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Investigations of the Trophic Relationships, Feeding Ecology and Feeding Behavior of Larval Spot, *Leiostomus Xanthurus* Lacepede, and Atlantic Croaker, *Micropogonias Undulatus* (Linnaeus) (Pisces:Sciaenidae)

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INVESTIGATIONS OF THE TROPHIC RELATIONSHIPS, FEEDING ECOLOGY AND FEEDING BEHAVIOR OF LARVAL SPOT, *LEIOSTOMUS XANTHURUS* LACEPÈDE, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS* (LINNAEUS) (PISCES: SCIAENIDAE)

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ABSTRACT

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The feeding ecology and trophic relationships of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae were evaluated and compared inter- and intraspecifically.

Based on six morphometric measurements, the nutritional condition of spot larvae collected in the northern Gulf of Mexico was determined to be high, with no larvae classified as starving and with the vast majority of larvae classified as fed. This was probably due to an inability to sample starving larvae at sea because of strong predation pressure on larvae weakened by starvation or was indicative of favorable feeding conditions and therefore a relative absence of starving larvae in the collection area. Also, in spite of the similarities in gross morphology of the larvae of both species, significant differences in morphometry and overall body shape were found. These differences may manifest themselves in differential swimming abilities and result in differences in the feeding behavior and diet composition of the larvae, although this was not tested.

The two species demonstrated a convergence in diet with age, with the diets of preflexion larvae being the most dissimilar. The degree of interspecific dietary overlap, however, was relatively high for both developmental stages. In spite of the high degree of dietary overlap, inter- and intraspecific competition were probably not important

determinants of feeding behavior among the larvae because of the apparent high abundance and availability of prey.

The larvae fed predominantly on all life stages of copepods as well as other crustaceans but demonstrated consistently strong selection for the copepods *Oithona* spp. and *Paracalanus* spp., while showing strong negative selection for *Acartia tonsa*. In contradistinction to the pattern of overall dietary convergence, the degree of food selection increased with age in both species, with preflexion larvae of the two species exhibiting very similar patterns of food selection. Although the actual patterns of food selection were variable both intra- and interannually, larvae always fed selectively among the prey organisms that were available. Selective behavior was plastic enough on both spatial and temporal scales to accommodate the high spatiotemporal variability of the plankton community.

Finally, as food selectivity increased with larval age, larvae added larger prey organisms to their diets while still feeding on smaller prey. Overall prey size and shape were important factors in determining diet composition and food selection among the larvae, with the larvae eating prey that were, on average, larger than those available in the ambient plankton. The precise relationship between prey size and shape and feeding behavior was probably not one of size-limited ingestion, but instead of visual profile and reactive distance. These results were in accordance with predications made by optimal foraging theory and two other mechanistic models of food selection.

The feeding incidence of three age classes of larval spot, *Leiostomus xanthurus*, on the rotifer *Brachionus plicatilis* was investigated in the laboratory under six different spectral regimes. Red, yellow, green and blue plastic filters with broadly overlapping spectral signatures were used to render prey those colors. Feeding incidence was also measured under white light conditions (control) at an irradiance equal to the colored filters ($\approx$3.0 $\mu mol \cdot m^{-2} \cdot sec^{-1}$) and at an ambient laboratory irradiance level six times greater than the control. Significant ($P < 0.001$, ANOVA) sources of variation were at-

tributed to age, spectral regime and an interaction term. The incidence of feeding was different for the three age classes. Feeding incidence increased with age in all but the red spectral regime. This increase was attributed to increased visual and swimming abilities, previous feeding experience and gut capacity. Two-to-three week old larvae did not demonstrate a higher feeding incidence in any treatment when compared to the control. Seven and ten week old larvae demonstrated a higher feeding incidence in the yellow and green spectral regimes when compared to the other regimes. It was hypothesized that those larvae possessed two pigments of different maximal absorption that were matched to typical background spacelight in nature facilitated contrast vision, resulting in higher feeding incidence . Differences in feeding incidence between the age classes indicated that the ability to perceive increased with age.

DEDICATION

für meine Grossmutter

Toni Ella Herrmann

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I am beholden to Vera Adams, who brought me back to life when I was dead and tired. She was always unselfishly by my side with love, support, and with a patience that I tried all too often. She saw me through to the bitter end and I would never have finished this manuscript without that support. I love her with all my life.

My interest in larval fish feeding ecology began with my reading of the doctoral work of Joanne Laroche (*née* Lyczkowski) published in *Fishery Bulletin* in 1982. Her work on larval marine sculpins stimulated my desire to investigate the feeding behavior of spot and Atlantic croaker larvae and to develop a better understanding of their food selection. I have often reread that fine paper whenever I felt lost or in need of encouragement and I am most grateful to her for unknowingly providing me with that incentive.

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FOREWORD

In the study of the profession to which he looked forward all his life he found irritation and vacuity as well as serene wisdom; he saw no one clear path to Truth but a thousand paths to a thousand truths far-off and doubtful.

Sinclair Lewis, 1924
Arrowsmith

None but those who have experienced them can conceive of the enticements of science. In other studies you go as far as others have gone before you, and there is nothing more to know, but in a scientific pursuit there is continual food for discovery and wonder.

Victor, in *Frankenstein*
Mary Shelley, 1818

I am the wiser in respect to all knowledge and the better qualified for all fortunes for knowing that there is a minnow in the brook. Methinks I have need even of his sympathy and to be his fellow in a degree. I would even know the number of their fin rays and how many scales compose the lateral line.

Henry David Thoreau

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PREFACE

The past two decades have seen a great deal of diverse research on the early life history of marine fishes, including studies of development, ecology and behavior, as well as the critical period concept and recruitment. Much of that work has dealt with attempts to evaluate mortality and factors that affect survival of fish larvae at sea, with the ultimate goal of correlating those factors with recruitment. This has been done so that predictive models of the annual strength of important fish stocks could be developed. This is not to say that all such work has had as its purpose the goal of fisheries management, but certainly, fisheries biology has had a significant impact on the nature of how larval fish biology has been studied.

Research has focused on the food and feeding behavior of larval fishes and has evaluated feeding incidence, starvation and nutritional condition, as well as demonstrated that larvae are generally selective in their feeding behavior. However, the nature and strength of food selection as a behavioral trait remains poorly understood. This has been for two primary reasons. First, little is known about the plasticity of the larval diet. Second, past studies have fallen short of determining what factors affect food selection and in what order of importance they do so.

Therefore, the present study had two major purposes. The first was to undertake a quantitative analysis of food selection of two marine sciaenids, spot, *Leiostomus xanthurus* Lacepède, and Atlantic croaker, *Micropogonias undulatus* (Linnaeus), from collections made in the Northern Gulf of Mexico in December 1981, and by comparing these data with data from the two previous winters, to make a quantitative assessment of interannual variability in food selection by those larvae. In addition, the relationship between the shape of the prey organism and food selection was investigated (Chapter I).

Second, it was the purpose of this study to investigate in the laboratory, the role of prey color on feeding behavior of spot (Chapter II).

CHAPTER ONE

THE FEEDING ECOLOGY AND TROPHIC RELATIONSHIPS AMONG LARVAL SPOT, *LEIOSTOMUS XANTHURUS* LACEPÈDE, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS* (LINNAEUS) (PISCES: SCIAENIDAE), IN COASTAL WATERS OF THE NORTHERN GULF OF MEXICO

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INTRODUCTION

The Critical Period Concept

It has long been supposed that annual recruitment success and the resulting year-class strength of pelagic fish stocks are dependent on cohort survivorship during early life history stages, when the larvae are particularly vulnerable to unstable oceanographic conditions, starvation and predation (Hjort 1914, 1926; Beverton 1962; Gulland 1965; Cushing and Harris 1973; Lasker 1975, 1978a, 1978b; Hunter 1976; Hunter 1981; McCullough and Stanley 1981; Wroblewski 1984; Wroblewski et al. 1989; Houde 1989). This early period in the life-history of fishes has been termed the "critical period." Darwin (1859) suggested that the high fecundity exhibited by many organisms and especially those with an aquatic existence reflects a high rate of mortality. In fishes, it is during the critical period that mortality is most intense and that year-class strength is determined (Gulland 1965; Beyer 1989).

The critical period concept has received much attention since it was first proposed by Fabre-Domergue and Biétrix (1897) and was originally used to describe the time of complete yolk absorption, when these authors observed high mortality among marine fish larvae in their laboratory studies of ichthyoculture (May 1974). The most widely accepted definition of the critical period concept was put forth by Hjort (1914, 1926) in his now classic study of North Sea herring and cod stocks. Hjort believed that successful recruitment, as a consequence of cohort survivorship through the critical period, is dependent on the availability of planktonic food just before total yolk-sac absorption (see May [1974], for a thorough review of Hjort's hypothesis). Hjort (1914) postulated that differential rates of mortality among the larvae were perhaps responsible for the large-scale interannual fluctuations in stock size that he observed.

More recently, Balon (1984) suggested that fishes may encounter many "critical periods" during their early life histories that are dependent on the timing of major ontogenetic events. As a fish larva grows, its ecological requirements change and so does its vulnerability to the abiotic and biotic determinants of survival. In principal, it is possible that larvae must face several bottlenecks during their ecological and developmental ontongeny (Houde 1989) and that these periods of variable vulnerability would be reflected in overall mortality rates. The ontogenetic events that accompany these ecological bottlenecks include the sequential development of morphological structures such as a swim bladder, functional digestive system, full fin compliment and functional sensory organs, as well as specific behaviors such as exogenous feeding, active swimming and schooling.

So far, no empirical evidence whatsoever exists for multiple critical periods outside of freshwater, low-fecundity spawners with demersal or adhesive eggs. Survivorship curves for highly fecund marine species with planktonic eggs are smooth and negatively exponential, not saltatory or punctuated as Balon's (1984) hypothesis might predict. Mortality rate shows a steady decline with increasing age of the larva. In addition, most of the survivorship curves available at the time of May's (1974) review of the critical period concept did not show an increased mortality at the point of yolk absorption (i.e., when exogenous feeding becomes obligatory).

In any case, survival through any number of critical periods must be dependent on both density-independent abiotic factors such as advection and stable ocean conditions, and density dependent biotic factors such as competition, starvation and predation. Presumably, it is also dependent on an interplay between the two, as well as on the physiological and ontogenetic state of the larva. Like growth, survival should be facilitated by a successful feeding history because feeding success would afford the larva a higher level of physical condition. The critical period concept has had a great influence

on how the ecology of larval fishes has been approached for the last 20 years, as evidenced by the number of authors who have invoked Hjort's work.

Larval Fish Feeding Ecology

The three main causes of mortality during the early life-history of marine fishes are starvation, predation and transport away from water masses with conditions favorable for survival and growth or away from areas suitable for settlement of transforming juveniles (e.g., coral reefs or estuaries). As regards feeding and starvation, the last 10-15 years of research on the early life history of fishes has produced numerous studies dealing with descriptions of the diet of, and the trophic relationships between, different species of larval fishes (see Turner [1984] for an extensive taxonomic review of this literature). Many such studies have included brief discussions of larval feeding ecology in relation to survival, the critical period concept or recruitment processes (e.g., Shelbourne 1962; Hunter 1972; Laurence 1974; Laurence 1978; Laurence et al. 1981; Lasker 1975; Lasker and Zweifel 1978; Arthur 1976; Ehrlich et al. 1976; Scura and Jerde 1977; Houde 1978; Ellerston et al. 1981; McCullough and Stanley 1981; Werner and Blaxter 1981; Crecco and Blake 1983; Govoni et al. 1983; Wroblewski 1984; Malhotra and Munshi 1985; Martin et al. 1985; Courtois and Dodson 1986; Taggart and Leggett 1987). Many others have undertaken their work in terms of the critical period concept with the intention of addressing the specific problem of early feeding environment and survival of the larvae (e.g., Lasker 1975; Lasker and Zweifel 1978; Arthur 1976; Houde 1978; Ellersten et al. 1981; Sinclair et al. 1985; Peterman et al. 1988).

Past work on the feeding ecology of larval fishes has (1) demonstrated that larvae often attempt to eat the largest prey items possible; (2) measured feeding incidence, relative to starvation and condition, and selectivity; and (3), if multiple coexisting species were studied, compared the diets of the target species qualitatively as well as quantitatively (e.g., Kjelson et al. 1975; Last 1978a, 1978b, 1980; Laroche 1982; Govoni et al.

1983; Govoni et al. 1986a; Jenkins 1987). For example, Laroche (1982) described the diets and trophic relationships among five species of marine cottids, measured feeding incidence and overlap, and related her findings to the effects of prey size, vertical distribution of the larvae and possible interspecific competition. In another study, Monteleone and Peterson (1986) described the feeding ecology of the American sand lance (*Ammodytes americanus*) and found, as others have (e.g., Last [1980]; Laroche (1982); Sherman et al. [1981]; Govoni et al. [1983, 1986a]), that as larvae grow, they consume a broader range of prey sizes. In laboratory studies of the growth and survival of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) conducted at variable prey densities, Laurence et al. (1981) investigated interspecific competition between these two species. They found distinct differences between the two species, with *G. morhua* exhibiting 2-2.5 times greater growth rate and significantly greater survival. These results were attributed to predation by cod larvae on haddock, cannibalism by cod on themselves, and size selective predation on the prey by both species. In a large scale study of the feeding of 20 species of marine fishes from the northeast coast of England, Last (1980) investigated diurnal and seasonal variations in feeding, and the relationship between prey size and the age of the larvae. Not surprisingly, he found distinct differences in the diets of demersal, pleuronectiform larvae as compared to pelagic larvae. The former fed predominantly on appendicularians and the latter predominantly on copepods.

The temporal dynamics and ecological determinants of diet composition remain poorly studied. Most studies have usually restricted their analyses to a single season and have not investigated feeding behavior between years. When data from successive years were available (Laroche 1982; Roblin and Burslé 1984), researchers usually grouped their data and investigated feeding behavior without regard to possible interannual variation. Often, too little material was available for statistically valid multiple-year comparisons. However, in investigating two winters of data (1979-81) collected in the Gulf

of Mexico, Govoni et al. (1983) found no obvious interannual variation in diet exhibited by larval spot (*Leiostomus xanthurus*) or Atlantic croaker (*Micropogonias undulatus*), although feeding incidence of Gulf menhaden (*Brevoortia patronus*) on dinoflagellates changed from year to year. In observations made on the food and feeding of larval herring (*Clupea harengus*) over a period of three years, Sherman and Honey (1971) found that the diet of this species changed seasonally with changes in the composition and abundance of the copepod community. They concluded that food selection is often opportunistic with larvae exploiting new resources as they become available in the plankton. The subject of temporal variability in food selection remains poorly studied, however.

Other factors that affect cohort survivorship, such as predation and some unfavorable abiotic conditions, are directly related to feeding through growth (Cushing 1975; Houde 1978; Wroblewski 1984). Larvae that feed successfully have the potential to grow rapidly and are probably more successful in avoiding the heavy predation that operates during the larval period (O'Connell and Raymond 1970; Ware 1975; Houde and Schekter 1981; Hunter 1981). In fact, Wroblewski (1984) reported that it is generally recognized that predation, rather than starvation, is the major cause of mortality among marine fish larvae. However, he did allow that nutritional state and growth rate, which are dependent on feeding history, determine vulnerability to predation. Larvae are presumably more resilient to unfavorable abiotic conditions, particularly during early life, if they are in good physical condition. Although poorly understood, starvation has been the most extensively studied of the three major factors affecting survivorship among fish larvae.

Starvation

It is generally accepted that starvation is responsible for a high degree of mortality among marine fish larvae (May 1974; Laurence 1974; Braum 1967; Wroblewski

1984), although it has been difficult to document that phenomenon conclusively in the field. Work by Hunter (1972, 1981) and Lasker (1975, 1978a, 1978b) has suggested that the overall, average abundance of planktonic food may be less critical for the survival of marine fish larvae than the spatiotemporal distribution of food. Starvation and survival are affected by both spatial and temporal factors associated with plankton and larval fish patch dynamics. The patchy nature of plankton distributions, including both larval fishes and their planktonic food, suggests that the co-occurrence of fish larvae and their food may be infrequent and episodic (for discussions of this subject see Govoni et al. [1985] and Al-Yamani [1988]). Larval fish survival may be dependent on the frequency and duration of patch interactions (Hjort 1914, Lasker 1975, 1981a, 1981b; Lasker and Zweifel 1978; Houde and Schekter 1978; Hunter 1981). In light of this fact and from knowledge regarding the natural interannual variation in spatial distribution and timing of plankton productivity, it is likely that the diet of successive cohorts may consist of somewhat different taxa from year to year. Indeed, their menus and diets may differ considerably (e.g, see Sherman and Honey [1971]).

It remains unknown to what degree larval diets reflect the temporal variability of the plankton community or to what degree successive cohorts of larvae are able to modify their diets as the availability of specific plankters changes from year to year. Cushing (1975) proposed that the magnitude of survival and recruitment into a fishery is dependent on the match or mismatch of the time of spawning by the fish to the seasonal production of their planktonic food (temporal synchrony). He termed the supposed relationship between that temporal synchrony and recruitment into the fishery as the "match-mismatch hypothesis." Intuitively this relationship seems obvious, but the relationship between larval and prey patch coincidence (both spatial and temporal, although Cushing's (1975) hypothesis regarded only temporal considerations) and cohort survivorship has been difficult to demonstrate. Frank and Leggett (1982) suggested that the major difficulty that has inhibited researchers from uncovering direct evidence sup-

porting the relationship between spatial and temporal synchrony of larvae and their food, and their survivorship, has been an inability to quantify the *in situ* developmental history of a single cohort from spawning to first feeding and beyond. If the developmental history of a cohort could be followed, the researcher might be able to measure directly the determinants of survivorship as well as recruitment. In studying the effects of environment on growth rate, efficiency and swimming performance of larval capelin (*Mallotus villosus*), Frank and Leggett (1982) demonstrated that environmental conditions during the yolk sac stage influenced not only growth rate and the size that larvae attained at first feeding, but also prey capture ability. This in turn affected the size, quantity and quality of food available to the larvae before and after the onset of exogenous feeding.

A practical problem with finding support for the match/mismatch hypothesis has been an inability to demonstrate that larval fishes actually starve to death at sea. Specifically, it has been difficult to resolve the spatial distribution and patchiness of fish larvae and their prey and to evaluate either the nutritional condition or mortality of the larvae. Laboratory studies that have investigated feeding efficiency and growth of marine fish larvae (Blaxter 1965; Lasker et al. 1970; O'Connell and Raymond 1970; Houde 1978; Houde and Schekter 1981) and field studies that have experimentally estimated zooplankton abundance (Beers and Stewart 1967, 1969; Lasker 1975), suggest that prey densities necessary for survival and growth occur infrequently under natural conditions. Furthermore, survival and growth are functions of the frequency and temporal duration of such patch coincidence between fish larvae and their prey (Hunter 1972; Vlymen 1977; Houde and Schekter 1978; Lasker and Zweifel 1978; Govoni et al. 1985). Lasker et al. (1970) and Lasker (1975, 1978a) showed that water that contained cell concentrations of the naked dinoflagellate (*Gymnodinium splendens*) high enough to support feeding by the northern anchovy (*Engraulis mordax*) were almost exclusively restricted to the chlorophyll maximum layer. Feeding incidence was quite low in surface waters that did not contain food items of the appropriate size or density. In laboratory studies on the

functional responses of the larvae of three species of marine fishes to variable prey densities, Houde and Schekter (1978, 1980, 1981) demonstrated that prey density had a direct effect on growth rate and efficiency of these larvae and consequently, on the duration of the larval stage. Also, they found noticeable differences in the abilities of two of the species to exploit temporary patches that contained high concentrations of prey. The sea bream (*Archosargus rhomboidalis*), although more sensitive to variable prey density in terms of the amount of time spent in the larval phase than the bay anchovy (*Anchoa mitchilli*), was better able to exploit temporary patches of prey once they were discovered. Food patch discovery and exploitation may not always ensure a diet of food items of optimal quality, however. Duration and frequency of patch coincidence must be sufficiently long and frequent enough for development to occur, otherwise larval mortality can be high (Lasker et al. 1970; Hunter 1981).

It has been suggested that stable ocean conditions are necessary for the maintenance of patch coincidence (Hjort 1914, 1926; Cushing 1975; Lasker 1975, 1978a; Wroblewski 1984, 1989; Owen 1989). In fact, part of Hjort's (1914) original critical period concept included conjecture about the probable relationship between abiotic factors and the coincidence of prey organisms and aggregations of fish larvae. Certain natural, large-scale phenomena, such as upwelling, storms and El Niño, may render the local environment unstable, thereby transporting larvae and their food away from the larval feeding or nursery grounds (Bakun 1973; Lasker 1975, 1978a, 1978b). In a survey of 37 years of survival data of the Pacific mackerel (*Scomber japonicus*), Sinclair et al. (1985) concluded that survivorship during the early life history of these larvae was perhaps influenced to a greater extent by hydrographic processes than by biological interactions. Specifically, they found a direct correlation between variable survivorship in *S. japonicus* to age 1 yr and sea level. Poor survivorship was associated with strong southward flow of the California Current and lower sea levels during years of weak El Niño events.

Small scale circulation patterns may also affect cohort survivorship during any given year. For example, when Owen (1989) sampled microplankton on fine- (< few meters) and microscales (< 1 m), he found that plankton concentrations often varied more than two-fold between adjacent collections, supporting the contention that patches of plankton with densities capable of supporting larval fishes may in fact exist and underscoring the degree of patchiness characteristic of the prey. Maintenance of these patches was probably dependent upon hydrographic events operating on a scale similar to that of the distribution of the plankton. In his studies of the feeding environment of the northern anchovy (*Engraulis mordax*), Lasker (1975, 1978a) witnessed the alternating effects of storm-driven mixing of nearshore waters, which obliterated the plankton-rich chlorophyll maximum layer and subsequent storm senescence and upwelling, which replenished surface waters with the nutrients necessary for primary production. He concluded that the timing and duration of upwelling events responsible for maintaining patch integrity were decisive determinants for survival and recruitment of those larvae.

More recent work by Wroblewski et al. (1989) suggests that some level of wind-generated turbulence is necessary for upwelling and redistribution of nutrients into depleted surface waters in order to sustain primary and secondary production, and thus for promoting optimal feeding conditions for fish larvae. Wroblewski et al. (1989) suggested that conditions optimal for feeding by *Engraulis mordax* existed when a "wind event" strong enough to downwell the upper mixed layer into the nutricline was followed by a period of calm. In relating environmental determinants of mortality in larval bay anchovy (*Anchoa mitchilli*) and striped bass (*Morone saxatilis*) to Hjort's (1914) critical period concept, Houde (1989) differentiated between episodic mortalities, which may or may not be catastrophic to recruitment, and more subtle variability in daily growth and mortality rates of eggs and larvae. He suggested that it is the subtle changes in mortality, caused by variable day-to-day predation and starvation rates, that have the greatest effect on recruitment rather than massive advective losses of eggs and larvae, failed egg

production or acute pollution effects. Although recent work has added to our knowledge and understanding of starvation, much remains unknown.

Food Selection

Although past studies investigating the feeding behavior and diet of larval fishes have described the diets and trophic relationships of these fishes and demonstrated that they feed selectively, they have fallen short of determining what factors affect selectivity and in what order of importance. In his now famous work on the feeding ecology of fishes, Ivlev (1961) proposed that it is the abundance of prey the regulates the degree of food selection among fishes. Specifically, greater prey diversity leads to increased trophic specialization among the predators (Rajasilta and Vuorinen 1983). It remains unclear, however, why fish larvae eat what they do and what factors affect their choice. Prey selection is a complex phenomenon directly dependent on a number of physiological limitations and behavioral patterns of both the forager and the prey, as well as on variable environmental conditions that often affect the temporal and spatial duration of the interaction between them. Such interactions have been conveniently described as a cycle of sequential events: encounter (detection), attack (pursue), capture and ingestion (Werner and Hall 1974). It is an interplay between behavior, physiology and environment that determines the success of predator or prey.

Larval fishes are predominantly photopic visual predators, relying almost exclusively on cone-containing simplex retinae to detect prey (Blaxter and Staines 1970; Blaxter 1968a, 1968b, 1975, 1986; Sandy and Blaxter 1980). Their feeding success and diet selection may be dependent on such visually related factors as the size, shape, elusiveness and perhaps color of the prey organism (Arthur 1976; Checkley 1982; Stoecker and Govoni 1984; Govoni et al. 1986a), as well as ambient light intensity and turbidity (Boehlert and Morgan 1985; Breitburg 1988). Those factors are known to influence prey visibility (Eggers 1982; Rajasilta and Vuorinen 1983) and it follows that they

are probably important in terms of food selection (Stoecker and Govoni 1984; Govoni et al. 1986a). Characteristics associated with the prey's appearance are particularly important during early feeding experiences or when encountering novel prey, because those factors enable the predator to establish a search image of the prey (Checkley 1982) and reinforce prey recognition with increased experience (Ware 1971).

Prey Size and Shape

Several investigators have suggested that the width of a food item is the most important factor in food selection by larval fishes, with the predators attempting to ingest the largest (widest) prey items possible (Shelbourne 1962; Brooks and Dodson 1965; Brooks 1968; Werner and Hall 1974; Confer and Blades 1975; Zaret and Kerfoot 1975; Eggers 1977, 1982; O'Brien 1979; Beyer 1980; Vinyard 1980; Gardner 1981; Luecke and O'Brien 1979; Breck and Gitter 1983; Butler and Bence 1984; Li et al. 1985; Wetterer and Bishop 1985). Much recent work has investigated the behavioral and theoretical bases for size selective predation by planktivorous fishes, but no consensus has been reached regarding the underlying causes of such selection (e.g., Brooks and Dodson 1965; Brooks 1968; Werner and Hall 1974; Confer and Blades 1975; Zaret and Kerfoot 1975; O'Brien 1976, 1979; O'Brien et al. 1976; Vinyard and O'Brien 1976; Eggers 1977, 1982; Vinyard 1980; Gardner 1981; Luecke and O'Brien 1981; Breck and Gitter 1983; Butler and Bence 1984; Li et al. 1985; Wetterer and Bishop 1985). The earliest work on selective predation by planktivorous fishes (i.e., the size-efficiency hypothesis of Brooks and Dodson 1965) emphasized both conspicuousness of the prey and energetics of the predator as important determinants of size-selective predation.

Three basic models of size selective predation in planktivorous fishes have been developed and tested. The resulting argument concerns whether the observed feeding patterns are consistent with predictions made by optimal foraging theory (OFT; Werner and Hall 1974) or with those made by two more mechanistic models termed the apparent

size model (ASM; O'Brien et al. 1976) and the reactive field volume model (RFVM) (Werner and Hall 1974; Butler and Bence 1984). OFT predicts that the diet chosen should maximize the energy gained by the predator per unit of foraging time. Generally, fish should eat the largest food items available in order to maximize their energy gain per unit effort. The ASM predicts that when given a choice, the predator should chose the prey item that appears largest – i.e., that subtends the greatest visual angle on the eye – regardless of whether it really is largest. Apparent prey size is a function of absolute prey size as well as the proximity of the prey to the predator. Diet ultimately depends, then, on visual acuity and environmental factors such as turbidity and light level, both of which are related to prey appearance and to prey encounter probability. Predators do not always eat the largest prey available, and the ASM may explain instances when predators deviate from the size-selection paradigm. Large prey are selected by the predator because of energetic considerations and because of environmental (e.g., turbidity) and physiological considerations (e.g., type of retina) affecting how fish perceive their prey. The RFVM (or the encounter rate hypothesis of Confer and Blades 1975) and the greatest stimulus model (GSM) are models of passive selection (Wetterer and Bishop 1985) that predict that prey should be selected in accordance with the rate of encounter, which is calculated as the product of the relative field volume (the volume of water surrounding the fish within which a particular prey is visually detected) and the prey density. These models, however, unjustifiably assume uniform dispersion of prey outside the reactive distance (RD). That is, the maximum distance from the eyes of the fish at which a particular prey item can be visually detected. These models predict that the size distribution of prey items eaten by the fish should reflect their relative densities in the perceptual field of the fish (Werner and Hall 1974). All four models assume that each prey item has the same probability of being attacked by the predator once they have been visually detected (Confer and Blades 1978).

From this literature, it is apparent that no single model adequately explains size-selective feeding patterns for all species, all feeding conditions, or all life history stages. Selection depends on the density of food items and on the turbidity of water (which enhances or inhibits feeding activity, depending on contrast and RD), and varies ontogenetically depending on visual acuity and hence the ability of larvae to detect smaller prey. In addition, selection by planktivores is not always size dependent (e.g., Sherman and Honey 1971; Feller and Kaczynski 1975; Drenner et al. 1978; Drenner and McComas 1980; Sumida and Moser 1980; Hansen and Wahl 1981; Checkley 1982; Rajasilta and Vuorinen 1983; Mills et al. 1984, 1986). In those cases in which prey size does play a major role, deviations in the size-selection model are often evident (Drenner et al. 1978; Durbin 1979; Drenner and McComas 1980; Vinyard 1980). Although food width is undoubtedly an important determinant of dietary preference, other factors are also important determinants of food selection. For example, in laboratory experiments, Byron (1982) found that juvenile rainbow trout (*Salmo gairdneri*) selectively fed on darkly pigmented copepods even when much larger unpigmented copepods were available. This was not the case in their field studies, though, where fish exhibited classic size selective predation patterns. That may be explained by the different light regimes between the laboratory experiments and the field. Different photic environments would result in differences in apparent prey size or conspicuousness. In studying the seasonal variations of food and feeding in larval herring (*Clupea harengus harengus*), Sherman and Honey (1971) concluded that larvae were selective for prey size only in the earliest stages of growth when much of the plankton community is unavailable to them because of the relatively small size of the larvae. Selectivity in planktivorous fishes has been viewed almost exclusively in terms of the prey size-selection paradigm, and little attention has been given to other factors, particularly the complex matter of prey catchability. Clearly, prey width only explains part of the variation observed in food selection.

In light of the large body of literature dealing with size selection, it is surprising that no similar effort has been made on the subject of shape. The single linear dimension of food item width is an important determinant of selection inasmuch as it is affected by the morphological constraints associated with gape and the dimensions of the predator's buccal cavity. From a behavioral point of view, the three-dimensional resultant of length, width and height (i.e., shape) may be equally important, especially in cases where the size-selection paradigm in not valid. Fish larvae probably integrate several dimensions into a complex variable such as shape when discriminating among the variety of food items they encounter. Prey shape may play a major role in recognition of food items, learning and catchability, and the "flatness," "oblongness," or "roundness" of a food organism may be important in forming a search image that will be reinforced by experience.

Feeding selection may be dependent on behavioral and physiological limitations of the predator and prey organisms, and may reflect a hierarchical sequence of effectors, operating within the framework of optimal foraging theory. Conspicuousness, size, shape, color and catchability may all be important in determining the selective feeding patterns of the predator and at different times in the predation sequence. In addition, these factors may produce variable effects throughout the ontongeny of the predator, under different environmental conditions and may be dependent on the identity of the prey organism.

Studies that examine the food habits and trophic relationships of commercially important marine fishes and also address such ecological questions as inter- and intraspecific competition; dietary, spatial and temporal overlap; dietary preference; ontogenetic changes in diet composition; and starvation among marine fish larvae will add to our present knowledge of their early life histories. Because survivorship and feeding are related through growth, feeding studies have practical ecological importance.

Kjelson et al. (1975) and Govoni and his colleagues (Govoni 1981; Govoni et al. 1983, 1985, 1986a) have described the diets of both larval spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*), investigated ontogenetic development of the digestive system and ontogenetic changes in diet, and discussed the trophic relationships of the two species. Larvae of these two species of sciaenids rely almost exclusively on zooplankton, particularly all life stages of copepods (Kjelson et al. 1975), as well as pteropods and pelecypod veligers, for food (Govoni et al. 1983). The phytoplankton (predominantly dinoflagellates and centric diatoms) infrequently found in the guts of *L. xanthurus* and *M. undulatus* are believed to have been ingested incidentally with zooplankton. Because most crustacean zooplankters macerate their food, those phytoplankton (i.e., their siliceous frustules and thecae) are probably not released into the gut as whole organisms during digestion of the zooplankton that consumed them. *M. undulatus* occasionally eats the large armored dinoflagellate *Dinophysis* as a single and discrete food item, but their relative metabolic contribution is unknown. Govoni et al. (1986a) have demonstrated that spot and Atlantic croaker feed selectively among the multitude of planktonic food available to them and that the two species have significantly different diets, although they overlap somewhat. This overlap is particularly true for larvae less than five millimeters (SL) and is apparent not only from the prey taxa eaten, but also from the size distribution of the prey consumed. The digestive tract and associated organs of spot do not become functional until the time of complete yolk-sac absorption (≈30 h after hatching at 20°C) and change little during the larval phase (Govoni 1980; Govoni et al. 1986b). Indeed, yolk-sac larvae (1.6-2.5 mm NL) have undifferentiated guts and nonfunctional mouths, and larvae (2.5-7.0 mm NL) do not begin feeding until total yolk-sac absorption is nearly completed (Govoni 1980). In *L. xanthurus*, the oil globule lingers well after (1-2 d) complete yolk-sac absorption (J.J. Govoni, pers. comm.) and may afford the larvae a "last respite" in satisfying metabolic energy demands

before obligatory exogenous feeding commences. Larvae undergo transformation approximately 2 months after hatching (7.0-18.0 mm SL).

In the Gulf of Mexico, spot larvae eat copepods, pelecypod veligers and pteropods (predominantly *Limacina trochiformis*), whereas Atlantic croaker larvae eat primarily copepods. Both species feed selectively and predominantly on the cyclopoid copepods *Oncaea* spp. and the calanoid copepods *Paracalanus* spp. (Govoni et al. 1983, 1986a). *Micropogonias undulatus* also eats the calanoid copepod *Acartia tonsa* and the cyclopoid copepods *Corycaeus* spp. in appreciable numbers. All these copepods are common winter zooplankters in the neritic waters of the Gulf of Mexico (Minello 1980; Ortner et al. 1989). The apparent dissimilarity in diets is unexpected in light of the striking morphological similarity between spot and Atlantic croaker larvae.

Ontogenetic changes in selectivity apparently occur as the larvae grow, with larvae selecting smaller prey than they are capable of handling. As they grow, larvae add increasingly larger (i.e., wider) food items to their diets (Last 1980; Sherman et al. 1981; Laroche 1982), but do not exclude smaller food items. Govoni et al. (1986a) report that spot larvae (1.5-3.0 mm NL) consume food items of 20-300 μm in width, whereas Atlantic croaker of the same size consume food items of a narrower range (60-200 μm). Larger spot larvae (5-7 mm NL) eat food items of 60-500 μm, whereas similarly sized Atlantic croaker eat food items of 100-460 μm in width. Kjelson et al. (1975) have shown that prejuvenile spot ($\overline{TL}$ = 19 mm) eat copepodites ranging in size from 300-1200 μm (average $\approx$ 600 μm) as well as adult copepods, and that approximately 32% of the total prey taxa in the guts were harpacticoid copepods. By contrast, Govoni et al. (1983, 1986a) did not find appreciable numbers of harpacticoids in the diets of larval spot. The differences in these author's findings may be explained by the fact that Kjelson et al. (1975) analyzed older transforming (17-22 mm) larvae. As spot grow, they become increasingly oriented toward the substrate, a behavioral shift accompanied by a change in

the position of the mouth from terminal to inferior and concomitant changes in diet (Govoni 1987).

The actual behavioral mechanisms of prey selection are not understood and have not been addressed experimentally. Govoni et al. (1986a) however, speculated about the importance of several possible determinants of food selection in *Leiostomus xanthurus* and *Micropogonias undulatus* larvae, specifically prey width, swimming ability and color. Chapter two of this study summarizes results from laboratory experiments that test the relationship between feeding incidence and prey color.

Study Objectives

The general objective of this study was to investigate the diet and trophic relationships of larval spot, *Leiostomus xanthurus* Lacepède, and Atlantic croaker, *Micropogonias undulatus* (Linnaeus).

Specifically, I sought to:

1) investigate interannual patterns of variation in the diets of both species;

2) evaluate the apparent incidence of starvation among both species by using an index of nutritional state;

3) measure quantitatively and compare the nutritional condition interspecifically by developmental stage by using the same index of nutritional state;

4) compare differences in interspecific foraging behavior as reflected by diet relative to the shape of prey eaten; and

5) quantitatively analyze dietary preference and overlap between preflexion and flexion-postflexion spot and Atlantic croaker larvae.

MATERIALS AND METHODS

Field Collections

Spot and Atlantic croaker larvae and associated microzooplankton samples were collected by members of the Beaufort Laboratory, Southeast Fisheries Center (SEFC), Beaufort, North Carolina in December of 1981. Collections were made at nine stations on three transects located approximately at the 5.5, 27 and 55 m isobaths in the coastal shelf waters of the northern Gulf of Mexico, adjacent to Galveston Bay, Texas, the Mississippi River delta and Cape San Blas, Florida (Fig. I-1). At each station, collections were made at three discrete depths: surface, middle of the upper-mixed layer, and at or just above the pycnocline with casts at 6:00, 12:00, 18:00 and 24:00 hours made at each depth. Collections were made with a multiple opening and closing net and environmental system (MOCNESS - Wiebe et al. 1976). The MOCNESS was fished for 2-3 minutes at each depth, resulting in a relatively constant sampled water volume of approximately 140 m^3. The gear was equipped with nine 1.0 × 1.4 m, 505 μm mesh Nitex plankton nets to sample ichthyoplankton and with a 0.25 × 0.35 m, 67 μm mesh net mounted inside each of those nets to sample microzooplankton. Flowmeters mounted inside the mouth of each net provided a measure of sampling effort. When fished at discrete depths for short periods of time (several minutes) and accompanied by synoptic physical data, the MOCNESS provides real-time information regarding the specific parcel of water being sampled and ensures that the collections are both horizontally and vertically discrete. A short tow time alleviates many of the problems of scale associated with separately collecting ichthyoplankton and their planktonic food. Samples were preserved in 5% buffered (sodium tetraborate) formalin.

Analysis of MOCNESS Samples

All samples collected with the 505 μm mesh nets were sorted for spot and Atlantic croaker larvae (N = 25 collections). Specimens were then archived in 5% buffered formalin (mono- and dibasic sodium phosphate) for future analysis of gut contents. Microzooplankton samples that corresponded to the ichthyoplankton samples designated for gut content analysis were enumerated following the coefficient of variation stabilizing (CVS) method of Alden et al. (1982). This method provides estimates of abundance with equal precision for rare and common species. The CVS method involves the size fractionation of plankton samples into size classes of 2000, 850, 600, 300 and 200 μm. Because of the constraints of time and because very few (1.76%) of the prey items identified from the guts of postflexion larvae were >850 μm in length, only plankton from the 600, 300 and 200 μm splits that were ≤850 μm in length were processed. Each of these three size fractions was then repeatedly split with a Folsom plankton splitter until the sample size of the dominant zooplankter fell within a 95% prediction interval corresponding to the chosen level of precision of 35%. This level of precision was achieved with a prediction interval of 20-42 plankters per split and was chosen because of time constraints. Only those prey taxa that were identified from the gut content analysis of the larvae (see below) were identified and enumerated from each split. The abundance of the most numerous subdominant plankter whose abundance was below the chosen prediction interval was noted and the split containing the sample size of this plankter that fell within the chosen prediction interval (i.e., 20-42) was identified by back-calculating its abundance. This split was then enumerated as before (without the original dominant plankter) and all additional species encountered were counted, but not to the same level of precision. Relative abundances (proportions) of each plankter in each collection (not abundance per unit volume sampled) were computed by back calculating the data obtained from each split using the formula $2^n \times N$, where n was the split number that was

enumerated and N was the number of individuals of a particular plankter counted in that split. Calculation of actual abundance (e.g., per m^3) was not necessary because relative abundance was sufficient to calculate diet overlap and food selection among the larvae.

Larval Morphometrics and Nutritional Condition

Standard length (or notochord length), head length, eye diameter and body depth at the anus, the cleithral symphysis and the base of the pectoral fin were measured (following Powell and Chester [1985]) to the nearest 0.01 mm with an ocular micrometer for 275 spot and 275 Atlantic croaker larvae. Upper jaw length was measured from the anterior end of the premaxilla to the posterior-most edge of the maxilla. This was begun after a number of larvae had already been dissected and so these data were available for fewer than the total number of larvae (i.e., 151 spot and 196 Atlantic croaker). Means were computed from all morphometric measurements as well as from measurements (without upper jaw length) taken from spot larvae that were reared in the laboratory under three different feeding regimes (Tables I-1, I-2). The latter measurements (data provided by Alex Chester, SEFC, Beaufort, NC) were used to calculate a multivariate morphometric index of nutritional condition for spot larvae (Powell and Chester 1985). A similar multivariate index has been used for larval jack mackerel, *Trachurus symmetricus* (Theilacker 1978), larval Atlantic cod, *Gadus morhua* (Koslow et al. 1985) and spot, *Leiostomus xanthurus* (Powell et al. in press). The relative condition of only spot larvae was determined because calibration data were unavailable for Atlantic croaker. A multivariate analysis of variance (MANOVA) was used to evaluate differences in the morphometric characters between spot (not corrected for preservation effects) and Atlantic croaker, as well as between field-caught spot larvae of unknown nutritional condition (corrected for preservation effects) and those spot larvae reared in the laboratory (Tables I-3, I-4). These data were not standardized for standard length prior to this analysis, but the analysis was instead performed separately on preflexion and flexion-

postflexion larvae (see Powell and Chester [1985] for a discussion of the problems associated with normalizing morphometric data).

The six morphometric measurements were regressed against standard length and plotted for both species to demonstrate morphological similarities that exist between the species (Figs. I-2, I-3). Size and shape similarities between the species were further investigated using discriminant analysis.

Discriminant analysis is a multivariate procedure used to separate two or more groups of individuals given measurements for these individuals on several highly correlated variables (Manly 1986). Classification results are then compared with the original groupings designated *a priori* by the researcher and results are reported as percentage correctly classified into each group. Classification results (discriminant functions) can then be used to classify individuals whose group membership is unknown. Discriminant analysis was used in the present study to classify larvae based on nutritional condition and diet composition because it can be an effective means of separating larvae based on their morphometrics and diets.

Discriminant analysis was used to develop classification functions from $\log_{10}(X+1)$ transformed morphometric measurements (same as above) made on 805 spot larvae reared under three different feeding regimes. That analysis follows Analysis I, as described by Powell and Chester (1985). I chose to rerun their analyses in order to insure the integrity of my own programming and to construct classification coefficients based on SAS (SAS Institute, Cary, NC) instead of relying on their published coefficients, which were based on the BMBP statistical software. Larvae were then classified according to their nutritional condition as indexed by the six morphometric variables (Table I-5). The three feeding regimes consisted of larvae fed daily on rotifers (*Brachionus plicatilis*), larvae moderately starved (unfed to the point of 50% mortality) and larvae starved beyond 50% mortality (see Powell and Chester [1985]). Classification functions were derived separately for preflexion (SL $\leq$3.8 mm, N = 471) and flexion-

postflexion larvae (SL >3.8 mm, N = 334) because of the difference in susceptibility to starvation between these developmental stages. For this reason, every analysis performed in this study was done separately for these two developmental stages. The standard length at which notochord flexion occurs appears to be a function of feeding history (see Powell and Gordy [1980]), and instead of using limits derived from laboratory-reared larvae (e.g., Powell and Chester 1985), limits for field-caught larvae obtained from the literature were used (see Fruge and Truesdale [1978] and Powles and Stender [1978]). These limits were: preflexion <4.4 mm SL≤ flexion-postflexion.

Discriminant analysis had some difficulty correctly predicting preflexion larvae that were moderately starved and starved (52% and 63% correctly classified) as well as flexion-postflexion larvae that were fed and moderately starved (73% and 55% correctly classified). In order to increase classification accuracy in their study, Powell and Chester (1978) combined the aforementioned groups and reanalyzed the data with discriminant analysis. That analysis was performed in the present study as well and corresponds to their Analysis II (Table I-5).

Classification functions derived from Analyses I and II were then applied to the six morphometric measurements obtained from the spot larvae investigated in this study, to classify those larvae according to their relative nutritional condition (Table I-6). Analysis of nutritional condition was restricted to MOCNESS samples that contained both species of larvae. In order to equate field measurements with the laboratory measurements used to derive the discriminant classification functions, morphometric measurements taken from these larvae were corrected for shrinkage due to formalin preservation by applying the following experimentally derived algorithms to the data (A. Chester, unpublished data):

$$SL = SL(0.974663) + 0.357501 \quad (1)$$

$$HL = HL(0.961518) + 0.096281 \quad (2)$$

$$ED = ED(0.901197) + 0.024444 \quad (3)$$

$$BDA = BDA(0.952436) + 0.052276 \quad (3)$$

$$BDC = BDC(0.979201) + 0.027079 \quad (4)$$

$$BDP = BDP(1.036991) + 0.025097 \quad (5)$$

where SL = standard length, HL = head length, ED = eye diameter and BDA, BDC and BDP are body depth at the anus, cleithral symphysis and base of the pectoral fin, respectively.

Similar data of nutritional condition and correction factors for preservation effects for Atlantic croaker do not exist. Because of striking gross morphological similarities between the species (e.g., see Figs. I-2, I-3), correction factors and classification functions based on the morphometrics of one species might be applied to the other. If no differences in shape exist between the species, the classification functions derived from laboratory-reared spot larvae could justifiably be applied to the classification of Atlantic croaker larvae of unknown nutritional condition. A one-way analysis of covariance (ANCOVA) was used to explore differences in the regression relationships between standard length and the other morphometric measurements between the two species. ANCOVA regressed the $\log_{10}(X+1)$ of each morphometric character against $\log_{10}(SL+1)$ inter- and intraspecifically (Figs. I-2, I-3, Table I-7). That analysis assumes homogeneity of slope between the regression lines being compared. An analysis of slope was performed, and in those cases where the slopes did not differ from unity, the regressions were investigated further for differences in intercept (Table I-8). An experimentwise error rate of $P < 0.02$ was chosen for the ANCOVA as a precaution against an inflated probability of Type I error due to the number of independent contrasts being made (see Kirk [1982]).

Two types of discriminant analysis were used to evaluate size and shape differences between the two species. Classification discriminant analysis was used to clas-

sify spot and Atlantic croaker larvae based on the morphometric characters (Table I-9) and canonical discriminant analysis was used to evaluate differences in shape between the species (Table I-10). Because differences in length existed between the two species for a given developmental stage, these analyses were performed without standard length and on data standardized for standard length. Standardization was accomplished by dividing each morphometric measurement by the corresponding standard length of the larva. Canonical discriminant analysis (CDA) is a data-reduction technique akin to both principal component analysis and canonical correlation analysis, and is used to derive canonical variables (uncorrelated linear combinations of the original variables) that summarize between-class variation much the way that principal components summarize total variation (SAS Institute, Inc. 1985). CDA was utilized in the present study because it performs pairwise comparisons with univariate and multivariate one-way ANOVA's by testing for differences in group means (Mahalanobis distance). CDA was also used because canonical scores contained in each canonical function (e.g., prey morphometrics or gut contents data) are amenable to statistical analysis.

Diet Comparison and Overlap

The analysis of gut contents was restricted to single MOCNESS samples that contained both species of larvae and usually to those samples collected during daylight or dawn hours. This protocol permitted an interspecific comparison of diet. Also, larvae collected during the day or early evening almost always had food in their guts. Following identification and morphometric measurement, the gastrointestinal tract (fore-, mid- and hindgut; Govoni et al. [1986a]) was removed from each larva. A drop of lactic acid pigmented with Chlorazol Black E (Sigma Chemical Co., St. Louis, MO) in 70% ethanol (Judkins and Fleminger 1972; Sumida and Moser 1980) was often added to the gut contents to stain crustacean cuticle and to facilitate identification of those food items. Each food item found in the gut was identified to the lowest taxon possible, counted, and its

maximum width, height and length were measured and recorded. When copepods were disarticulated (usually the cyclopoid copepods *Oncaea venusta* and *Oithona* spp.), urosomes and metasomes were paired according to relative lengths and species identification, and rearticulated as well as possible in order to obtain a length measurement. When that was not possible, the food item was not included in the analysis of prey morphometrics. For copepods, total length was measured from the anterior-most edge of the rostrum to the posterior end of the caudal rami. Body width was measured across the widest axis of the cephalothorax and body height was measured in lateral aspect at the deepest part of the body, including the pereiopods. The pereiopods were included irrespective of how far they were extended, because larvae undoubtedly see the legs of the copepod extended during detection and pursuit of the copepod. Other crustaceans (e.g., barnacle nauplii and cladocerans) were measured similarly. Antennae and setae were not included in these measurements. Measurements of other prey taxa identified from the gut contents of the larvae (e.g., pelecypod veligers, pteropods and tintinnids) were measured as follows. Unless an obvious anteroposterior axis could be identified, the longest axis of the body (or lorica) was measured as length. The next longest axis was measured as body width and the shortest axis as body height. Also, often 5-15% (roughly estimated by volume) of the gut contents consisted of unidentifiable chyme (i.e., crustacean appendages and setae). Instead of including that material in the gut content analysis as a meaningless category, which would bias the other prey taxa by resigning them less importance (indexed by percent and frequency of occurrence), it was not included in the analysis.

Diets were compared separately for preflexion and flexion-postflexion larvae (see above for a discussion of the efficacy of analyzing each developmental stage separately). The percent of the total number of food items (*%N*) and the percent frequency of occurrence (*%F*) of each food item among preflexion and flexion-postflexion larvae that contained at least two food items in their guts was computed (Pasch and Lyford 1972;

Laroche 1982; Govoni et al. 1983; Brodeur and Pearcy 1984; Maule and Horton 1984). The relative importance (RI) of each food item was indexed by the product of the *%F* and *%N* (Hyslop 1980; Laroche 1982; Govoni et al. 1983) separately for both developmental stages (Tables I-11, I-12). All diet categories that had at least one RI value ≥0.01 for a species and developmental stage were plotted to demonstrate differences in the relative importance of these categories in the diets of the different larvae (Fig. I-4). A cutoff of RI ≥0.01 was chosen because inspection of RI values for all diet categories demonstrated a distinct discontinuity in these values at RI ≈ 0.01 (Tables I-11, I-12).

Discriminant analysis was used to classify larvae according to the composition of their diet (Analysis A, Tables I-13, I-14). Stepwise discriminant analysis (Desselle et al. 1978; Carnes and Slade 1982; Govoni et al. 1983) was used to identify those prey taxa most effective in distinguishing the four larval groups by diet composition (Analysis A, Tables I-15, I-16). A moderate significance level of $P < 0.15$ was chosen as the singularity criterion for diet categories entering the stepwise model as a precaution against including more discriminators than could be reliably estimated at the given sample size (Costanza and Afifi 1979; SAS Institute, Inc. 1985). The results of the stepwise discriminant analysis were then used to undertake a second classification analysis of diet composition (Analysis B, Tables I-13, I-14), to evaluate what role diet items that were only rarely encountered in the gut contents analysis had in the discriminant model and to assess the collective discriminant power of those diet categories identified as poor discriminators when analyzed singularly. Analysis B included those diet categories that were significant ($P < 0.15$) discriminators in Analysis A and all other diet categories combined as a single category. Stepwise discriminant analysis (SDA) is a multivariate technique that selects a subset of quantitative variables (e.g., specific food categories from all those eaten) to produce a discrimination model that best distinguishes the classes being compared (e.g., larval groups). Variables are entered into the model in stepwise fashion and remain in the model only if they meet the criterion to stay (e.g., $P < 0.15$). When all

variables in the model meet that criterion and no other variables meet the criterion to enter, stepwise selection of remaining variables stops (SAS Institute, Inc. 1985). SDA was used in the present study because it provided an effective way of identifying those food categories most unique to each larval group.

Indices of diet overlap are used to assess differences in resource utilization among taxa which are spatiotemporally coincident. They can provide an estimation of the degree of trophic niche overlap between the taxa being investigated and are sometimes used to address questions of inter- and intraspecific competition (e.g., see Zaret and Rand [1971]; Wallace [1981]; Coates-Markle [1982]; Laroche [1982]; Govoni et al. [1983]; Brodeur and Pearcy [1984]). In the present study, inter- and intraspecific differences in diet composition were further investigated by computing two indices of diet overlap (Table I-17). The indices used were as follows:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^{n} |p_{xi} - p_{yi}| \right) \qquad (6)$$

$$L = (A/X \cdot Y) \sum_{i=1}^{n} x_i \cdot y_i / a_i \qquad (7)$$

where α is Schoener's (1970) index of percent overlap, p_{xi} and p_{yi} are the proportions of diet category i in the diets of species x and y, and x_i and y_i are the actual numbers of diet category i in the diets of species x and y. n is the total number of diet categories. A value of zero for α indicates no overlap between the groups being compared, while a value of one indicates complete overlap in utilization of resources. Contrary to common practice, values of α were not computed individually for each collection and then averaged, because very few collections contained enough larvae of two of the larval groups to make statistically meaningful calculations. Instead a single value of each index was computed from all larvae by developmental stage and species, irrespective of the collection, and was based on the total numbers of each diet category eaten by all larvae. α

was chosen so that a comparison could be made with values previously reported in the literature for spot and Atlantic croaker (e.g. Govoni et al. [1983])

L is a measure of niche overlap as defined Hurlbert (1978) and is unique among indices of overlap in that it takes into account the abundance of each diet category (a_i) in the ambient environment and can thus provide a different perspective of overlap that α. X, Y, and A are the sums of x_i, y_i and a_i within each collection. Calculation of L was restricted to those collections that contained at least five larvae of two of the larval groups and to 13 broad food categories (see below). L was chosen because several authors (e.g., Hurlbert 1978; Wallace 1981) have suggested that overlap indices are ecologically meaningful only if they include components of prey availability.

Prey Size and Shape

Inter- and intraspecific comparisons of diet composition were made with respect to the sizes and shapes of the prey eaten by the larvae as follows. Morphometric measurements of prey size (i.e., length, width and height) were not normally distributed for the groups being compared and no standard data transformation resulted in normality. Consequently, a Wilcoxon distribution-free rank sum test (WRT) of prey size was used to evaluate differences in the size of the prey eaten by the larvae. Means (± one standard deviation) of the morphometric measurements obtained from the prey items were computed from the total number of prey items consumed by each group (Table I-18).

A nonparametric nearest neighbor discriminant analysis was used to classify larvae according to the length, width and height of the prey items they consumed and thereby assess the discriminating power of prey morphometrics (Tables I-19, I-20). Classification results provided an insight into the relationship between the size of the prey consumed by the larvae and food selection. These results also provided a coarse es-

timate of overlap between, and distinctiveness among, the larvae, based on the overall size of the prey eaten.

Principal component analysis (PCA) was also used to investigate relationships between prey size and shape, and diet composition among the larvae. PCA is a multivariate technique used to evaluate relationships between several quantitative variables (e.g., prey morphometrics) by constructing linear combinations of the original variables (principal components) which explain the total variation among the original variables (SAS Institute, Inc. 1985). Like canonical discriminant analysis, PCA produces scores which are uncorrelated and thus amenable to statistical analysis. In the present study, PCA was used to determine the importance of each morphometric measurement in food selection by the larvae (Table I-21). Individual larvae were assigned principal component scores which represented the size and shape of the prey items eaten. Frequency distributions were constructed for the first two principal components and these size frequency distributions (SFD) were compared inter- and intraspecifically for differences with a chi-square goodness-of-fit test. This was done by arbitrarily selecting the overall SFD of one of the groups being compared as the expected frequency, and comparing it to the SFD of the other group (e.g., flexion-postflexion spot), which was treated as the observed frequency (Table I-22). Experimentwise error rates of $P = 0.001/2 = 0.005$ and $P = 0.01/2 = 0.05$ were chosen for chi square analysis as a precaution against an inflated probability of Type I error due to the number ($N = 2$) of independent contrasts being made (see Sokal and Rolf [1981] and Kirk [1982]). Finally, 95% confidence ellipses were plotted on the first two principal components for each of the four larval groups to demonstrate differences in the size and shape of the prey items eaten by the larvae (Fig. I-5).

Likewise, PCA, chi-squared analysis of homogeneity and independence (Brown and Hollander 1977) and 95% confidence ellipses were used to investigate food selection with respect to the sizes and shapes of the prey that were spatiotemporally coincident

with the larvae. In order to establish a baseline SFD from the ambient plankton, 20 individual plankters of each of the 13 broad food categories (see below) were randomly selected from the 600, 300 and 200 μm splits from 15 of 25 randomly selected MOCNESS collections in proportion to their overall abundance in those splits. The relative abundance of each of these plankters in the three sieve splits was determined and averaged for those 15 collections. Plankters were then randomly removed from the three splits of the remaining 10 collections in direct proportion to their mean relative abundances. This entailed removing two of each plankter from the remaining collections (2 plankters each $\times$ 10 remaining collections = 20 total plankters of each species). This was done to insure an accurate estimation and characterization of the prey sizes and shapes from among the 13 selected food categories in the ambient plankton. Their maximum length, width and height were measured and analyzed with a PCA as previously described (Tables I-23, I-24; Fig. I-6).

Food Selection

In addition to using the relative proportion of availability (p) and utilization (r) of each food category to compute selectivity indices (see below) these values can also be used to assess patterns of food selection by the larvae. Therefore, weighted (see above) means of $\log_{10}(X+1)$ transformed p and r values were computed from those MOCNESS collections and broad food categories mentioned above (Table I-25) and plotted (e.g., Costello 1990) inter- and intraspecifically to demonstrate linear differences in selectivity for these food items by the larvae (Fig. I-7). Plots of p and r provided the simplest and least abstract means of evaluating food selection by the larvae.

Selectivity indices have received much attention in the literature regarding their validity and reliability (e.g., see Paloheimo [1979]; Strauss [1979, 1982]; Johnson [1980]; Kohler and Ney [1982]; Lechowicz [1982]). These indices differ in their underlying assumptions, limitations and sensitivity to sampling error and to the presence of rare food

items in the diet. They also differ in their instability to changes in the relative abundance of food types in the environment and to the subjectivity used in determining which food items are truly available to the predator and which are not (see Johnson [1980] and Lechowicz [1982] for reviews of electivity indices).

Chesson's (1978) index of food selection (α) was computed for 13 broad diet categories from MOCNESS collections that contained at least five larvae of any one of the larval groups. α values were computed from the percent occurrence of each diet category in the guts of all the larvae in each collection by developmental stage and species. Each collection was thus treated as a single "gut" and compared to the availability of each diet category in the environment. This was done instead of computing individual indices for every larva in a collection, computing a mean value for each collection and then calculating a grand mean from all the collections, because the numbers and taxonomic diversity of food items in any single gut were typically quite low and would have perhaps resulted in fallacious mean index values if computed from individual larvae. Also, poorly resolved diet categories such as "calanoida" or "unidentified copepods" were not included in calculating α values and categories resolved to the species level were almost always combined with their congeners. For example, *Paracalanus crassirostris* and *P. quasimodo* were combined into a group called *Paracalanus* spp. Other diet categories (i.e., not copepods) were combined to a higher taxonomic level (e.g., cyclopoid and calanoid nauplii combined into a single group called copepod nauplii). Combining similar diet categories into broader and more meaningful groups was subjective and was based on knowledge of their general shape and swimming behavior as well as on their taxonomic relatedness. Combining food categories was necessary and justified because larvae presumably select prey items without regard to the taxonomy of the prey item but instead with regard to more biologically significant criteria. Also, errors in identification of gut contents at the species level would introduce an unresolvable error into the calculation of electivity indices that would over- and underestimate the selection of par-

ticular food items. That artifact was avoided by combing prey taxa to a higher taxonomic level. Chesson's α was calculated as follows:

$$\alpha_i = (r_i/p_i)/(\sum_{i=1}^{n} r_i/p_i) \qquad (8)$$

where r_i is the relative utilization of prey item i by the predator, p_i is the relative availability of prey item i in the environment and n is the total number of food categories in the environment. Chesson's α is derived from a simple model of prey encounter and capture probabilities and encompasses an arbitrary number of prey types of both constant and changing prey densities, thereby overcoming the problem of variation with the relative abundance of food items inherent in Ivlev's (1961) forage ratio (Chesson 1978, 1983). α is vulnerable to sampling error for rare food items in the environment but that problem is alleviated in part by restricting the analysis to the 13 broad food categories (see above). α was also computed in order to make comparisons with values reported in a previous study by Govoni et al. (1986a). This index varies between 0 and 1 with values of $\alpha > 1/n$ indicating preference and of $\alpha < 1/n$ indicating "avoidance." The mean number (rounded to the nearest whole number) of food categories out of 13 that were available to the larvae in each MOCNESS collection (n) were computed in order to value α with respect to $1/n$ Table I-26). Mean values (± standard deviation) of α, weighted by the number of available food categories in each MOCNESS collection, were computed for the 13 broad food categories and plotted by developmental stage, in order to demonstrate differences in selection for those food categories by the larvae (Table I-26; Figs. I-8, I-9).

Multiyear Comparison of Diet Composition

An interannual comparison of diet composition of all four larval groups was made by comparing data of larval diet composition from the present study (i.e., December 1981 = Year 3) with data from collections made in December 1979 and February 1980

(Year 1), and December 1980 and February 1981 (Year 2), previously published by Govoni et al. (1986a). Seasonal differences in diet composition are known to exist for larval herring, *Clupea harengus harengus* (Sherman and Honey 1971), but such differences (i.e., December versus February) were ignored, in the present study. Interstation (i.e., Galveston Bay versus Mississippi River delta) differences in plankton abundance and diet composition were also ignored, and data from two cruises each were combined to form years 1 and 2. This was done because too few data were available from each month or collection to make statistically valid comparisons. Fifteen diet categories that composed 5.6% and 6.4% of the total number of prey eaten by Atlantic croaker and spot larvae were deleted from year one and year two prior to analysis (see Table I-27 for rational). After that deletion, 29 diet categories remained and were available for analysis. A multivariate analysis of variance (MANOVA) was used to identify those diet categories in each larval group that were utilized in significantly ($P < 0.01$) different quantities between the three years (Table I-28). A MANOVA is a useful means of reducing a large data set prior to further multivariate analysis because it identifies *a priori* those variables that will best discriminate the groups being compared (e.g., see Birdsong et al. 1989). A canonical discriminant analysis was then applied to these data to elucidate interannual differences in diet composition (Table I-29). The 95% confidence ellipses were plotted on the first two canonical functions for all four larval groups to further demonstrate interannual differences in diet composition (Figs. I-10, I-11, I-12, I-13). An error value of $r > 0.70$ (r is the between-class correlation between the canonical variables and the original variables) was used to decide which diet categories to include on the confidence ellipses. This criterion level has been used by Birdsong et al. (1989) and serves as a somewhat arbitrary means of assigning significance to each canonical correlation. Finally, classification discriminant analysis was used to classify larvae according to their utilization of all 29 diet categories, and thereby assess interannual variability in diet composition among the larval groups (Table I-30).

All statistical analyses used in this study were run under the VM/XA-CMS (release 2) operating system on an IBM 3090-180 mainframe computer using the SAS (version 5.18) statistical package (SAS Institute, Cary, NC) excepting the chi-square analyses of goodness-of-fit, homogeneity and independence, which were calculated by hand or performed using the Statgraphics (version 3.1) statistical graphics system (Statistical Graphics Corp., Rockville, MD) on a personal computer.

RESULTS

Basic Morphometrics

Spot larvae of unknown nutritional condition were significantly larger ($P < 0.05$, Tukey's studentized range test) than their laboratory-reared counterparts for all morphometric characters except eye diameter among flexion-postflexion larvae (Table I-3). Also, those same spot larvae (measurements not corrected for preservation effects) were significantly ($P < 0.01$, Tukey's studentized range test) larger in all respects than Atlantic croaker larvae (Table I-4). This was probably because spot larvae complete notochord flexion at a later stage than croaker and are thus larger at the same developmental stage ($SL \geq 4.4$ mm for spot and $SL \geq 4.0$ mm for croaker, see Powles and Stender [1978]). Non-transformed means (± one standard deviation) and cell sample sizes for both field-caught larvae and laboratory-reared larvae are reported in tables I-1 and I-2.

Nutritional State

Initial classification of preflexion and flexion-postflexion spot larvae of known nutritional condition by discriminant analysis of six $\log_{10}(X+1)$ transformed morphometric characters produced results nearly identical to those reported by Powell and Chester (1985) in their analysis of the same data (Table I-5). Minor differences in the classification results between the present study and their analysis were attributed to several factors: differences in the statistical algorithms and rounding error associated with the different statistical procedures employed (i.e., SAS versus BMBP), as well as the different data transformation used in the two studies ($\log_{10}[X+1]$ versus $\log_{10}$).

Discriminant analysis correctly classified preflexion and flexion-postflexion larvae that were fed (77% and 73% correct), as well as flexion-postflexion larvae that were starved (82% correct), but classified the other groups with poorer accuracy (Analysis I, Table I-5). As Powell and Chester (1985) reported, classification results were vastly improved by combining moderately starved and starved preflexion larvae into a single category and likewise combining fed and moderately starved flexion-postflexion larvae. Classification of fed and starved preflexion larvae improved from 77% to 82% and from 64% to 84% correctly classified, while classification results of fed and starved flexion-postflexion larvae larvae improved from 73% to 87% and from 82% to 88% (Analysis II, Table I-5).

When preflexion and flexion-postflexion spot larvae of unknown nutritional condition were classified by discriminant functions derived from both Analyses I and II, 100% of the preflexion larvae were classified in the fed category while 93% of the flexion-postflexion larvae were classified as fed and 7% as moderately starved. No larvae were classified as starved. Classification results for flexion-postflexion larvae improved to 100% fed in Analysis II (Table I-6).

Interspecific Comparison of Larval Morphometrics

No analysis of nutritional condition was undertaken for Atlantic croaker larvae because significant differences ($P < 0.05$, ANCOVA) were found for three morphometric characters (i.e., head length and body depth at the anus and pectoral fin) between flexion-postflexion spot and Atlantic croaker larvae when they were regressed against standard length (Tables I-7, I-8). These results indicated that minor differences in body shape existed between the species. Furthermore, based on the five morphometric characters used to characterize nutritional condition, discriminant analysis correctly classified all four larval groups with relatively high levels of accuracy, thereby demonstrating interspecific differences in body shape (Table I-9). Highly significant ($P < 0.001$) dif-

ferences in overall body shape between the species were further demonstrated by canonical discriminant analysis, with Wilks' lambda (Λ) values and Mahalanobis distances showing significant separation between the species (Table I-10). Λ is the likelihood ratio statistic for testing the hypothesis that the means of the classes on the selected variables are equal in the population, and a value of zero for this statistic connotes complete separation between the groups (SAS Institute, Inc. 1985). Consequently, correction factors for preservation and classification functions from discriminant analysis derived for spot could not be applied to Atlantic croaker.

Diet Comparison and Overlap

Food items from 24 different taxonomic categories were identified from the guts of spot and Atlantic croaker larvae (Tables I-11, I-12). A total of 381 prey items were identified and measured from the guts of 100 preflexion croaker larvae, and 476 prey items from the guts of 110 preflexion spot larvae. A total of 769 prey items were identified and enumerated from the guts of 175 flexion-postflexion croaker larvae, while 651 prey items were processed from the guts of 165 flexion-postflexion spot larvae. The diets of the larvae consisted primarily of nauplier, juvenile and adult copepods, as well as pteropods, pelecypod veligers, cladocerans and invertebrate eggs, and represented a taxonomically less diverse group of diet items than previously reported for these species from the Gulf of Mexico (e.g., Govoni et al. 1983).

The percent frequency of occurrence (*%F*) and the percent total number (*%N*) of each diet category were computed and their product was taken as an index of relative importance (RI). RI values indicated that unidentified calanoid copepods, *Paracalanus* spp., *Oithona* spp. and *Oncaea venusta* were all important diet items for all four larval groups. RI values of most diet categories showed no discernible pattern with respect to developmental stage. Intraspecific patterns were evident however, for those diet categories with RI $\geq$ 0.01 (Fig. I-4). For both species, the importance of calanoid nauplii

and *Oncaea venusta* was lower for flexion-postflexion larvae than it was for preflexion larvae, while that of *Paracalanus* spp. was higher. Also, the importance of *Oithona* spp. and *O. plumifera* were higher for flexion-postflexion Atlantic croaker larvae than for preflexion larvae, while spot showed almost no difference in the importance of that genus as a diet category between developmental stages. In fact, the relative importance of many diet categories was less for flexion-postflexion larvae than for preflexion larvae, indicating that as larvae grew and added new food items to their diets, the relative importance of any single diet category decreased. *Oithona* spp. and *Paracalanus* spp. were consumed in larger numbers than other food items by the larvae, but were often in such an advanced state of digestion that it was impossible to reliably identify them to the species level. This was also true for the diet category Copepoda and the decreased importance of this category among postflexion larvae, as indicated by RI values, owes in part to the fact that prey items taken from older larvae were in better condition and were thus identified with greater resolution than those taken from preflexion larvae (Tables I-12, I-13). Prey items taken from older larvae also tended to be larger, which in turn facilitated their specific identification. Certain diet items were very rarely encountered and are represented by very low RI values that may actually represent only 1-4 individuals identified from all the guts dissected. Those diet items contributed little to an interspecific analysis of diet composition and in most cases, were absent from the diet of one species, while present in very low numbers in the other (e.g., dinoflagellates, cladocerans, copepod and barnacle nauplii and copepodites).

Based on diet composition, discriminant analysis classified Atlantic croaker larvae more accurately than it did spot larvae for both developmental stages. Regardless of developmental stage, the diet of croaker larvae was wider and more distinct than that of spot larvae (Analysis A, Table I-13). Croaker larvae, regardless of their developmental stage, utilized diet categories that spot did not. Conversely, spot larvae of both developmental stages shared a greater relative proportion of their diets with croaker than

croaker did with spot. Likewise, within both species of larvae, flexion-postflexion larvae were classified more accurately than preflexion larvae, demonstrating that the diet of the former group was more distinct and included a wider array of prey than that of the latter (Analysis A, Table I-14). Older larvae ate diet categories that were not utilized by preflexion larvae in addition to eating prey that were utilized by the younger larvae. Simply, larvae in the groups with the higher classification scores had more distinct diets and shared less of their diet composition with the larvae in the groups with the lower scores than they did among themselves.

In a second discriminant analysis of diet composition, in which all those diet categories determined as insignificant discriminators of larval group by a stepwise discriminant analysis of diet composition (see below) were combined into a single category, the general trends in classification were the same as those from Analysis A (Analysis B, Tables I-13, I-14). Interspecifically (Table I-13), Atlantic croaker larvae were classified correctly more often than spot larvae for both developmental stages (51% versus 77% for preflexion spot and croaker larvae, and 42% versus 84% for flexion-postflexion spot and croaker larvae). Classification scores between the two analyses were different. In comparing Analyses A and B, the classification of spot deteriorated from 65% to 51% for preflexion larvae and from 60% to 42% for flexion-postflexion larvae, while the classification scores of Atlantic croaker improved from 72% to 77% for preflexion larvae and from 69% to 84% for flexion-postflexion larvae. Prey items rarely eaten by spot and croaker larvae and that were poor discriminators of the larval groups were, as a group, more important (i.e., more unique) to the diet of croaker larvae than to that of spot larvae. Intraspecifically (Analysis B, Table I-14), flexion-postflexion larvae were classified more accurately than preflexion larvae (68% versus 44% for spot flexion-postflexion and preflexion larvae, and 63% versus 59% for croaker flexion-postflexion and preflexion larvae). Classification of both developmental stages deteriorated or remained the same in Analysis B (e.g., from 59% to 44% and 68% to 68% for spot, and from 63% to 59% and

75% to 63% for croaker, preflexion and flexion-postflexion larvae, respectively). The combined group of poor and rarely encountered discriminators from Analysis A did not provide better discrimination of either developmental stage of either species. Indeed, combining them as a single group only confused the intraspecific discrimination by diet composition and suggested that those diet categories were utilized similarly by both developmental stages.

Stepwise discriminant analysis identified the diet categories that were most important in distinguishing the four larval groups (Tables I-15, I-16). For the most part, the results of this analysis produced a diverse list of diet categories that included those categories that had the most divergent RI values. For example, among preflexion larvae, *Oithona nana* and unidentified calanoid copepods (probably *Paracalanus* spp.) were the most significant ($P < 0.005$) discriminators of larval species, whereas *Oithona* spp., barnacle nauplii and *O. nana* were the best ($P < 0.001$) discriminators of larval species among flexion-postflexion larvae (Analysis A, Table I-15). This analysis was actually more useful as a data reduction procedure than as a means of identifying important diet categories. When the significant discriminators were reanalyzed with all other diet categories combined in a single category (Analysis B), several diet categories that were included in the stepwise model from Analysis A were eliminated, suggesting that they were not important contributors to the diet of the larvae with respect to the combined group. This analysis did not result in significant discrimination by the combined group but did result in greater significance levels for several of the categories that remained in the model. For preflexion larvae, *Temora* spp., cyclopoid nauplii and *Oithona plumifera* were dropped from the discriminant model in Analysis B, as were *Acartia tonsa* and calanoid nauplii for flexion-postflexion larvae. The order of importance also changed between the two analyses for both developmental stages. Wilks' lambda values were relatively high for all discriminators but were highly significant ($P < 0.001$), showing good separation between the species for both developmental stages (Table I-15).

Calculation of two different indices of diet overlap showed greater overlap among both species of flexion-postflexion larvae than among preflexion larvae, indicating a convergence in the diet of the two species with age (Table I-17). Values for Schoener's (1970) index of percent overlap (α) demonstrated a 61% overlap among preflexion larvae and an 81% overlap among flexion-postflexion larvae. Values of Hurlbert's index of niche overlap (L) showed the same pattern with respect to developmental stage, giving mean values of 3.47 and 3.62 for preflexion and flexion-postflexion larvae. A value of zero for either index indicates no overlap between the species, whereas overlap is represented by any $\alpha \geq 0.60$ (Zaret and Rand 1971) and any $L > 1$ (Hurlbert 1978). These results are not in agreement with those obtained from a classification discriminant analysis of diet composition, which demonstrated a divergence in diet with age for both species (Table I-14). Intraspecifically, values of α showed greater dietary overlap among spot larvae (83%) than among Atlantic croaker larvae (62%), indicating a greater divergence of diet composition with age for croaker larvae. These results are in conformance with those obtained from a classification discriminant analysis of diet composition that demonstrated greater classification accuracy (i.e., greater divergence between flexion stages) for croaker (Table I-13). Mean values for L of 2.77 and 4.77 for spot and Atlantic croaker larvae however, show the opposite pattern.

Prey Size and Shape

Flexion-postflexion larvae of both species consumed prey items that were significantly larger ($P < 0.001$, Wilcoxon rank sum test) in all respects than those consumed by preflexion larvae (Table I-18). The larger the larva, the larger the food consumed. Interspecifically, preflexion spot larvae ate prey items that were significantly ($P < 0.001$) larger in all respects than did preflexion croaker larvae. That was undoubtedly due to the fact that spot larvae were significantly ($P < 0.01$, MANOVA, Table I-4) larger in all respects than croaker larvae. Flexion-postflexion spot larvae ate prey items significantly

(P <0.001) wider than did croaker larvae, but in spite of significant interspecific differences in the size of these larvae (Table I-4), there was no difference in the length or height of the prey items they consumed.

A nonparametric discriminant analysis of prey morphometrics demonstrated differences in the utilization patterns of the larvae based on the overall size of the prey (Tables I-19, I-20). Interspecifically, Atlantic croaker larvae were classified with a relatively high degree of accuracy with classification scores of 76% and 86% correctly classified for preflexion and flexion-postflexion larvae, whereas spot larvae were classified with very low accuracy, having scores of 38% and 21% correctly classified for preflexion and flexion-postflexion larvae (Table I-19). Croaker larvae, irrespective of developmental stage, had a wider but more distinct range of prey sizes that they exploited, whereas spot exploited a more narrow and less distinct size range that overlapped with that of croaker. Intraspecifically, flexion-postflexion larvae of both species were classified with greater accuracy than preflexion larvae (Table I-20). Among spot larvae, flexion-postflexion larvae had a classification score of 87%, while preflexion larvae had a score of only 18%, correctly classified. Likewise, croaker larvae had scores of 89% and 26% for flexion-postflexion and preflexion larvae. Thus, preflexion larvae had a narrow and overlapping diet composition relative to the broader but more distinct diet composition of flexion-postflexion larvae. The overall size distribution of prey items must have increased with age, with flexion-postflexion larvae eating prey sizes not utilized by preflexion larvae. In this analysis, the group with the lower classification scores exhibited a relatively narrow range of prey sizes from which they exploited relative to the other group. That relatively narrow range overlapped to a larger degree with that of the group with the higher score, and a high score indicated a more distinct diet (i.e., non-overlapping) that enabled discriminant analysis to effectively classify larvae based on prey morphometrics.

Principal component analysis (PCA) of prey morphometrics demonstrated that the overall size of the prey was the most important contributor to variation in diet composition among the larvae (Table I-21). Eigenvalues of the first two principal components (PC1 and PC2) explained 90% of the standardized variance in prey size among all four larval groups. PC1 had approximately equal, high positive eigenvectors for all three morphometric variables for all four larval groups, indicating equal contribution by those variables to overall prey size. For preflexion spot larvae, 84% of the standardized variance in prey shape was explained by PC1, while 8% was explained by PC2. A high positive eigenvector for prey width and moderate negative eigenvectors for prey length and height on PC2 indicated that prey width was also important in determining diet composition among those larvae. Among flexion-postflexion spot larvae, 64% of the standardized variance was explained by PC1 while 22% was explained by PC2. A high positive eigenvector for prey height and negative eigenvectors values for length and width on PC2, indicated a strong prey height component to prey items eaten by those larvae. Among preflexion croaker larvae, roughly 80% of the standardized variance was explained by PC1 while 13% was explained by PC2. Finally, among flexion-postflexion croaker larvae, 66% of the standardized variation in diet composition was explained by PC1 and 25% explained by PC2 among flexion-postflexion croaker larvae. Both developmental stages of croaker larvae exhibited strong positive eigenvectors for prey length for PC2, underscoring the importance of this morphometric variable in feeding selection by those larvae. Chi-square analysis demonstrated significant ($P < 0.05$) inter- and intraspecific differences in the frequency distributions of PC1 and PC2 further demonstrating that preflexion and flexion-postflexion larvae of both species fed on prey items that differed significantly in their overall size and shape (Table I-22).

Results from the PCA were clarified by plotting 95% confidence ellipses on PC1 and PC2. Flexion-postflexion larvae of both species ate larger prey items than preflexion larvae and these groups were strongly resolved on PC1 (Fig. I-5). Interspecific dif-

ferences were also evident with preflexion spot larvae eating larger prey items than preflexion Atlantic croaker larvae. A similar pattern was demonstrated by flexion-postflexion larvae, but a greater degree of overlap existed in the prey sizes utilized by those larvae. Those results are in accordance with the results from a Wilcoxon rank sum test of prey size previously described (Table I-18) and may reflect the significant intra- and interspecific differences in the size of the larvae (Table I-4). PC2 contributed weakly to resolving differences in the sizes and shapes of the prey eaten by the larvae, showing a large degree of overlap in the length, and height-width components of prey size (Table I-21). Other than overall prey size, there were no differences in the shapes of the prey items utilized by the four larval groups.

Prey Size and Shape in the Ambient Plankton

With one exception, results of a PCA of prey morphometrics with respect to the sizes and shapes of prey available to the larvae in the ambient plankton were very similar to those reported above from an inter- and intraspecific comparison of prey size and shape. Overall prey size was the most important contributor to the variation in diet composition (Table I-23). The only difference existed among flexion-postflexion larvae, in which prey length was replaced by prey height as the strongest eigenvector on PC2, indicating that these larvae ate wider prey than generally available. This change was accompanied by a change in the position of the 95% confidence ellipse along PC2 for these larvae. All larvae except preflexion Atlantic croaker larvae ate larger prey items than were generally available (Fig. I-6). This was particularly true for both species of flexion-postflexion larvae which showed almost complete overlap in the overall size of the prey they ate. These larger larvae were better resolved on PC2 with croaker larvae eating longer and wider prey than spot larvae and than were available in the ambient plankton.

Chi-square analysis of homogeneity and independence of the frequency distributions of PC1 and PC2 detected significant ($P < 0.001$) differences among those distribu-

tions for the four larval groups and ambient plankton (Table I-24). The four larval groups ate prey items that differed in their size and shape and that were different from the sizes and shapes available in the ambient plankton.

Food Selection

All four larval groups exhibited strong selectivity for specific diet categories while consuming other categories in relative proportions that were equal to, or lower than, the those that were available in the ambient plankton. The relative proportions of the availability (p_i) and utilization (r_i), of each food category demonstrated the degree and pattern of food selection by the larvae (Table I-25; Fig. I-7). The diagonal line in each graph represents a one-to-one relationship between p and r, and represents feeding in direct proportion to availability (i.e., $p = r$). Food categories that appear above the diagonal were exploited in greater proportion than they were available ($r > p$) while those plotted below the diagonal ($r < p$) were eaten in lesser proportion than they were available. The availability of *Acartia tonsa* was far greater than its utilization by all four larval groups. In fact, this food category was the most available in terms of relative abundance, but it was never an important contributor to diet composition (see Tables I-11, I-12). The copepods *Oithona* spp., *Paracalanus* spp. and *Oncaea* spp. were all eaten in greater proportions than they were available. Preflexion spot larvae showed weak preference for copepodites, pteropods, barnacle nauplii and *Oncaea venusta*, whereas preflexion croaker demonstrated a weak preference for pteropods, the harpacticoid copepod, *Microsetella* spp. and copepodites. Those larvae did exhibit a strong preference for *Oithona* spp., *O. venusta*, and copepod nauplii. Other food categories such as the copepods *Euterpina acutifrons*, *Corycaeus* spp. and *Temora* spp. as well as cladocerans were utilized very poorly or not at all by the larvae. These results are in general accordance with the relative importance indices computed for each diet category (Tables I-11,

I-12), as well as with results from a stepwise discriminant analysis that determined which diet categories were most important to each of the larval groups (Tables I-15, I-16).

Weighted means of Chesson's (1978) index of food selection (α) demonstrated differences in selectivity among the larvae of both species for the 13 broad food categories (Table I-26; Figs. I-8, I-9). Standard deviations of those means, however, were large and indicated a wide degree of variation in selectivity by the larvae between individual MOCNESS collections. α varies between 0 and 1, and values of $\alpha > 1/n$ indicate preference. Larvae in all four larval groups demonstrated a moderate-strong preference for the calanoid copepod *Paracalanus* sp. and the cyclopoid copepod *Oithona* sp. In addition, preflexion larvae of both species fed selectively on pteropods and the cyclopoid *Oncaea venusta*, whereas flexion-postflexion spot larvae showed a weak-moderate preference for cladocerans. Both developmental stages of Atlantic croaker showed a strong preference for *O. venusta*. Interspecifically, preflexion larvae of both species exhibited very similar patterns of food selection (Fig. I-8), whereas flexion-postflexion larvae did not (Fig. I-8). That pattern of dietary divergence with age between the two species was also demonstrated by a discriminant analysis of overall diet composition, in which flexion-postflexion larvae were more accurately classified than preflexion larvae (Table I-14). No discernible interspecific patterns in α were evident (Fig. I-9). With only minor exceptions α indicated patterns of food selection that were the same as those described for indices of relative importance (Tables I-11, I-12), results of a stepwise discriminant analysis (Tables I-15, I-16) and linear relationships between p and r (Fig. I-7).

Multiyear Comparison of Diet Composition

Both developmental stages of spot, as well as flexion-postflexion Atlantic croaker larvae, utilized a diverse group of diet categories in significantly ($P < 0.01$, MANOVA) different numbers between the three years (Table I-28). Among preflexion croaker

larvae, however, only pelecypod veligers, copepodites and *Paracalanus* spp. were utilized in significantly different numbers between the three years out of 29 diet categories. Those differences in utilization of prey resulted in highly significant ($P < 0.001$, canonical discriminant analysis) interannual differences in the overall pattern of utilization for both stages of spot and flexion-postflexion croaker larvae (Table I-29). It also demonstrated significant differences among preflexion croaker larvae between years two and three, but not between those years and year one. Exact patterns of interannual differences in prey utilization were clarified by plotting 95% confidence ellipses on the first two canonical functions for the four larval groups (Figs. I-10, I-11, I-12, I-13). No specific trends existed between the three years. In contrast, differences in variation within each year (denoted by the dimensions of each ellipse), as well as patterns of overlap between the years, were apparent. For all larvae except preflexion croaker larvae, year one showed the greatest variation in diet composition and year three showed the least. These results can be explained by the effects of sample size on variation, with year one having a small number of larvae (collections were limited to the inshore Mississippi River Delta station) and year three a much larger sample size (see Table I-30 for sample sizes). Differences in identification of gut contents between the present study (year 3) and Govoni et al. (1986a) may have also contributed to these results.

Discriminant analysis demonstrated similar patterns of distinctiveness in diet composition between the three years. With a single exception, year three was consistently classified more accurately than years 1 and 2, indicating a less diverse group of taxa and a smaller degree of variation of utilization in that year (Table I-30). Years two and three showed different degrees of accuracy in classification among the four larval groups, indicating greater similarity in the diet composition of the larvae among these two years when compared with year three.

The results of the MANOVA, PCA and discriminant analysis clearly demonstrated that spot and Atlantic croaker larvae had significantly different diets between the

three years, utilizing many of the same diet categories, but in different amounts. Also, differences in the numbers of larvae from each year may have affected the analysis, inasmuch as interannual variation in diet composition was overshadowed by intra-annual variation.

TABLE I-1.–Mean (± S.D.) measurements for seven morphometric characters of preflexion and flexion-postflexion[1] spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Measurements from spot larvae were corrected for effects of formalin preservation[2].

Morphometric character[3]	*Leiostomus xanthurus*		*Micropogonias undulatus*	
	Pre	Flex-post	Pre	Flex-post
Standard length	3.87±0.43	6.24±1.71	3.27±0.50	5.45±1.99
Head length	1.23±0.15	1.85±0.54	0.98±0.18	1.68±0.60
Eye diameter	0.38±0.04	0.49±0.08	0.38±0.05	0.52±0.10
Body depth at the:				
anus	0.86±0.17	1.43±0.43	0.76±0.16	1.33±0.46
cleithral symphysis	0.99±0.15	1.60±0.46	0.90±0.17	1.50±0.49
pectoral fin	1.10±0.16	1.77±0.52	0.97±0.18	1.59±0.52
Sample size	110	165	100	175
Upper jaw length	0.69±0.11	1.26±0.35	0.61±0.11	1.11±0.37
Sample size	55	97	72	124

[1]Limits for developmental stages were: preflexion <4.4 mm SL≤ flexion-postflexion for spot and preflexion <4.0 mm SL≤ flexion-postflexion for croaker and follow Powles and Stender (1978).

[2]Preservation-correction algorithms provided by Alex Chester, SEFC, NOAA/NMFS, Beaufort, NC.

[3]All measurements were made with an ocular micrometer to the nearest 0.01 mm and are reported in millimeters.

TABLE I-2.–Mean (±S.D.) measurements of six morphometric characters of preflexion and flexion-postflexion[1] spot (*Leiostomus xanthurus*) larvae reared under three different feeding regimes[2,3].

Morphometric character	Nutritional category					
	Starved		Moderately starved		Fed	
	Pre	Flex-post	Pre	Flex-post	Pre	Flex-post
Standard length	2.81±0.47	4.91±0.83	2.84±0.46	4.94±0.78	2.91± 0.42	4.88±0.91
Head length	0.61±0.16	1.32±0.30	0.63±0.16	1.34±0.29	0.65±0.14	1.30±0.32
Eye diameter	0.24±0.06	0.50±0.12	0.25±0.06	0.51±0.10	0.27±0.06	0.50±0.12
Body depth at the:						
anus	0.45±0.12	1.08±0.31	0.49±0.14	1.23±0.31	0.56±0.15	1.23±0.35
cleithral symphysis	0.51±0.10	1.20±0.35	0.53±0.12	1.25±0.31	0.57±0.14	1.24±0.35
pectoral fin	0.49±0.09	1.10±0.32	0.53±0.10	1.24±0.33	0.62±0.15	1.28±0.35
Sample size	115	65	141	96	215	173

[1]Feeding regimes corresponded to larvae fed daily (Fed), larvae starved to the point of 50% mortality (Moderately starved) and larvae starved beyond 50% mortality (Starved).

[2]Limits for developmental stages were: preflexion (Pre) ≤3.8 mm SL< flexion-postflexion (Flex-post).

[3]Data provided by Alex Chester, SEFC, NOAA/NMFS, Beaufort, NC.

TABLE I-3.–Results of a multivariate analysis of variance of six $\log_{10}(X+1)$ transformed morphometric characters of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) larvae of known and unknown nutritional condition[1,2]. Means were compared between nutritional categories and are preceded by a different superscript if significantly different ($P < 0.05$, Tukey's studentized range test).

Morphometric character	Nutrional category			
	Unknown	Fed	Moderately starved	Starved
Preflexion larvae:				
Standard length	^{A}0.7027	^{B}0.5897	^{B}0.2098	^{B}0.5777
Head length	^{A}0.1438	^{B}0.2149	^{B}0.2098	^{B}0.2052
Eye diameter	^{A}0.1438	^{B}0.1031	^{C}0.0962	^{C}0.0935
Body depth at the:				
anus	^{A}0.2792	^{B}0.1934	^{B,C}0.1837	^{C}0.1769
cleithral symphysis	^{A}0.3099	^{B}0.1910	^{C}0.1721	^{C}0.1599
pectoral fin	^{A}0.3324	^{B}0.2074	^{C}0.1836	^{D}0.1723
Sample size	110	215	141	115
Flexion-post flexion larvae:				
Standard length	^{A}0.8713	^{B}0.7642	^{B}0.7705	^{B}0.7675
Head length	^{A}0.4643	^{B}0.3573	^{B}0.3657	^{B}0.3619
Eye diameter	^{A}0.1755	^{A}0.1759	^{A}0.1775	^{A}0.1735
Body depth at the:				
anus	^{A}0.3959	^{B}0.3439	^{B}0.3483	^{B}0.3372
cleithral symphysis	^{A}0.4234	^{B}0.3436	^{B}0.3434	^{C}0.3126
pectoral fin	^{A}0.4517	^{B}0.3530	^{B}0.3454	^{C}0.3161
Sample size	165	173	96	65

[1]These data were corrected for effects of preservation with algorithms provided by Alex Chester, SEFC, NOAA/NMFS, Beaufort, NC.

[2]Feeding regimes correspond to larvae fed daily (Fed), larvae starved to the point of 50% mortality (Moderately starved) and larvae starved beyond 50% mortality (Starved). Data were provided by Alex Chester, SEFC. NOAA/NMFS, Beaufort, NC.

TABLE I-4.–Results of a multivariate analysis of variance of six $\log_{10}(X+1)$ transformed morphometric characters of preflexion and flexion-postflexion larval spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*). Means were compared between species and are preceded by a different superscript if significantly different ($P < 0.01$, Tukey's studentized range test).

Morphometric character	Means of $\log_{10}(X+1)$ transformed data	
	Leiostomus xanthurus[1]	*Micropogonias undulatus*
Preflexion larvae:		
Standard length	^{A}0.6793	^{B}0.6268
Head length	^{A}0.3269	^{B}0.2149
Eye diameter	^{A}0.1789	^{B}0.1031
Body depth at the:		
anus	^{A}0.2769	^{B}0.1934
cleithral symphysis	^{A}0.3088	^{B}0.1910
pectoral fin	^{A}0.3290	^{B}0.2074
Sample size	110	100
Upper jaw length[2]	^{A}0.2339	^{B}0.2065
Sample size	54	72
Flexion-post flexion larvae:		
Standard length	^{A}0.8589	^{B}0.7940
Head length	^{A}0.4604	^{B}0.4198
Eye diameter	^{A}0.3991	^{A}0.1813
Body depth at the:		
anus	^{A}0.4245	^{B}0.3605
cleithral symphysis	^{A}0.4454	^{B}0.3903
pectoral fin	^{A}0.3607	^{B}0.4066
Sample size	165	175
Upper jaw length[2]	^{A}0.3607	^{B}0.3177
Sample size	97	124

[1]These data were not corrected for effects of preservation.

[2]Measurements of this character were not obtained for all larvae.

TABLE I-5.–Percent and total number of larvae classified by a discriminant analysis of six $\log_{10}(X+1)$ transformed morphometric characters taken from preflexion and flexion-postflexion spot (*Micropogonias undulatus*) larvae[1] reared under three different feeding regimes[2,3].

		Predicted nutrional category							
		Preflexion				Flexion-postflexion			
Analysis[4]	Actual nutritional category	Fed	Moderately starved	Starved	*N*	Fed	Moderately starved	Starved	*N*
I	Fed	77%	19%	4%	215	73%	24%	5%	173
	Mod-starved	16%	52%	32%	141	28%	55%	17%	96
	Starved	3%	33%	64%	115	5%	14%	82%	65
	Total number				471				334
II	Fed	82%	—	18%	215	87%	—	13%	269
	Starved	16%	—	84%	256	12%	—	88%	65
	Total number				471				334

[1]Limits for developmental stages were: preflexion ≤3.8 mm SL< flexion-postflexion.

[2]Data provided by Alex Chester, SEFC, NOAA/NMFS, Beaufort, NC.

[3]Feeding regimes corresponded to larvae fed daily (Fed), larvae starved to the point of 50% mortality (Moderately starved) and larvae starved beyond 50% mortality (Starved).

[4]These analyses follow Powell and Chester (1985). In Analysis II, moderately starved and starved preflexion larvae were combined as were fed and moderately starved flexion-postflexion larvae.

TABLE I-6.–Percent of spot (*Leiostomus xanthurus*) larvae of unknown nutritional condition classified into three nutritional categories by discriminant analysis of six $\log_{10}(X+1)$ transformed morphometric characters [1,2].

Analysis[3]	Developmental stage	*N*	Nutritional category		
			Fed	Moderately starved	Starved
I	Preflexion	110	100%	0	0
	Flexion-postflexion	165	93%	7%	0
	Total number	275			
II	Preflexion	110	100%	—	0
	Flexion-postflexion	165	100%	—	0
	Total number	275			

[1]Preservation-correction algorithms and data provided by Alex Chester, SEFC, NOAA/NMFS, Beaufort, NC.

[2]Feeding regimes corresponded to larvae fed daily (Fed), larvae starved to the point of 50% mortality (Moderately starved) and larvae starved beyond 50% mortality (Starved).

[3]These analyses followed Powell and Chester (1985). In Analysis II, moderately starved and starved preflexion larvae were combined as were fed and moderately starved flexion-post flexion larvae.

TABLE I-7.–Results of a linear regression of six $\log_{10}(X+1)$ transformed morphometric characters of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae regressed against $\log_{10}$(standard length + 1)[1].

Morphometric character	*Leiostomus xanthurus*			*Micropogonias undualtus*		
	Slope	Intercept	r^2	Slope	Intercept	r^2
Preflexion larvae:						
Head length	0.6602	-0.1216	0.7560	0.6996	-0.1429	0.8418
Eye diameter	0.2057	0.0092	0.4142	0.2461	-0.0150	0.5862
Body depth at the:						
anus	0.6450	-0.1293	0.7210	0.6060	-0.1019	0.6900
cleithral symphysis	0.6991	-0.1980	0.5945	0.6149	-0.1420	0.6849
pectoral fin	0.6033	-0.0808	0.6899	0.6155	-0.930	0.6659
Sample size		110			100	
Upper jaw length	0.4871	-0.0901	0.8231	0.4583	-0.758	0.7719
Sample size		55			72	
Flexion-post flexion larvae:						
Head length	0.7839	-0.2129	0.9533	0.7369	-0.1653	0.9463
Eye diameter	0.2053	0.0065	0.7321	0.2078	0.0163	0.7159
Body depth at the:						
anus	0.7023	-0.1787	0.9153	0.6536	-0.1287	0.9112
cleithral symphysis	0.7048	-0.2063	0.8736	0.6555	-0.1600	0.8945
pectoral fin	0.7228	-0.1754	0.9178	0.6691	-0.1247	0.9133
Sample size		165			175	
Upper jaw length	0.6142	-0.1861	0.9428	0.5857	-0.1512	0.9036
Sample size		97			124	

[1]All regression relationships were highly significant ($P < 0.001$, ANOVA).

TABLE I-8.–Results of a one-way analysis of covariance of six $\log_{10}(X+1)$ transformed morphometric characters of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae regressed against $\log_{10}$(standard length + 1)[1].

Morphometric character	Source	Type III[2] SS	*F*	*P*[*]
Preflexion larvae:				
Head length	Slope	0.0002	0.69	NS
	Intercept	0.0001	0.47	NS
Eye diameter	Slope	0.0002	1.65	NS
	Intercept	0.0002	1.37	NS
Body depth at the:				
anus	Slope	0.0002	0.48	NS
	Intercept	0.0002	0.54	NS
cleithral symphysis	Slope	0.0009	1.47	NS
	Intercept	0.0009	1.50	NS
pectoral fin	Slope	0.0000	0.04	NS
	Intercept	0.0000	1.10	NS
Sample size			210	
Upper jaw length	Slope	0.0001	0.42	NS
	Intercept	0.0004	0.25	NS
Sample size			126	
Flexion-postflexion larvae:				
Head length	Slope	0.0019	5.85	0.0161
	Intercept	—	—	—
Eye diameter	Slope	0.0000	0.03	NS
	Intercept	0.0001	0.68	NS
Body depth at the:				
anus	Slope	0.0200	4.43	NS
	Intercept	0.0031	6.65	0.0103
cleithral symphysis	Slope	0.0021	3.88	NS
	Intercept	0.0026	4.16	NS
pectoral fin	Slope	0.0025	5.27	NS
	Intercept	0.0031	6.69	0.0101
Sample size			340	
Upper jaw length	Slope	0.0005	1.29	NS
	Intercept	0.0009	2.58	NS
Sample size			221	

[1]All regression relationships were highly significant ($P < 0.001$, ANOVA).

[2]Type III sum of squares was adjusted for covariate (i.e., standard length) effects.

[*]Significance investigated at $P = 0.05/6$ groups $= .0083 \times 2 \approx 0.02$ (see Kirk [1982]).

TABLE I-9.–Classification results from a discriminant analysis of five $\log_{10}(X+1)$ transformed morphometric characters taken from preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae[1].

Actual group	Predicted group					
	Preflexion			Flexion-postflexion		
	Spot	Croaker	*N*	Spot	Croaker	*N*
Spot	73%	27%	110	79%	21%	165
Croaker	30%	70%	100	29%	71%	175

[1]All data were standardized for standard length. Data from spot were not corrected for preservation effects.

TABLE I-10.–Results of a canonical discriminant analysis of five $\log_{10}(X+1)$ transformed morphometric characters used to determine differences in body shape between spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae.

Analysis[1]	Mahalanobis distance	*P*	Canonical correlation	Wilks' lamda (Λ)	*F*	df	*P*
Preflexion larvae: (*N* = 126)	8.4389	*	0.9729	0.0534	351.480	6	*
Flexion-postflexion larvae: (*N* = 221)	10.7169	*	0.9829	0.0338	1018.028	6	*

[1]All data were standardized for standard length. Spot data were not corrected for preservation effects.
*All probabilities were significant ($P < 0.001$, ANOVA).

TABLE I-11.–Inventory of prey taxa or category identified from the guts of preflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae expressed as the percent frequency of occurrence (*%F*), percent of the total number of food items in the diet (*%N*) and their product, taken as an index of relative importance (RI).

	Micropogonias undulatus			*Leiostomus xanthurus*		
Diet category	*%F*	*%N*	RI	*%F*	*%N*	RI
dinoflagellates[1]	0.0100	0.0026	*	—	—	—
Tintinnida						
Stenosemella sp.	0.0600	0.0315	0.0019	0.0091	0.0042	*
Pteropoda						
Limacina trochiformis	0.0300	0.0262	0.0008	0.0273	0.0126	0.0003
pelecypod veligers[1]	0.0200	0.0079	0.0002	0.0091	0.0021	*
Cladocera[1]	0.0100	0.0052	0.0001	—	—	—
Copepoda[1]	0.0100	0.0026	*	0.0364	0.0483	0.0018
calanoid nauplii	0.1500	0.0997	0.0150	0.1091	0.0819	0.0089
Eucalaus nauplii	—	—	—	0.0091	0.0021	*
cyclopoid nauplii	0.0400	0.0105	0.0004	—	—	—
copepodites	0.0100	0.0026	*	0.0273	0.0084	0.0002
Calanoida[1]	0.4200	0.2520	0.1085	0.2182	0.0819	0.0179
Paracalanus spp.	0.3100	0.1837	0.0570	0.3818	0.2836	0.1083
P. quasimodo	0.0100	0.0052	0.0001	0.0273	0.0063	0.0002
Temora spp.	0.0200	0.0052	0.0001	—	—	—
Acartia tonsa	0.0100	0.0030	*	—	—	—
Harpacticoida						
Microsetella sp.	0.0100	0.0026	*	—	—	—
Euterpina acutifrons	0.0100	0.0026	*	—	—	—
Cyclopoida[1]	0.0800	0.0289	0.0023	0.0545	0.0147	0.0008
Oithona spp.	0.3000	0.1706	0.0512	0.0200	0.0903	0.0181
O. nana	0.0100	0.0052	0.0001	0.1909	0.1828	0.0349
O. plumifera	0.0600	0.0157	0.0009	0.1727	0.0714	0.0123
Oncaea venusta	0.2500	0.1181	0.0295	0.1818	0.0945	0.0172
Cirripedia[1]						
barnacle nauplii	—	—	—	0.0364	0.0105	0.0004
invertebrate eggs[2]	0.0400	0.0184	0.0007	0.0091	0.0042	0.0004
Total number of prey items		381			476	
Total number of guts		100			110	

[1]Unidentified due to advanced stage of digestion.

[2]These were not copepod eggs.

*Indicate RI values < 0.0001.

—Indicate diet categories not utilized by the larvae.

TABLE I-12.–Inventory of prey taxa or category identified from the guts of flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae expressed as the percent frequency of occurrence (*%F*), percent of the total number of food items in the diet (*%N*) and their product, taken as an index of relative importance (RI).

	Micropogonias undulatus			*Leiostomus xanthurus*		
Diet category	*%F*	*%N*	RI	*%F*	*%N*	RI
Tintinnida						
Stenosemella sp.	0.0057	0.0039	*	0.0121	0.0031	*
Pteropoda						
Limacina trochiformis	—	—	—	0.0121	0.0061	*
Cladocera[1]	0.0171	0.0078	0.0001	0.0121	0.0215	0.0003
Copepoda[1]	0.0343	0.0234	0.0008	—	—	—
calanoid nauplii	0.0857	0.0442	0.0038	0.0634	0.0200	0.0007
cyclopoid nauplii	0.0286	0.0091	0.0003	0.0121	0.0061	*
copepodites	—	—	—	0.0242	0.0138	0.0003
Calanoida[1]	0.2686	0.1274	0.0342	0.2303	0.1060	0.0244
Paracalanus spp.	0.4629	0.3121	0.1445	0.5576	0.3026	0.1687
P. crassirostris	0.0286	0.0026	*	0.0303	0.0353	0.0011
P. quasimodo	—	—	—	0.0182	0.0061	0.0001
Temora spp.	0.0171	0.0039	*	0.0061	0.0046	*
Temora turbinata	0.0171	0.0208	0.0004	0.0303	0.0077	0.0002
Acartia tonsa	0.0229	0.0052	0.0001	0.0303	0.0169	0.0005
Harpacticoida[1]	—	—	—	0.0061	0.0015	*
Euterpina acutifrons	0.0057	0.0013	*	0.0121	0.0046	*
Cyclopoida[1]	0.0686	0.0273	0.0019	0.0667	0.0200	0.0013
Oithona spp.	0.3714	0.2172	0.0807	0.1758	0.0952	0.0167
O. nana	0.0571	0.0195	0.0011	0.1697	0.1244	0.0211
O. plumifera	0.1314	0.0793	0.0104	0.1394	0.0722	0.0101
Oncaea venusta	0.1600	0.0702	0.0112	0.1212	0.1014	0.0123
Corycaeus spp.	0.0114	0.0026	*	0.0242	0.0061	0.0001
Cirripedia[1]						
barnacle nauplii	—	—	—	0.0727	0.0230	0.0017
invertebrate eggs[2]	0.0057	0.0013	*	0.0061	0.0015	*
Total number of prey items		769			651	
Total number of guts		175			165	

[1]Unidentified due to advanced stage of digestion.

[2]These were not copepod eggs.

*Indicate RI values < 0.001.

—Indicate diet categories not utilized by the larvae.

TABLE I-13.–Classification results from an interspecific discriminant analysis of diet composition of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Diet was characterized by the $\log_{10}(X+1)$ transformed number of prey items eaten from each of 23 diet categories.

		Predicted group					
		Preflexion			Flexion-postflexion		
Analysis[1]	Actual group	Spot	Croaker	*N*	Spot	Croaker	*N*
A	Spot	65%	35%	110	60%	40%	165
	Croaker	28%	72%	100	31%	69%	175
B	Spot	51%	49%	110	42%	58%	165
	Croaker	23%	77%	100	16%	84%	175

[1]Analysis A included all diet items (*sans* unknown copepods) encountered in the gut contents analysis. Analysis B included those diet items which were selected by stepwise discriminant analysis as significant ($P < 0.15$) discriminators of flexion stage and species by diet composition with all other diet items combined as a single category.

TABLE I-14.–Classification results from an intraspecific discriminant analysis of diet composition of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Diet was characterized by the $\log_{10}(X+1)$ transformed number of prey items eaten from each of 23 diet categories.

		Predicted group					
		Spot			Croaker		
Analysis[1]	Actual group	Pre	Flex-post	*N*	Pre	Flex-post	*N*
A	Preflexion	59%	46%	110	63%	37%	100
	Flex-post	32%	68%	165	25%	75%	175
B	Preflexion	44%	56%	110	59%	41%	100
	Flex-post	32%	68%	165	37%	63%	175

[1]Analysis A included all diet items (*sans* unknown copepods) encountered in the gut contents analysis. Analysis B included those diet items which were selected by stepwise discriminant analysis as significant ($P < 0.15$) discriminators of flexion stage and species by diet composition with all other diet items combined as a single category.

TABLE I-15.–Stepwise discriminant analysis results listing those diet categories most important in discriminating between spot and Atlantic croaker larvae by diet composition. Diet categories are listed in decreasing order of discriminating power. The singularity criterion for variables entering into the stepwise model was $P < 0.15$.

Diet category	F	P	Wilks' lambda (Λ)	P
Analysis A[1]				
Preflexion larvae:				
Oithona nana	18.39	<0.001	0.9188	<0.001
Calanoida	8.37	<0.005	0.8831	<0.001
Paracalanus spp.	6.76	<0.010	0.8550	<0.001
barnacle nauplii	4.49	<0.05	0.8366	<0.001
O. plumifera	4.31	<0.05	0.8194	<0.001
Temora spp.	3.99	<0.05	0.8036	<0.001
cyclopoid nauplii	3.98	<0.05	0.7880	<0.001
copepodites	2.33	<0.15	0.7790	<0.001
Flexion-postflexion larvae:				
Oithona spp.	17.52	<0.001	0.9506	<0.001
barnacle nauplii	11.48	<0.001	0.9192	<0.001
O. nana	12.30	<0.001	0.8866	<0.001
copepodites	3.65	<0.10	0.8770	<0.001
calanoid nauplii	4.24	<0.05	0.8660	<0.001
Paracalanus quasimodo	3.31	<0.10	0.8574	<0.001
Acartia tonsa	2.55	<0.15	0.8509	<0.001
Analysis B[1]				
Preflexion larvae:				
Oithona nana	32.33	<0.001	0.9442	<0.001
barnacle nauplii	18.46	<0.001	0.9133	<0.001
copepodites	6.20	<0.05	0.9030	<0.001
Calanoida	4.68	<0.05	0.8953	<0.001
Paracalanus spp.	2.67	<0.15	0.8910	<0.001
Overall model	7.84	<0.001	0.8843	<0.001
Flexion-postflexion larvae:				
Oithona nana	32.33	<0.001	0.9442	<0.001
barnacle nauplii	18.46	<0.001	0.9133	<0.001
Oithona spp.	12.86	<0.005	0.8923	<0.001
copepodites	6.18	<0.005	0.8822	<0.001
Paracalanus quasimodo	2.35	<0.05	0.8784	<0.001
Overall model	9.79	<0.01	0.8733	<0.01

[1]Analysis A includes all the diet items (*sans* unknown copepods) encountered in the gut contents analysis. Analysis B includes those diet items which were selected by stepwise discriminant analysis as significant discriminators of larval species by diet composition with all other diet items combined as a single category.

TABLE I-16.–Stepwise discriminant analysis results listing those diet categories most important in discriminating between developmental stages of spot and Atlantic croaker larvae by diet composition. Diet categories are listed in decreasing order of discriminating power. The singularity criterion for variables entering into the stepwise model was $P < 0.15$.

Diet category	*F*	*P*	Wilks' lambda (Λ)	*P*
Analysis A				
Spot:				
calanoid nauplii	6.88	<0.01	0.9753	<0.01
Temora turbinata	3.16	<0.10	0.9640	<0.01
Corycaeus spp.	3.21	<0.10	0.9526	<0.01
Paracalanus crassirostris	2.67	<0.15	0.9432	<0.01
Acartia tonsa	2.47	<0.15	0.9346	<0.01
Croaker:				
Paracalanus spp.	9.51	<0.01	0.9665	<0.01
Calanoida	7.72	<0.01	0.9399	<0.001
calanoid nauplii	5.32	<0.05	0.9219	<0.001
Pteropoda	5.47	<0.05	0.9036	<0.001
Stenosemella sp.	5.88	<0.05	0.8844	<0.001
Oithona nana	3.43	<0.10	0.8732	<0.001
dinoflagellates	3.16	<0.10	0.8630	<0.001
P. crassirostris	2.77	<0.10	0.8542	<0.001
Temora turbinata	2.43	<0.15	0.8465	<0.001
Oncaea venusta	2.10	<0.15	0.8398	<0.001
Paracalanus quasimodo	2.11	<0.15	0.8331	<0.001
Analysis B				
Spot:				
calanoid nauplii	9.01	<0.005	0.9838	<0.005
Parcalanus crassirostris	4.87	<0.05	0.9751	<0.001
Acartia tonsa	4.19	<0.05	0.9676	<0.001
Corycaeus sp.	4.16	<0.05	0.9603	<0.001
Temora turbinata	3.06	<0.10	0.0549	<0.001
Overall	4.33	<0.001	0.9542	<0.001
Croaker:				
calanoid nauplii	9.01	<0.01	0.9838	<0.005
Paracalanus spp.	8.81	<0.01	0.9682	<0.001
P. crassirostris	5.72	<0.05	0.9581	<0.001
Pteropoda	4.56	<0.05	0.9502	<0.001
Stenosemella sp.	3.95	<0.05	0.9433	<0.001
Temora turbinata	3.34	<0.10	0.9375	<0.001
dinoflagellates	2.13	<0.15	0.9338	<0.001
Calanoida	2.13	<0.15	0.9302	<0.001
Oncaea venusta	2.24	<0.15	0.9263	<0.001
Overall	3.81	<0.001	0.9214	<0.001

[1]Analysis A includes all the diet items (*sans* unknown copepods) encountered in the gut contents analysis. Analysis B includes those diet items which were selected by stepwise discriminant analysis as significant ($P < 0.15$) discriminators of flexion stage by diet composition with all other diet items combined as a single category.

TABLE I-17.–Indices of diet overlap for preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae.

Species and developmental stage	Index of diet overlap[1]		
	Schoener[2] α	Hurlbert $L \pm$S.D.	N
Spot × croaker:			
Preflexion	0.6079	3.47±2.22	5
Flexion-post flexion	0.8109	3.62±1.91	4
Preflexion × flexion-postflexion:			
Spot	0.8392	2.77±1.60	4
Croaker	0.6190	4.77±4.00	4

[1]Indices were Schoener's (1970) percent overlap and Hurlbert's (1978) index of niche overlap.

[2]Calculations were based on consumption of 24 diet categories by 275 larvae of each species.

[3]Mean values of L were computed from collections that contained at least five larvae of any two larval groups (N) and were restricted to 13 broad food categories.

TABLE I-18.–Results of a Wilcoxon distribution-free rank sum test of prey length, width and height taken from prey items identified from the guts of spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Comparison of means were made interspecifically and intraspecifically. Means not preceded by the same superscript were significantly different at $P < 0.001$ except those denoted by *, which were significantly different at $P < 0.05$.

Species and developmental stage	Total number of prey items eaten[1]	Prey morphometrics (mm)		
		Length	Width	Height
Spot:				
Preflexion × Flexion-postflexion	479	^{*A}418.74±104.05	^{A}146.49±27.79	^{*A}152.02±37.84
	668	^{*B}462.42±234.52	^{B}156.47±34.57	^{*B}164.49±67.89
Croaker:				
Preflexion × Flexion-postflexion	386	^{A}348.82±117.72	^{A}135.05±31.33	^{A}141.84±41.60
	784	^{B}456.85±208.85	^{B}151.74±33.81	^{B}161.35±47.01
Preflexion:				
Spot × Croaker	479	^{A}418.74±104.05	^{*A}146.49±27.79	^{A}152.02±37.84
	386	^{B}348.82±117.72	^{*B}135.05±31.33	^{B}141.84±41.60
Flexion-postflexion:				
Spot × Croaker	668	^{A}462.42±234.52	^{A}156.47±34.57	^{A}164.49±67.89
	784	^{A}456.85±208.85	^{B}151.47±33.81	^{A}161.35±47.01

[1]Cell sizes were N = 110 and 100 for preflexion spot and croaker, and N = 165 and 175 for flexion-postflexion spot and croaker.

TABLE I-19.–Classification results from a nonparametric discriminant analysis of prey length, width and height taken from prey items identified from the gut contents of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Classification scores were compared interspecifically by developmental stage.

Actual group	Predicted group					
	Preflexion			Flexion-postflexion		
	Spot	Croaker	N^1	Spot	Croaker	N^1
Spot	38%	62%	479	21%	79%	668
Croaker	24%	76%	386	14%	86%	784

[1]These are the total number of prey eaten by all larvae in each group. Groups sizes of larvae were N = 110 and 100 for preflexion spot and croaker, and N = 165 and 175 for flexion-postflexion spot and croaker.

TABLE I-20.–Classification results from a nonparametric discriminant analysis of prey length, width and height taken from prey items identified from the gut contents of preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Classification scores were compared intraspecifically.

Actual group	Predicted group					
	Spot			Croaker		
	Pre	Flex-post	N^1	Pre	Flex-post	N^1
Preflexion	18%	82%	479	26%	74%	386
Flex-post	13%	87%	668	11%	89%	784

[1]These are the total number of prey items eaten by all larvae in each group. Sample sizes of larvae are N = 110 and 100 for preflexion spot and croaker, and N = 165 and 175 for flexion-postflexion spot and croaker.

TABLE I-21.–Results of a principal component analysis of prey length, width and height taken from prey items eaten by spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae.

Species	Developmental stage	Original variable[1]	Correlation			Eigenvectors[2]		
			L	W	H	PC1	PC2	PC3
Spot	Preflexion	L	1.0000	0.7569	0.7674	0.5781	-0.4400	0.6929
		W	—	1.0000	0.7577	0.5756	0.8172	0.0280
		H	—	—	1.0000	0.5783	-0.3826	-0.7205
					Eigenvalue:	2.5214	0.2461	0.2326
					Proportion:	0.8405	0.0820	0.0775
	Flexion-preflexion	L	1.0000	0.5333	0.3444	0.5629	-0.6619	0.4950
		W	—	1.0000	0.4985	0.6207	-0.0570	-0.7820
		H	—	—	1.0000	0.5458	0.7474	0.3788
					Eigenvalue:	1.9220	0.6570	0.4210
					Proportion:	0.6407	0.2190	0.1403
Croaker	Preflexion	L	1.0000	0.6075	0.6963	0.5569	0.7859	0.2686
		W	—	1.0000	0.7582	0.5756	-0.5984	0.5573
		H	—	—	1.0000	0.5988	-0.1558	-0.7856
					Eigenvalue:	2.3765	0.3995	0.2240
					Proportion:	0.7922	0.1332	0.0747
	Flexion-preflexion	L	1.0000	0.3299	0.3777	0.4578	0.8869	0.0622
		W	—	1.0000	0.7146	0.6221	-0.3696	0.6902
		H	—	—	1.0000	0.6351	-0.2773	-0.7209
					Eigenvalue:	1.9723	0.7444	0.2833
					Proportion:	0.6574	0.2481	0.0944

[1]L, W and H are prey length, width and height measured to the nearest 0.01 mm.

[2]Eigenvectors represent actual loadings of each principal component on the original morphometric variables and indicate the importance of each original variable to the respective principal component. Proportions are the amount of variation in the original variables accounted for by each eigenvalue.

TABLE I-22.–Results of a chi-square goodness-of-fit analysis of the frequency distributions of the first and second principal component scores derived for each prey item eaten by spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae by a principal component analysis of prey length, width and height.

Species and developmental stage	χ^2	df	P^*
First principal component-overall size of the prey:			
Spot × croaker:			
Preflexion	1251.51	16	<0.005
Flexion-post flexion	915.55	14	<0.005
Preflexion × flexion-postflexion:			
Spot	2878.58	14	<0.005
Croaker	242.79	14	<0.005
Second principal component-prey height and width:			
Spot × croaker:			
Preflexion	476.52	8	<0.005
Flexion-post flexion	21.22	8	<0.05
Preflexion × flexion-postflexion:			
Spot	747.14	7	<0.005
Croaker	238.90	8	<0.005

*Significance adjusted to $P = 0.001/2$ comparisons $= 0.005$ and $P = 0.01/2 = 0.05$ (see Kirk [1982]).

TABLE I-23.–Results of a principal component analysis of morphometrics obtained from prey items in 13 broad food categories eaten by spot and Atlantic croaker larvae, and from the ambient plankton.

Group		Original variable[1]	Correlation			Eigenvectors[2]		
			L	W	H	PC1	PC2	PC3
Spot	Preflexion	L	1.0000	0.7534	0.7596	0.5776	-0.4895	0.6533
		W	—	1.0000	0.7549	0.5764	0.8112	0.0982
		H	—	—	1.0000	0.5780	-0.3199	-0.7507
					Eigenvalue:	2.5119	0.2478	0.2403
					Proportion:	0.8373	0.0826	0.0801
	Flexion-preflexion	L	1.0000	0.6884	0.4911	0.6132	-0.2842	-0.7370
		W	—	1.0000	0.4352	0.5969	-0.4443	-0.6680
		H	—	—	1.0000	0.5173	0.8496	0.1028
					Eigenvalue:	2.0844	0.6081	0.3075
					Proportion:	0.6947	0.2027	0.1025
Croaker	Preflexion	L	1.0000	0.5431	0.6703	0.5484	0.7846	0.2891
		W	—	1.0000	0.7487	0.5741	-0.6047	0.5521
		H	—	—	1.0000	0.6080	-0.1368	-0.7821
					Eigenvalue:	2.3116	0.4647	0.2238
					Proportion:	0.7705	0.1549	0.0746
	Flexion-preflexion	L	1.0000	0.6848	0.6745	0.5853	-0.0832	-0.8066
		W	—	1.0000	0.7146	0.5749	-0.6589	0.4851
		H	—	—	1.0000	0.5718	0.7476	-0.3378
					Eigenvalue:	2.3316	0.3628	0.3056
					Proportion:	0.7772	0.1209	0.1019
Ambient plankton		L	1.0000	0.6599	0.7420	0.5487	0.8152	0.1856
		W	—	1.0000	0.8611	0.5816	-0.5317	0.6157
		H	—	—	1.0000	0.6006	0.2298	-0.7658
					Eigenvalue:	2.5117	0.3604	0.1278
					Proportion:	0.8372	0.1201	0.0426

[1]L, W and H are prey length, width and height measured to the nearest 0.01 mm.

[2]Eigenvectors represent actual loadings of each principal component on the original morphometric variables and indicate the importance of each original variable to the respective principal component. Proportions are the amount of variation in the original variables accounted for by each eigenvalue.

TABLE I-24.–Results of a chi-square test of homogeneity and independence of the frequency distributions of the scores of the first and second principal components derived from a principal component analysis of prey morphometrics. Morphometrics were obtained from plankters from 13 broad food categories eaten by spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae and from the ambient plankton.

Principal component	χ^2	df	*P*
First principal component overall size of the prey:	532.51	64	<0.001
Second principal component prey length and width:	174.67	48	<0.001

TABLE I-25.–Weighted mean values (±S.D.) of the $\log_{10}(X+1)$ transformed relative availability (p) and utilization (r) of 13 broad food categories eaten by preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Leiostomus xanthurus*) larvae. This analysis was restricted collections that contained at least five larvae in any one of the four larval groups.

Broad food category	*Leiostomus xanthrus*				*Micropognonias undulatus*			
	Preflexion		Flexion-postflexion		Preflexion		Flexion-postflexion	
	p	r	p	r	p	r	p	r
Pteropoda	0.003±0.024	0.018±0.136	0.003±0.024	0.012±0.081	0.003±0.024	0.018±0.109	0.003±0.024	0.003±0.024
Cladocera	0.041±0.213	0	0.041±0.213	0.001±0.009	0.041±0.213	0.007±0.065	0.041±0.213	0
Copepoda								
copepod nauplii	0.018±0.076	0.020±0.107	0.018±0.077	0.013±0.089	0.018±0.076	0.078±0.307	0.018±0.076	0.023±0.107
copepodites	0.003±0.029	0.027±0.085	0.003±0.029	0.004±0.028	0.003±0.029	0.004±0.025	0.003±0.029	0
Calanoida								
Acartia tonsa	0.106±0.291	0.012±0.121	0.106±0.291	0.003±0.022	0.106±0.291	0.002±0.016	0.106±0.291	0.005±0.336
Paracalanus spp.	0.079±0.192	0.103±0.273	0.079±0.192	0.133±0.345	0.079±0.192	0.106±0.244	0.079±0.192	0.079±0.247
Temora spp.	0.030±0.134	0	0.030±0.134	0.003±0.028	0.030±0.134	0.003±0.019	0.030±0.134	0.030±0.192
Cyclopoida								
Corycaeus spp.	0.027±0.084	0	0.027±0.084	0.004±0.036	0.027±0.084	0	0.027±0.084	0.004±0.029
Oithona spp.	0.028±0.097	0.159±0.345	0.028±0.097	0.147±0.327	0.028±0.097	0.087±0.206	0.028±0.097	0.075±0.258
Oncaea venusta	0.018±0.051	0.042±0.242	0.018±0.051	0.027±0.144	0.013±0.051	0.083±0.261	0.018±0.051	0.080±0.300
Harpacticoida								
Euterpina acutifrons	0.017±0.077	0	0.017±0.077	0	0.017±0.077	0.004±0.028	0.017±0.077	0.003±0.023
Microsetella spp.	0.002±0.012	0	0.002±0.012	0	0.002±0.012	0.004±0.035	0.002±0.012	0
Cirripedia								
barnacle nauplii	0.010±0.060	0.036±0.238	0.010±0.060	0.019±0.142	0.010±0.060	0	0.010±0.060	0

[1]Means were weighted by the number of available food categories in each MOCNESS collection.

TABLE I-26.–Weighted[1] mean values (±S.D.) of Chesson's index of food selection for spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. This analysis was based on utilization of 13 broad food categories by the larvae and was restricted to collections that contained at least five larvae in any one of the four larval groups.

Broad food category	Spot		Croaker	
	Preflex (*n*)[2]	Flex-post (*n*)	Preflex (*n*)	Flex-post (*n*)
Pteropoda	**0.211±1.270 (11)	0.007±0.048 (12)	*0.101±0.831 (11)	—
Cladocera	—	*0.106±1.010 (11)	0.001±0.011 (11)	—
Copepoda				
copepod nauplii	*0.095±0.493 (11)	0.016±0.106 (11)	0.099±0.380 (11)	0.092±0.510 (10)
copepodites	*0.084±0.453 (12)	0.032±0.206 (11)	0.069±0.435 (12)	—
Calanoida				
Acartia tonsa	*0.099±0.964 (11)	0.012±0.115 (10)	0.009±0.080 (11)	0.001±0.003 (10)
Paracalanus spp.	**0.145±0.541 (11)	*0.171±0.803 (10)	*0.160±0.892 (11)	**0.312±0.982 (10)
Temora spp.	—	0.097±0.150 (10)	0.011±0.098 (11)	0.033±0.167 (10)
Cyclopoida				
Corycaeus spp.	—	0.097±0.834 (10)	— (8)	0.043±0.451 (10)
Oithona spp.	*0.246±0.814 (11)	**0.495±1.252 (10)	**0.458±1.265 (11)	**0.244±0.926 (10)
Oncaea venusta	*0.177±0.651 (11)	0.091±0.375 (10)	**0.218±0.954 (11)	**0.318±1.194 (10)
Harpacticoida				
Euterpina acutifrons	—	—	0.006±0.045 (11)	0.006±0.046 (10)
Microsetella spp.	—	—	0.003±0.024 (11)	—
Cirripedia				
barnacle nauplii	0.059±0.390 (12)	0.010±0.104 (11)	—	—

[1]Means were weighted by the number of available food categories in each MOCNESS collection.

[2]*n* are the mean number of food categories out of 13, rounded to the nearest whole number, that were available to the larvae in collections that contained each food category.

—Indicate food categories not utilized by larvae in those samples in which the food category was available.

*Indicate values > 1/*n* and indicate weak-moderate preference for these food categories.

**Indicate values >> 1/*n* and indicate strong preference for these food categories.

TABLE I-27.–List of those diet categories deleted from the database of Govoni et al. (1986a) in order to permit an interannual comparison of diet composition for spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae with data from the present study.

Diet category[1]	Reason for deleting
chlorophytes diatoms tintinnids (not *Stenosemella*) rotifers	Undersampled by the 67 μm mesh net and their abundances would be grossly under estimated. Chlorophytes and diatoms were probably not eaten intentionally by the larvae but were instead ingested incidentally with zooplankton. These groups were never encountered in the present study. Likewise, rotifers and tintinnids were only rarely encountered in the present study.
chyme unidentified	Larvae do not eat these categories. Chyme is a by-product of digestion and "unidentified" is an artifact of the researcher's inability to identity the gut contents.
chaetognaths (*Sagitta* sp.)	This may have been an important group in both data sets, but because of rapid digestion and disarticulation, it was nearly impossible to obtain accurate counts.
Eucalanus sp. *Labidocera* sp. *Undinula* sp. *Lubockia* sp. *Saphirella* sp. Amphipoda crabs	These groups were never or very rarely recovered from gut contents in the present study and were rarely encountered in Govoni et al. (1986a). Their contribution to diet distinctiveness was therefore minimal and would have been dropped automatically by the discriminant analyses[2].

[1]These data were 5.6% and 6.4% of the total number of prey eaten by Atlantic croaker and spot larvae.

[2]Classification and canonical discriminant analyses automatically drop any variable (i.e., diet category) that has constant values and would thus offer no discrimination to the groups being compared.

TABLE I-28.–Results of a multivariate analysis of variance of diet composition of spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae between three years[1], listing those diet categories that were utilized in significantly different ($P < 0.01$) numbers[2].

Leiostomus xanthurus		*Micropogonias undulatus*	
Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
Stenosemella spp.	Pteropoda	pelecypod veligers	dinoflagellates
Pteropoda	Pelecypoda	copepodites	copepodites
pelecypod veligers	copepod nauplii	*Paracalanus* spp.	Calanoida
copepodites	*Eucalanus* nauplii		pelecypod veligers
Calanoida	Calanoida		*Paracalanus* spp.
Paracalanus spp.	*Paracalanus* spp.		*P. quasimodo*
Cyclopoida	*P. crassirostris*		*Temora* spp.
Oithona spp.	*Oncaea venusta*		*Oithona* spp.
O. nana	Harpacticoida		Harpacticoida
O. plumifera	*Microsetella* sp.		*Euterpina acutifrons*
invertebrate eggs	Ostracoda		barnacle nauplii
	invertebrate eggs		Ostracoda
			invertebrate eggs

[1]Year one corresponded to 12/79 and 02/80, year two corresponded to 12/80 and 02/81, and year three corresponded to 02/81.

[2]Data were the $\log_{10}(X+1)$ transformed number of each prey item eaten by the larvae.

TABLE I-29.–Results of a canonical discriminant analysis of diet composition of spot and Atlantic croaker larvae between three different years. This analysis was based on the $\log_{10}(X+1)$ transformed number of prey eaten in those diet categories selected by a multivariate analysis of variance as being utilized in significantly different ($P < 0.01$) numbers between the three years[1].

Larval group	Mahalanobis distance	*P*	Canonical correlation		Multivariate test			
			Can1	Can2	Wilks' lambda	*F*	df	*P*
Preflexion spot:			0.7650	0.5174	0.3037	14.586	22	<0.001
Year 1 × 2	3.454	<0.001						
Year 1 × 3	3.709	<0.001						
Year 2 × 3	2.397	<0.001						
Flexion-postflexion spot:			0.7548	0.5495	0.3003	12.716	24	<0.001
Year 1 × 2	4.521	<0.001						
Year 1 × 3	3.001	<0.001						
Year 2 × 3	3.445	<0.001						
Preflexion croaker:			0.5357	0.1206	0.7026	8.556	6	<0.001
Year 1 × 2	0.906	N.S.						
Year 1 × 3	1.008	N.S.						
Year 2 × 3	1.496	<0.001						
Flexion-postflexion croaker:			0.7017	0.5664	0.3447	11.413	26	<0.001
Year 1 × 2	3.179	<0.001						
Year 1 × 3	3.085	<0.001						
Year 2 × 3	2.590	<0.001						

[1]Year 1 corresponded to 12/79 and 02/80, year 2 corresponded to 12/80 and 02/81 and year 3 corresponded to 02/81.

TABLE I-30.–Classification results from an interannual[1] comparison of diet composition by discriminant analysis for preflexion and flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Diet was characterized by the $\log_{10}(X+1)$ transformed number of prey items from 29 diet categories identified from the gut contents of the larvae.

Species and developmental stage	Actual Group	Predicted group			
		Year 1	Year2	Year 3	*N**
Spot:					
preflexion	Year 1	57%	43%	0%	7
	Year 2	3%	93%	4%	94
	Year 3	3%	14%	83%	110
flexion-postflexion	Year 1	40%	0%	60%	10
	Year 2	4%	76%	20%	25
	Year 3	2%	4%	94%	165
Croaker:					
preflexion	Year 1	83%	17%	0%	6
	Year 2	32%	45%	23%	31
	Year 3	10%	1%	89%	100
flexion-postflexion	Year 1	60%	7%	33%	15
	Year 2	6%	69%	25%	36
	Year 3	3%	1%	96%	175

[1]Year one corresponded to 12/79 and 02/80, year two corresponded to 12/80 and 02/81, and year three corresponded to 02/81.

**N* are the total number of larvae in each group from each of the three years.

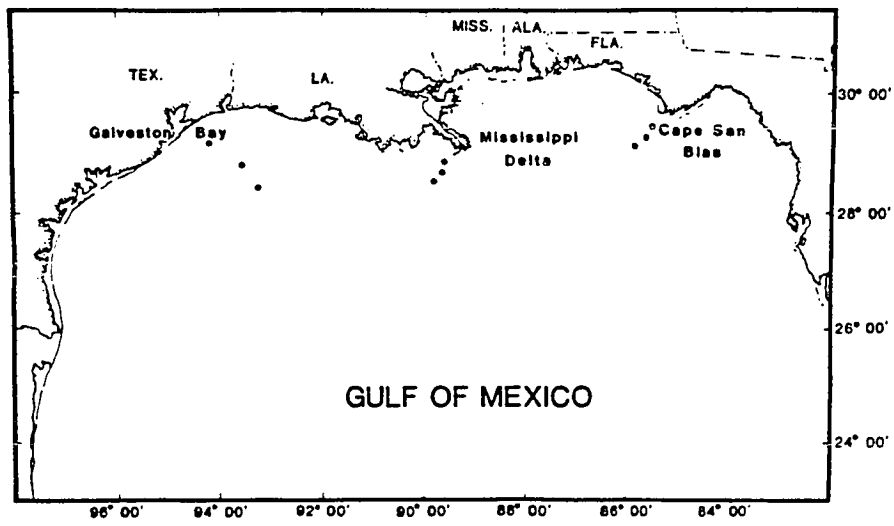

FIGURE I-1.–Map showing location of stations and transects where spot, *Leiostomus xanthurus*, and croaker, *Micropogonias undulatus*, larvae were collected in the northern Gulf of Mexico (from Govoni et al. [1983]).

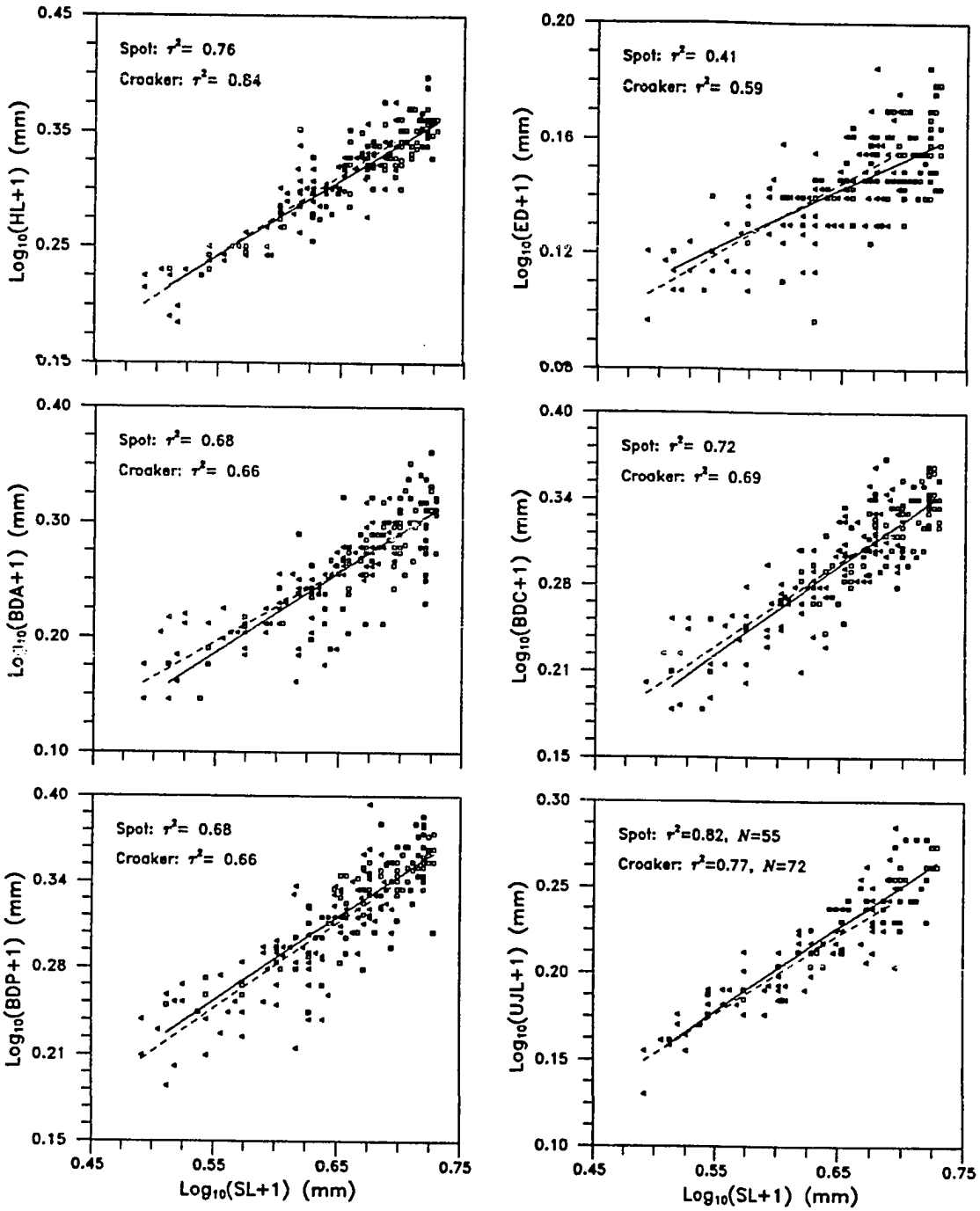

FIGURE I-2.–Relationship between six $\log_{10}(X+1)$ transformed morphometric characters and standard length of preflexion spot and Atlantic croaker larvae. Dashed lines and triangles denote croaker and solid lines and squares denote spot. BDA, BDP and BDC are body depth at the anus, pectoral fin and cleithral symphysis, and UJL is upper jaw length. N=110 for spot and N=100 for croaker except where noted.

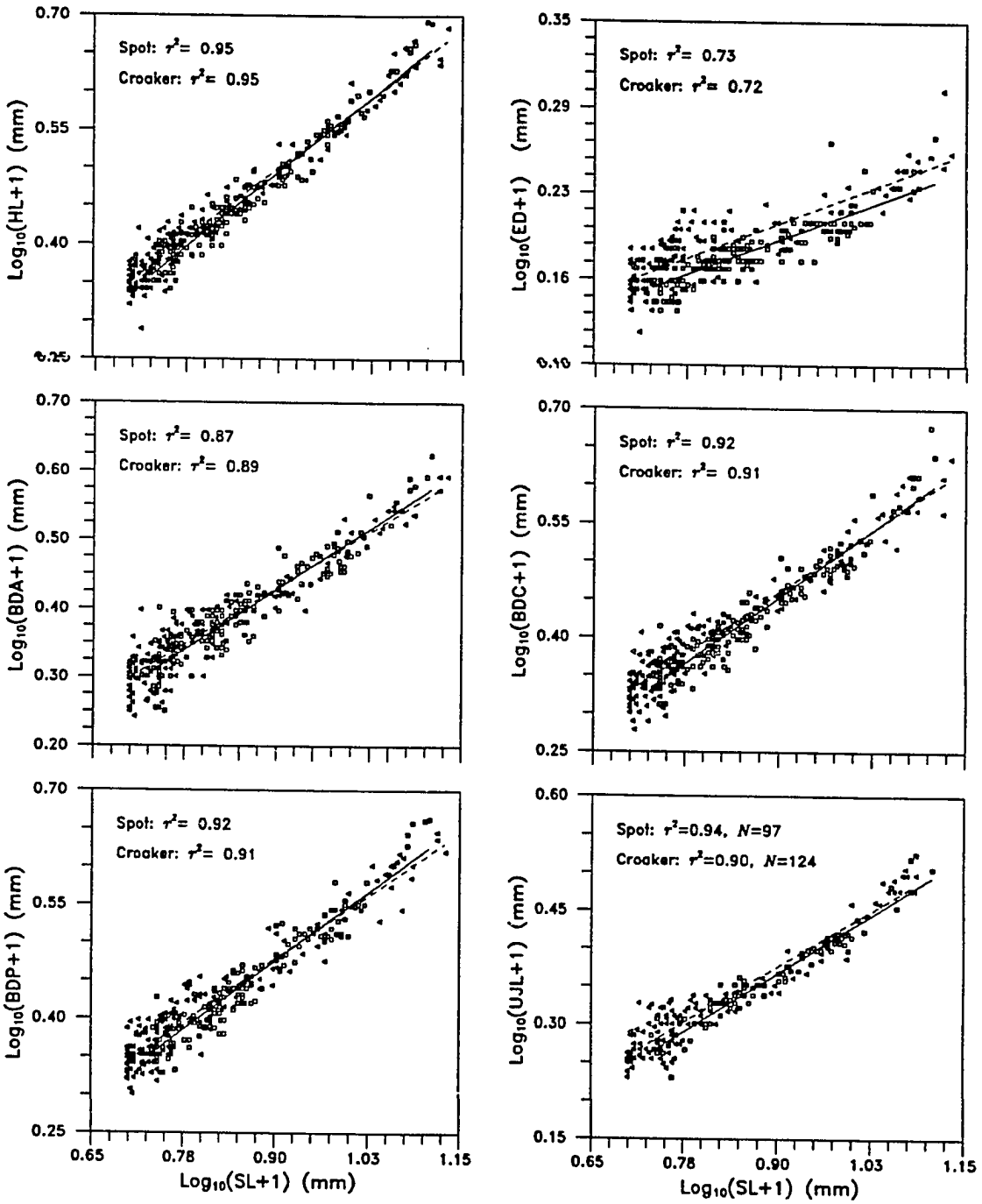

FIGURE I-3.–Relationship between six $\log_{10}(X+1)$ transformed morphometric characters and standard length of flexion-postflexion spot and Atlantic croaker larvae. Dashed lines and triangles denote croaker and solid lines and squares denote spot. BDA, BDP and BDC are body depth at the anus, pectoral fin and cleithral symphysis, and UJL is upper jaw length. N=165 for spot and N=175 for croaker except where noted.

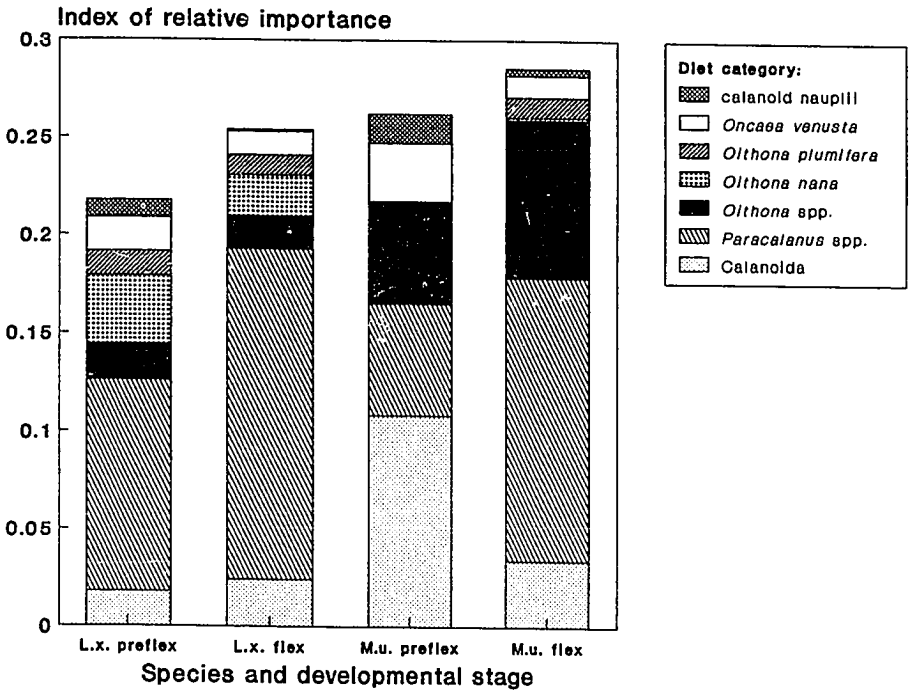

FIGURE I-4.–Relative importance indices (RI) of seven diet categories from preflexion and flexion-postflexion spot and Atlantic croaker larvae. RI values are the product of the percent frequency of occurrence (*%F*) and the percent total number (*%N*) of food items in the diet for each diet category. Diet categories with RI values ≥ 0.01 for at least one larval groups were plotted. L.x. is spot, M.u. is croaker, preflex is preflexion and flex is flexion-postflexion.

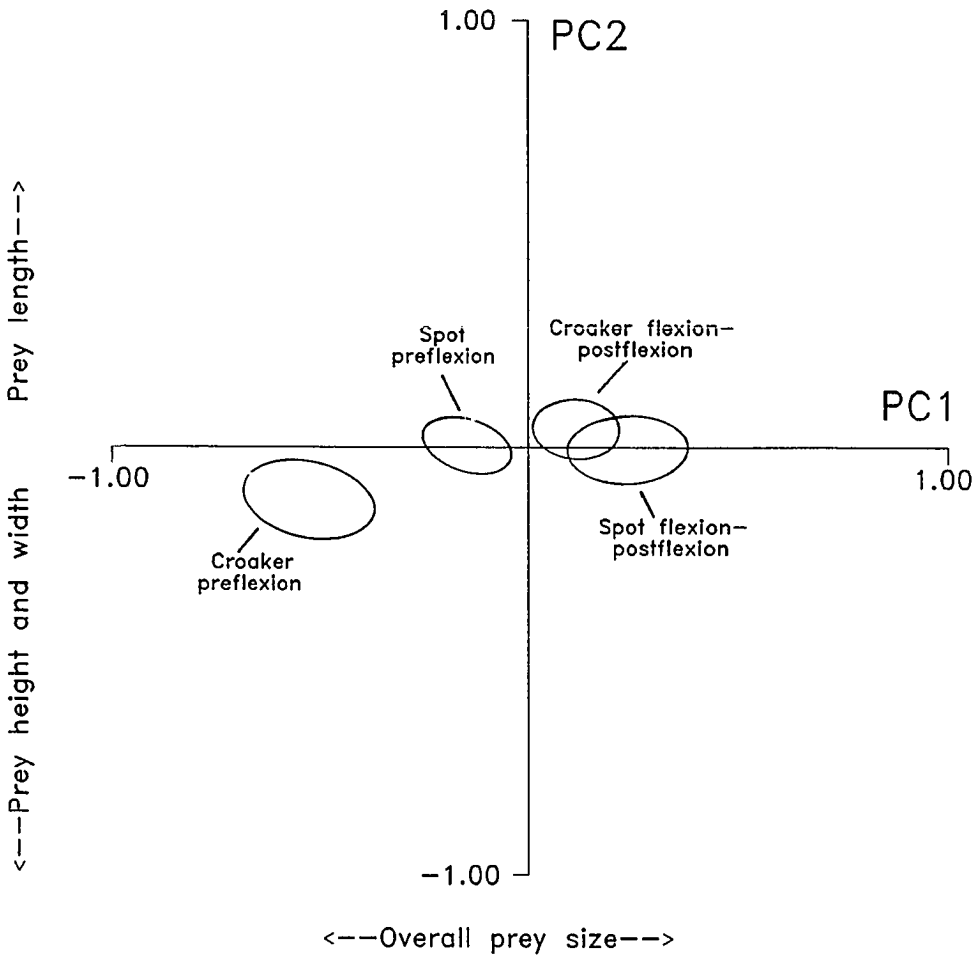

FIGURE I-5.–Plot of the 95% confidence ellipses on the first two principal components derived from a principal component analysis of prey morphometrics taken from prey items eaten by preflexion and flexion-postflexion spot and Atlantic croaker larvae. Morphometrics included prey length, width and height measured to the nearest 0.01 mm.

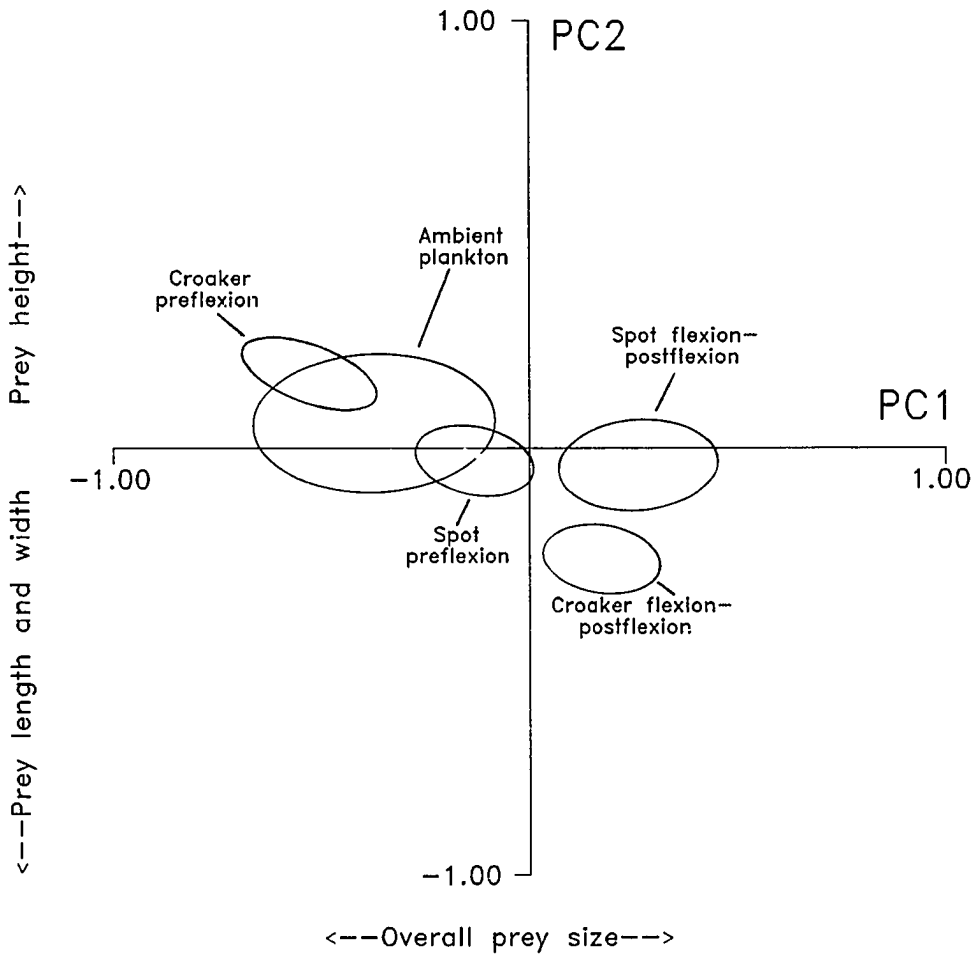

FIGURE I-6.–Plot of the 95% confidence ellipses on the first two principal components derived from a principal component analysis of prey morphometrics taken from prey in 13 broad food categories eaten by preflexion and flexion-postflexion spot and Atlantic croaker larvae, and from the ambient plankton. Morphometrics included prey length, width and height measured to the nearest 0.01 mm.

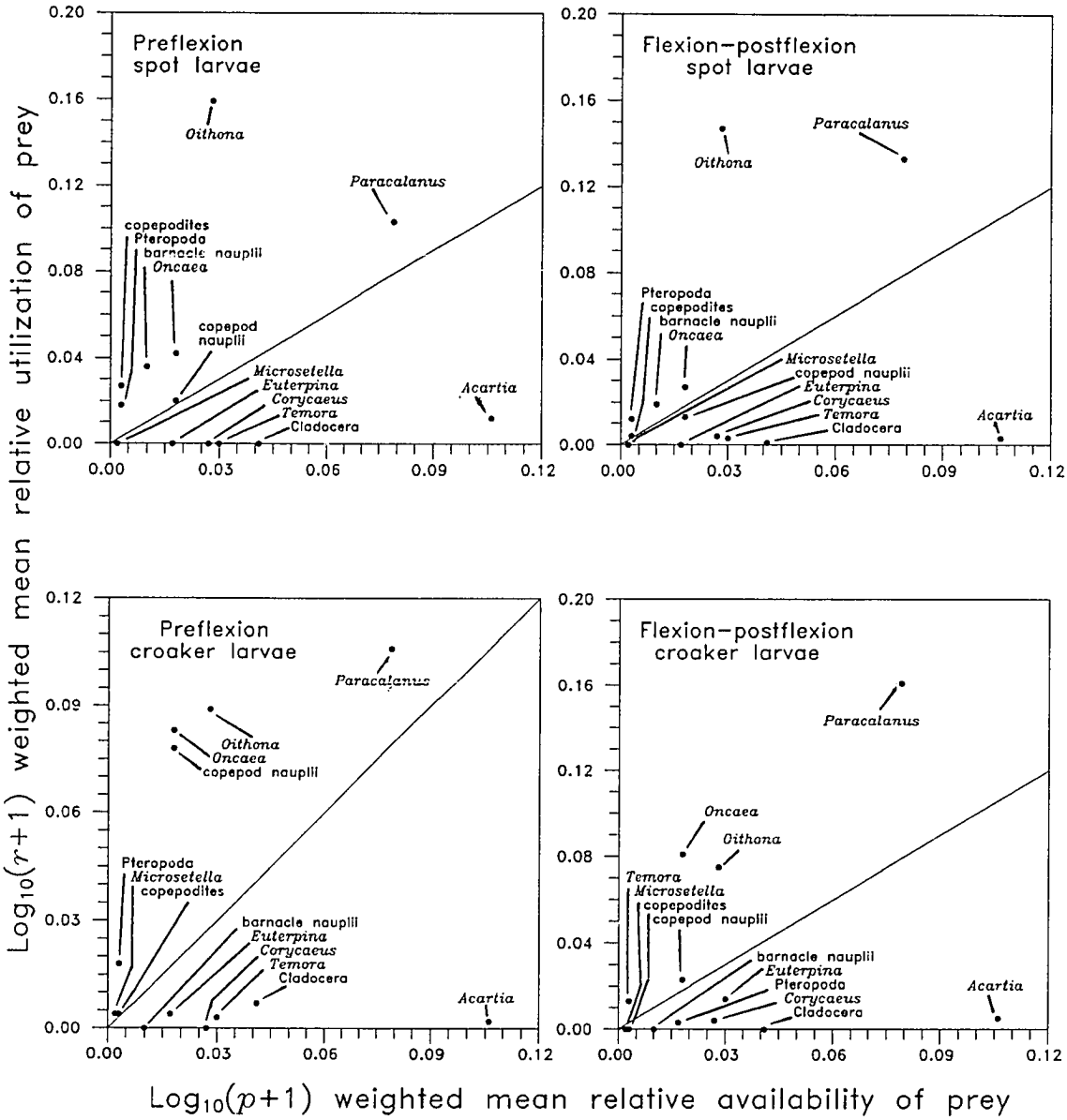

FIGURE I-7.–Relationship between the $\log_{10}(X+1)$ transformed weighted means of the relative percent utilization (r) and relative percent availability (p) of 13 broad food categories from the diets of preflexion and flexion-postflexion spot and Atlantic croaker larvae. Diagonal lines represent random ($p = r$) feeding. Points above the diagonal indicate selection ($p < r$) and points below the diagonal indicate avoidance ($p > r$).

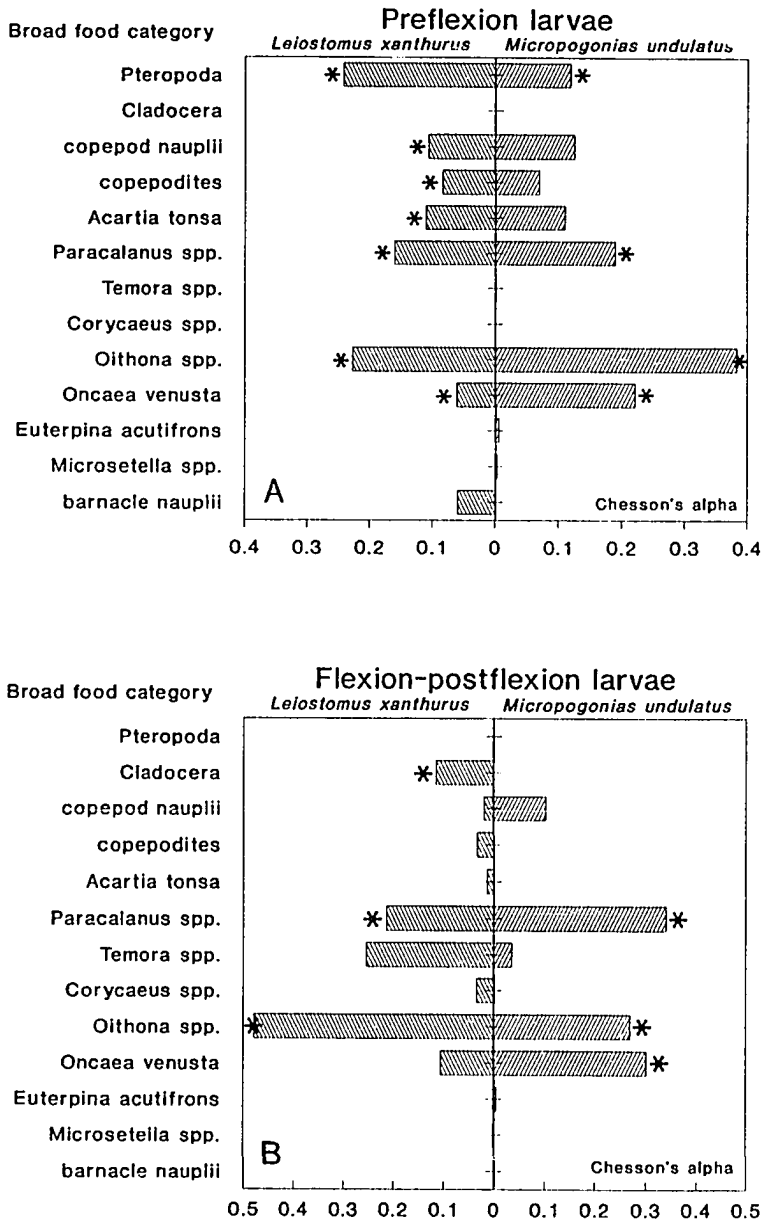

FIGURE I-8.–Weighted mean values of Chesson's index of food selection for (A) preflexion and (B) flexion-postflexion spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) larvae. Mean values were calculated for 13 broad food categories from collections that contained at least five individuals of one of the larval groups and were weighted by the number of available food categories in each collection. Values denoted by * represent index values > $1/n$.

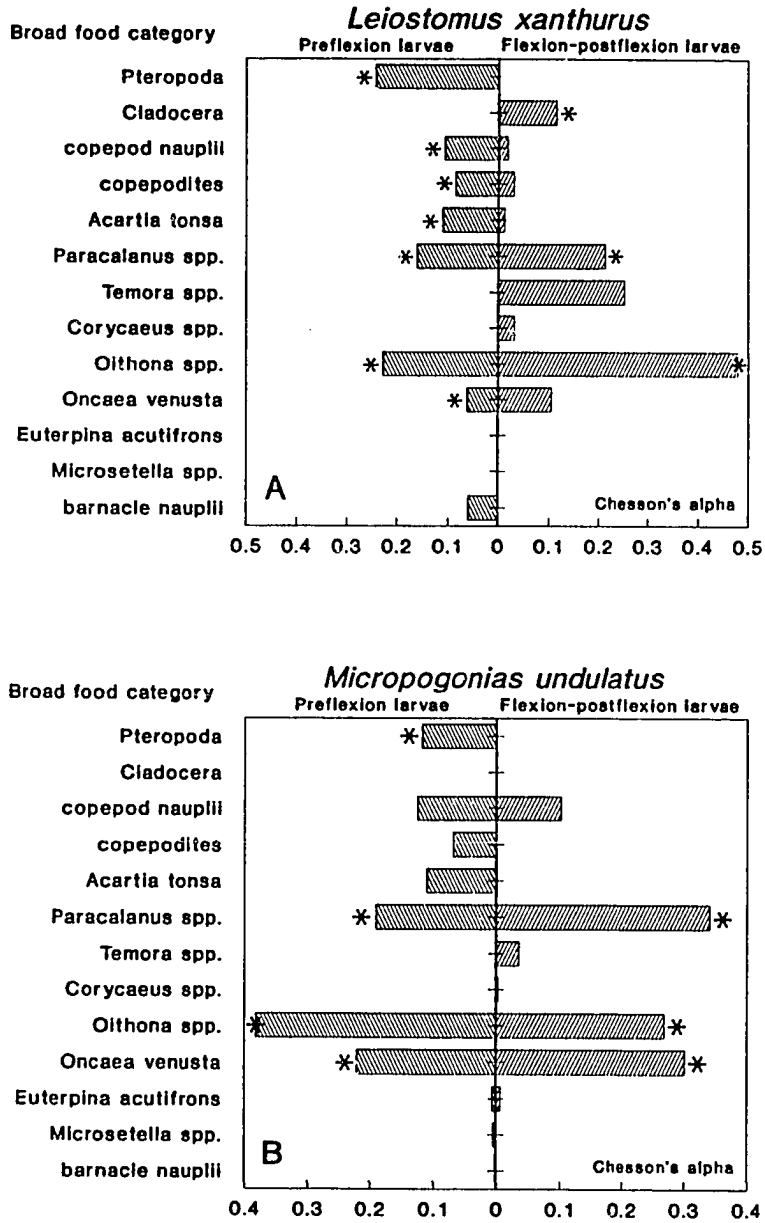

FIGURE I-9.–Weighted mean values of Chesson's index of food selection for (A) spot (*Leiostomus xanthurus*) and (B) Atlantic croaker (*Micropogonias undulatus*) larvae. Mean values were calculated for 13 broad food categories from collections that contained at least five individuals of one of the larval groups and were weighted by the number of available food categories in each collection. Values denoted by * represent index values > $1/n$.

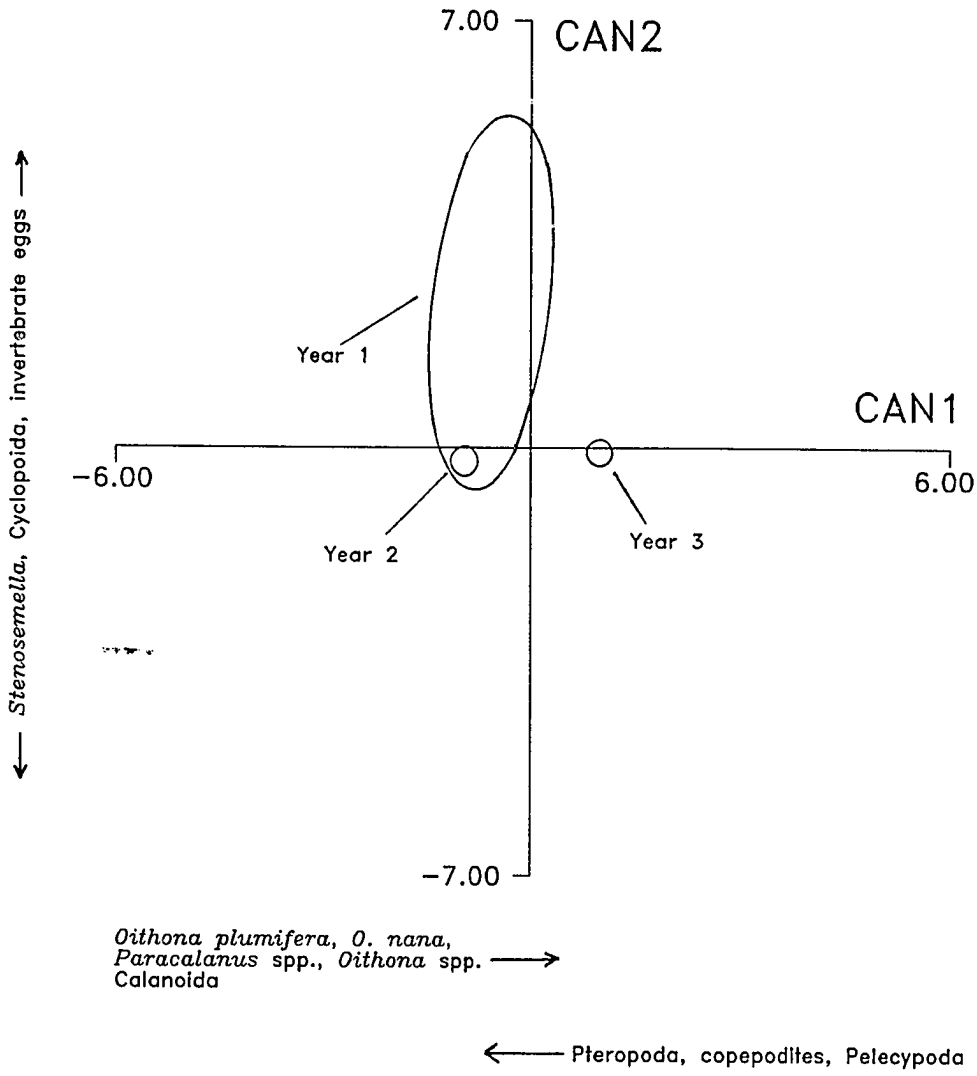

FIGURE I-10.–Plot of the 95% confidence ellipses on the first two canonical functions derived from a canonical discriminant analysis of diet composition of preflexion spot (*Leiostomus xanthurus*) larvae from three different years in the northern Gulf of Mexico.

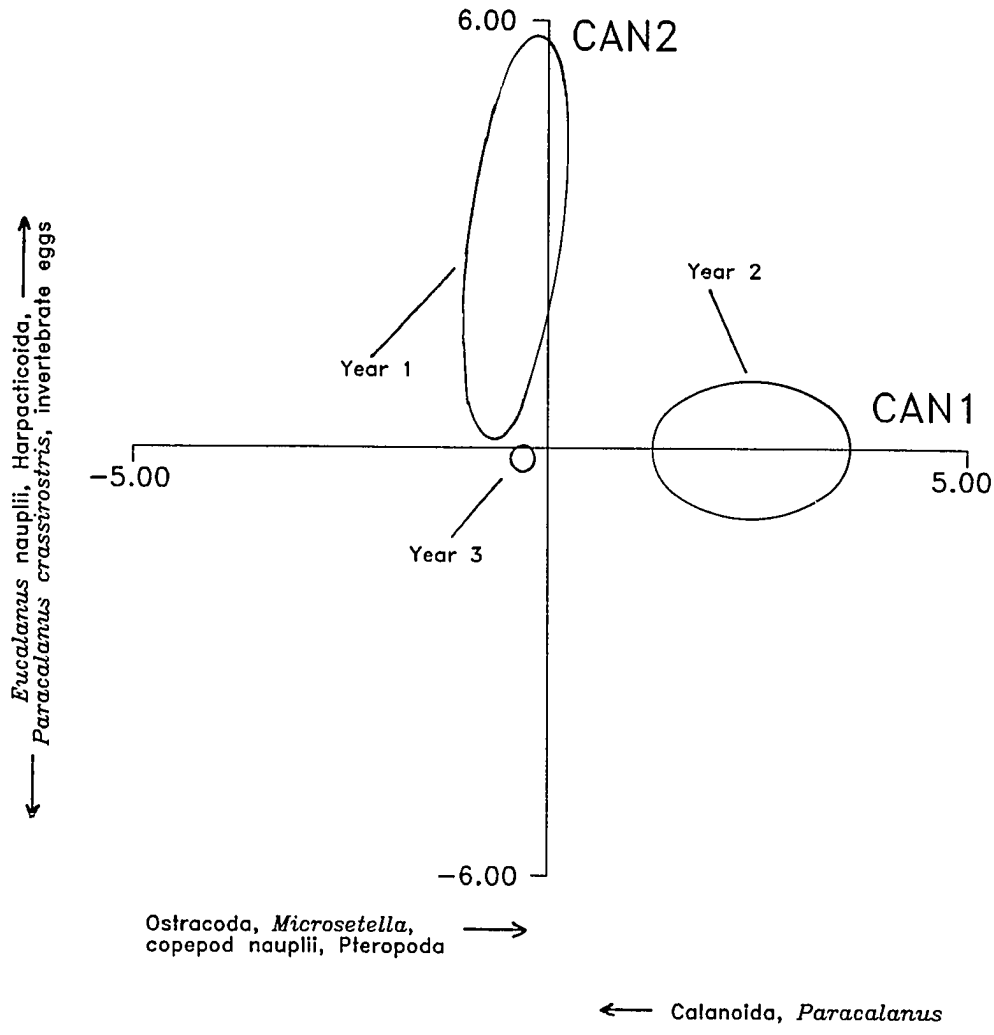

FIGURE I-11.–Plot of the 95% confidence ellipses on the first two canonical functions derived from a canonical discriminant analysis of diet composition of flexion-postflexion spot (*Leiostomus xanthurus*) larvae from three different years in the northern Gulf of Mexico.

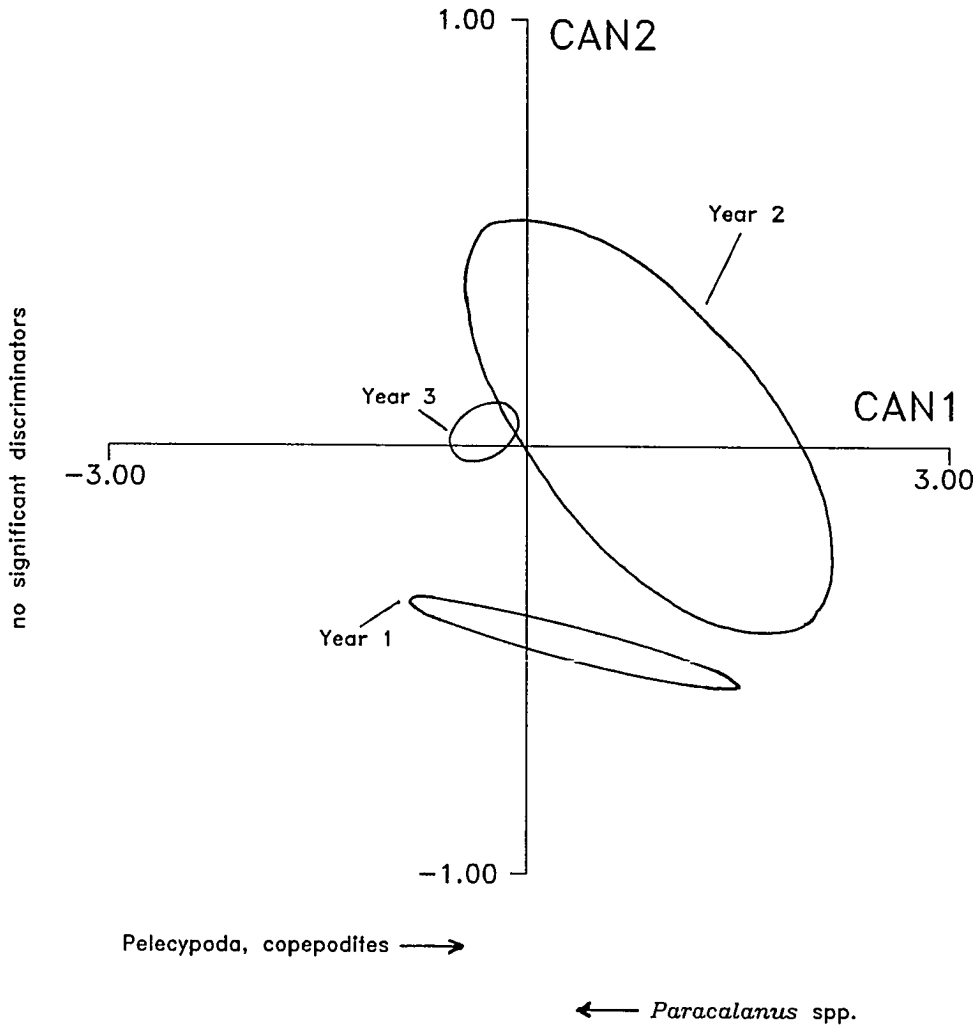

FIGURE I-12.–Plot of the 95% confidence ellipses on the first two canonical functions derived from a canonical discriminant analysis of diet composition of preflexion croaker (*Micropogonias undulatus*) larvae from three different years in the northern Gulf of Mexico.

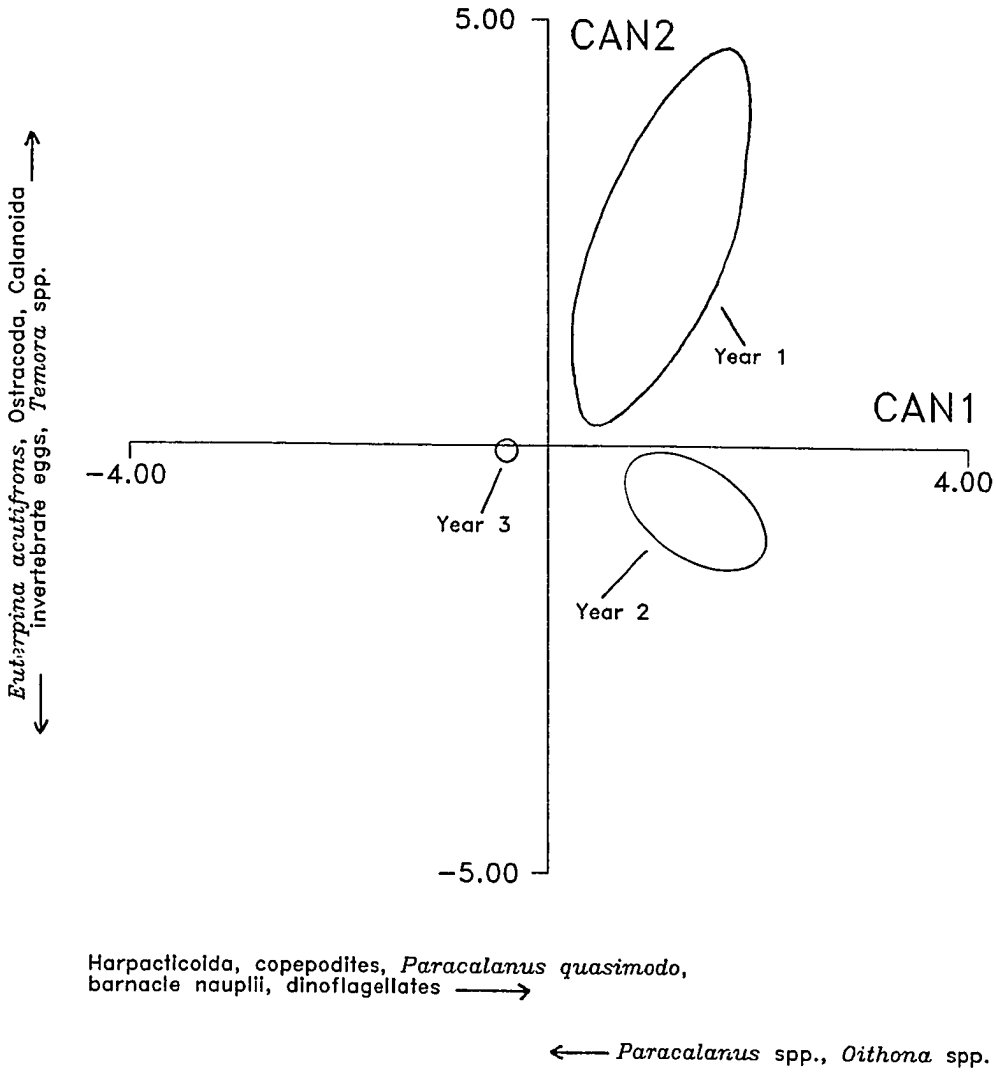

FIGURE I-13.–Plot of the 95% confidence ellipses on the first two canonical functions derived from a canonical discriminant analysis of diet composition of flexion-postflexion croaker (*Micropogonias undulatus*) larvae from three different years in the northern Gulf of Mexico.

DISCUSSION

Nutritional State

Starvation in marine fish larvae has been demonstrated for several species by histological (Theilacker 1978; O'Connell 1980) as well as morphometric methods (Theilacker 1978; Koslow et al. 1985; Powell et al. in press). Theilacker (1978) reported that 45% of larval jack mackerel (*Trachurus symmetricus*) collected in the open ocean were starving, whereas O'Connell (1980) encountered nearshore patches of larval northern anchovy (*Engraulis mordax*) in which the starvation rate approached 60%. Powell et al. (in press) reported values of 13 - 59% starvation for spot larvae along the Mississippi River plume front. In the present study, however, spot larvae were never classified as being starved and only 7% of flexion-postflexion spot larvae were classified as moderately starved (Table I-6). The fact that no starving larvae were found can be explained in several ways. Feeding conditions in the study area may have been adequate to afford the majority of the larvae a high level of nutritional condition and therefore, starvation was not a significant effector of mortality among these larvae at the time of collection.

If Lasker and Zweifel (1978), Houde and Schekter (1978) and Hunter (1981) are correct in suggesting that the co-occurrence of fish larvae and their planktonic prey is infrequent and episodic, then starvation might also be episodic. If this is so, the majority of larvae in a particular patch should exhibit a similar state of nutritional condition that reflects a common feeding history. Starved larvae should therefore be encountered in patches (e.g., O'Connell 1980) or not at all. On the other hand, some level of starvation might have been present among the larvae, but remained undetected by the morphometric index. Morphometrics may provide only a crude measure of nutritional status

(Koslow et al. 1985), and the degree of resolution provided by three coarsely defined nutritional groups (i.e., starved, moderately starved and starved) may not have been sufficient to evaluate differences in nutritional condition among larvae from the wild. Starvation may be a gradual and continual process dependent on the periodicity and duration of patch co-occurrence and not punctuated in the same way as the index (i.e., fed versus starved). Also, by the time starvation manifests itself as significant changes in body shape, the larva has probably already died or has been eaten.

Physical condition is known to influence swimming performance in young fishes (Bams 1967; Laurence 1972), and larvae in a poor nutritional state are probably swimming and feeding at reduced efficiency. For example, in studying the swimming abilities of larval largemouth bass (*Micropterus salmoides*), Laurence (1972) demonstrated that fed larvae had significantly different swimming speeds and behavior than did larvae starved for four days. He related his findings to the potential search volume of the larvae and concluded that poorly fed larvae were at a disadvantage during unfavorable feeding conditions because of their diminished swimming performance. Changes in morphology (i.e. body shape) as well as weakened sensory and muscular systems must all affect swimming behavior. Larvae that are weakened by starvation probably quickly succumb to predation pressure; therefore, it may be difficult to sample them. This reasoning does not reconcile the results of the present study with those of Powell et al. (in press), in which the same morphometric index of nutritional condition for spot was utilized. The results of that study suggest that their morphometric index is indeed sensitive to starvation among spot larvae at sea, and therefore it is somewhat unlikely that the lack of starving larvae in the present study was an artifact of their index. Those authors reported a wide degree of variation in the incidence of starvation during a single year. In comparing their results with the results from the present study, it appears that the degree of starvation among these larvae can be quite variable from year to year as well. That variability is undoubtedly dependent upon the past feeding history of the larvae, as well

as on the quality of the feeding conditions in the area the larvae are collected. Considering the size of the study area, it is surprising that no starving larvae were found among the 275 individuals collected.

Interspecific Comparison of Larval Morphometrics

The original purpose of comparing the morphologies of larval spot and Atlantic croaker was to determine the validity of applying a nutritional condition index to croaker larvae that was derived in the laboratory for spot. Significant interspecific differences in the size and shape between the two species existed, and consequently, the nutritional condition among croaker could not be evaluated from that index. That analysis, however, was also useful for evaluating differences in body shape and making general inferences to swimming performance, feeding success and diet composition.

Except for minor differences in pigmentation, larval spot and Atlantic croaker are morphologically indistinguishable (Lippson and Moran 1974). Fruge and Truesdale (1978) reported that no significant differences in body depth at the anus, the cleithrum, or in head length, existed for these species. Interspecific differences in eye diameter did exist by 4.5 mm SL and in preanal length by 8.5 mm SL, however (larvae $\approx 1.5 \leq$ SL ≤ 10.7 mm). In the present study, no interspecific differences in eye diameter were found when these data were regressed against standard length. In fact, significant differences ($P < 0.05$) were only found for three morphometric characters among flexion-postflexion larvae when standard length was treated as a covariate (Table I-8). Although only minor differences in body size were evident, two types of discriminant analysis demonstrated distinct interspecific differences in body shape in preflexion and flexion-postflexion larvae (Tables I-9, I-10). These differences may be attributed to the cumulative effect of subtle or minor (i.e., not statistically significant) differences in the five dimensions of body size between the species. Shape is the three-dimensional resultant of several

single-dimensional linear measurements, and discriminant analysis will maximize such subtle multivariate differences in the groups being compared.

Interspecific differences in body size and shape are significant because they undoubtedly affect the swimming performance of the larvae (Webb and Corolla 1981; Batty 1984; Webb and Weihs 1986) and may therefore affect pursuit and capture of prey as well as food selection. Like their planktonic prey, larval fishes are restricted to viscous and intermediate hydrodynamic regimes because of their small size and low swimming speeds (Kerfoot et al. 1980; Hunter 1981; Chia et al. 1984; Fuiman 1986; Fuiman and Webb 1988). Objects moving through a fluid are subjected to forces arising from their velocity, length (and shape), and the kinematic viscosity of the fluid they occupy. Such hydrodynamic conditions are evaluated in terms of turbulence and indexed as the ratio of the viscous forces to the inertial forces in the form of a dimensionless variable called the Reynolds number (R_e), which is expressed as follows:

$$R_e = \nu \cdot L \cdot \nu^{-1} \tag{9}$$

where

$$\nu = \rho \cdot \mu^{-1} \tag{10}$$

ν is the fish's velocity, L is its length and ν is the kinematic viscosity of the water, which is determined by computing the ratio of the density (ρ) to the viscosity (μ). During routine swimming activity, larval zebra danios (*Danio rerio*) spend approximately 98% of their time in viscous (R_e <30) and intermediate (30< R_e <200) hydrodynamic regimes (Fuiman and Webb 1988). Only during the height of critical activities such as escape and food capture do these larvae enter the inertial hydrodynamic regime (R_e >270) in which adult fish reside (Fuiman 1986). As such, they and their food are generally influenced by the fluid's viscosity and not by inertial forces caused by the turbulent flow of swimming.

Consequently, interspecific differences in body shape or those changes in shape induced by starvation, can directly affect the swimming abilities and feeding performance of fish larvae. These differences would be reflected in differences in diet composition and food selection. Even though the exact relationship between larval body shape, swimming ability and diet composition was not investigated, the results obtained from the morphometric analysis may be related to the differences found in the diets of the four larval groups.

Diet Composition and Overlap

Fish larvae that co-occur are potential competitors for the same food resources (Laurence et al. 1981; Crecco and Blake 1983; Kane 1984). Although both spot and Atlantic croaker larvae collected in discrete water masses demonstrated significant differences in the composition and breadth of their diets (Tables I-13 to I-17), they shared many of the same diet categories. As such, they were potential competitors for those resources (Tables I-11, I-12). Divergence in diet, as well as spatial and temporal segregation, are means of avoiding inter- and intraspecific competition for resources (Schoener 1970, 1982; Zaret and Rand 1971; Laroche 1982), but as Laroche (1982) pointed out, inferring competition from information about dietary divergence may be inappropriate. This has not, however, inhibited researchers from assessing the possibility of inter- and intraspecific competition with respect to the degree of dietary overlap between closely related species (e.g., Laurence et al. 1981; Laroche 1982; Crecco and Blake 1983; Kane 1984). Other authors (e.g., Hurlbert 1978; Abrams 1980) have indicated that caution is necessary when attempting to make inferences between overlap and competition, particularly if food resources are not limiting. Percent dietary overlap is known to vary directly with plankton abundance (Zaret and Rand 1971; Laroche 1982) and is dependent upon the degree of trophic specialization (i.e., selectivity) among the predators (Ivlev 1961). Dietary overlap indices are therefore only indirectly related to

the level of competition and perhaps serve only as indicators of temporal changes in competition (Kane 1984), as well as the potential for competition.

The large degree of dietary overlap between and among both species of larvae (Table I-17) and the apparent convergence of diet with age were not unexpected. Similar levels of dietary overlap (i.e., 0-0.85) and convergence in diet composition with age, were previously demonstrated for both species by Govoni et al. (1983). Those authors demonstrated that diets were most distinct among the youngest larvae (SL ≤5.00), at a time when prey size strongly coincided. In the present study, older larvae exploited diet categories that were not exploited, or were poorly exploited, by preflexion larvae (Table I-15). Because those diet categories, as a combined group, were not significant discriminators of species, they were probably not important (see below) to either developmental stage. Consequently, it was those categories identified by stepwise discriminant analysis that were utilized differently by the four larval groups (Tables I-14, I-15, I-16). Also, as larvae grew and added new diet categories to their diets, the relative importance of any single category already in the diet decreased (Tables I-11, I-12). Spatial segregation as well as significant differences in diet composition among these species prompted Govoni et al. (1983) to conclude that these larvae were not competing for food. The high level of nutritional condition exhibited by the larvae in the present study suggests that food resources were probably not limiting in the study area. Consequently, the high level of dietary overlap exhibited by the larvae, particularly among flexion-postflexion larvae, was probably not indicative of interspecific competition, but instead of an abundant food supply. Hunter (1981) suggested that the tendency for younger larvae to feed upon a greater diversity of prey and the subsequent specialization on stages of copepods (i.e., larger prey) by the larvae as they grow, may be due to the existence in the sea of a greater variety of small organisms of the proper size.

The observed pattern of interspecific convergence in diet with age is somewhat paradoxical. At the onset of exogenous feeding, when preflexion spot and Atlantic

croaker larvae are morphologically identical, it would be expected that larvae would attempt to eat whatever prey possible. That behavior should be reflected in a higher degree of overlap among the younger larvae. The fact that this was not the case might be explained by differences in the distribution of the larvae and their prey at different times during the life history of the larvae. Although there is no empirical evidence to support this hypothesis, it is possible that at the time of spawning, eggs and newly hatched (i.e., preflexion larvae) of these two species are probably spatially segregated to a greater extent than when the larvae are older. Initially, the pattern of larval distribution is dependent on the spatiotemporal proximity of spawning activity of the two species but as the larvae migrate shoreward and enter plankton-rich estuarine waters during development, spatial segregation is bound to deteriorate and the potential for competition increases. Finally, the pressure of interspecific competition might be relieved somewhat by monopolizing certain diet categories while at the same time sharing others. For example, diet categories that were infrequently encountered in the gut contents were more important to the diet of croaker larvae than to those of spot (Table I-13). Although this combined group of diet categories was not identified as being a significant discriminator of larval species, differential utilization of this group by the two species in addition to those categories that were significant discriminators of species (Table I-15), would have reduced the potential for competition. Kane (1984) described a similar convergence of diet composition with age for two species of larval gadid, the cod (*Gadus morhua*) and the haddock (*Melanogrammus aeglefinus*). He suggested that the higher level of partitioning of resources among younger larvae decreases the chances of competition during a period when starvation is relatively high and the larvae can ill afford the pressure of competition. With growth, larvae were better suited for competition and better able to share resources.

Finally, there was a lower degree of overlap among the two developmental stages of Atlantic croaker larvae than among spot, suggesting that intraspecific competition was

perhaps relatively more intense among spot. Similar intraspecific differences were demonstrated in larval cod and haddock by Kane (1984). As croaker larvae grew, their diet changed to a greater extent than did the diet of spot. It is difficult to evaluate this difference in ecological terms, but it is important to note that the changes in diet of both species resulted in greater overlap between the two species.

In addition to changes in the taxonomic composition of the diet of the two species associated with growth, changes in the size of the prey eaten by the larvae also occurred. Govoni et al. (1983) demonstrated that diet was most distinct among preflexion Atlantic croaker and spot larvae, even though the size of the prey eaten was most similar among these larvae. It has been shown that as larvae grow, they add progressively larger prey to their diets, but do not discontinue feeding on smaller prey (Sherman and Honey 1971; Hunter 1981; Govoni et al. 1983, 1986a; Kane 1984). This pattern is often characterized by a change in diet of copepod eggs and nauplii to one containing copepodites and adult copepods (Laroche 1982; Govoni et al. 1983). Similar results were obtained in the present study. Flexion-postflexion larvae ate significantly larger prey than did preflexion larvae (Table I-18). Therefore, in terms of the composition (see above) and size distribution of prey in the diet, larger larvae should have a more distinct diet than smaller larvae. This is because larger larvae share many diet categories with the smaller larvae, while at the same time exploiting new and larger prey. This was found to be the case in the present study. A discriminant analysis of prey size classified flexion-postflexion larvae with much greater accuracy than it did preflexion larvae, indicating that the older larvae had a relatively more distinct diet than did their preflexion counterparts (Table I-20). Interspecific differences in the size of prey consumed also existed. In spite of the larger degree of dietary overlap, spot and croaker larvae ate significantly different sizes of prey (Table I-18). Croaker larvae exploited sizes of prey that were not in the diet of spot larvae, while spot larvae shared a large part of the size distribution of their prey with croaker (Table I-19). These differences cannot be related to differences in the size of

the larvae. Spot larvae were significantly larger than croaker larvae for both developmental, stages and as such, they should have exploited a wider distribution of prey sizes. As was the case in the analysis of diet composition mentioned above, smaller larvae had a more distinct diet. A more quantitative discussion of prey size and shape, and food selection will follow.

Food Selection

Selective feeding has been demonstrated in many species of larval fishes (see Turner [1984] for a review), and spot and Atlantic croaker are no exception. Results of the present study demonstrated conclusively that these species feed selectively on certain plankters (Figs. I-7 to I-9) and these results are in good agreement with results reported by Govoni et al. (1986a) for the same species. Direct comparison between the two studies is difficult, however, because of several procedural differences. In the present study, all the larvae in a single collection were treated as a single "gut" and the analysis of food selection was performed for 13 broad food categories by the flexion stage of the larvae. In contrast, Govoni et al. (1986a) computed individual index scores for each larva and then computed a mean value. Those authors also performed their analysis on food groups that were combined somewhat differently than in the present study and were based on 5.00 mm (SL) size classes of larvae.

Several notable differences, however, could not be attributed to procedural differences between the two studies. In the present study, larvae in all four groups exhibited variable degrees of food selection for the 13 broad food categories, and demonstrated strong selectivity for the copepods *Oithona* spp. and *Paracalanus* spp. (Figs. I-7 to I-9). On the other hand, Govoni et al. (1986a) reported that smaller spot (1.00 - 5.00 mm) and larger croaker (5.00 - 10.00 mm) larvae did not, on average, selectively feed on *Oithona* spp., but instead fed upon pelecypods, a diet category that was rarely encountered in plankton samples and rarely eaten by larvae in the present study.

Also, the calanoid copepod *Acartia tonsa* had the greatest availability of all plankters, but was almost always absent from the diets of the larvae in the present study (Fig. I-7). In contrast, Govoni et al. (1986a) reported a high degree of selection for this food item among both young croaker larvae and older spot larvae. This is a notable difference between the two studies and it is unclear why feeding incidence for *A. tonsa* was so low in the present study. Other authors have similarly reported selection against *A. tonsa* (e.g., Checkley 1982; Peterson and Ausubel 1984; Monteleone and Peterson 1986; Jenkins 1987). Jenkins (1987) suggested that a negative correlation in the distribution of *A. tranteri* with other plankters was responsible for the observed selection against that plankter by two larval pleuronectids. This may or may not have been the case in the present study. Although MOCNESS collections of short duration and discrete depth simultaneously sampled larvae and their planktonic prey, information regarding the spatial scale of the patches of plankton being sampled were not available and therefore it is not possible to evaluate this factor. Checkley (1982) attributed selective avoidance in Atlantic herring (*Clupea harengus*) to greater burst speed, visibility and escape capability on the part of *A. tonsa*, and perhaps these factors also played a role in the present study. Govoni et al. (1986a) correlated diet composition among spot and croaker larvae with published data on the swimming behavior and color of prey. These authors suggested that the relatively slower, irregular and zigzag swimming behavior characteristic of smaller calanoid copepods such as *A. tonsa* might explain their abundance in the diets of these larvae. The actual relationship between the swimming behavior of the prey and larval diet composition remains untested. Short of direct observation of predator and prey, it is difficult to evaluate the specific role of microplankton swimming behavior in food selection by larval fishes. Govoni et al. (1986a) reported that *Paracalanus* spp. was not selected by smaller spot and croaker larvae, but in the present study, this prey species was the most frequently encountered in the gut content analysis. It is unclear why these

differences exist between the present study and the work of Govoni et al. (1986a), but in a very broad sense they underscore an inherent variability in selective behavior.

In spite of the fact that the diets of both species converged with age (Tables I-14, I-17), preflexion larvae of both species showed a greater similarity in their patterns of food selection (i.e., based on Chesson's α-index of food selection) than did flexion-postflexion larvae (Fig. I-8). This paradox is difficult to explain, inasmuch as diets should diverge with age (see above). The fact that the patterns for α between spot and Atlantic croaker diverged with age is not surprising and probably reflects ontogenetic divergences in the behavior and morphology of the two species. What is surprising is that there was no concomitant divergence in diet composition. It would seem that older spot and croaker larvae selected different prey, but not in sufficient numbers to result in dietary divergence. Some other factors must be enhancing dietary convergence, but it is unclear what those factors might be.

Inter- and Intrannual Comparison of Food Selection

The degree of food selection for each of the 13 broad food categories was quite variable between MOCNESS collections for all four larval groups. Standard deviations computed for mean Chesson's α values were always at least one order of magnitude greater than the actual means (Table I-26). Govoni et al. (1986a) reported similar large ranges and standard deviations for α. The results of the present study indicate conclusively, that as a behavioral trait, food selection among spot and Atlantic croaker larvae was quite plastic, and that patterns of food selection probably reflected differences in local plankton abundance, as well as variable hydrographic conditions. The possibility that differences in past feeding experience among the larvae may have affected their food selection (e.g., learning) can not be discounted. The results also indicate that regardless of variable plankton abundances or learned behavior, the larvae always fed selectively among the prey that were available. In fact, although the actual pat-

terns of food preference differed between collections and were different between the present study and Govoni et al. (1986a), the larvae always demonstrated strong preference for certain food categories. This fact suggests that in a broad sense, food selection may be a genetically determined behavior, but that larvae can modify their feeding strategy in response to changes in the availability of specific prey.

Considering the wide degree of intrannual variation in food selection and diet composition among the larvae, it is not surprising that significant interannual differences in diet composition were also manifest (Figs. I-10 to I-13, Tables I-29, I-30). Although the specific differences in diet composition between the three years were somewhat different for the four larval groups, the results clearly demonstrated that diet composition was temporally variable. Only among preflexion croaker were the differences somewhat indeterminate (Table I-29).

The procedural difficulties that exist in comparing the present study with data from Govoni et al. (1986a), did not exist in the discriminant analysis of diet composition because all the data were analyzed using the same criteria (Table I-27). There were, however, two potential sources of error in the discriminant models. The first was associated with the sample size of data available from year one. Collections made in December 1979 were restricted to a single station in the Mississippi River plume and provided very few larvae from each of the four larval groups (Table I-30). The relatively small sample sizes and the restricted geographical range of collection from that year may have affected the results obtained from the discriminant analyses of diet composition. The reliability and accuracy of separating two or more groups by discriminant analysis is directly related to the number of individuals being compared. The possible effect of a small sample size is supported by the fact that in all but one instance, the accuracy of classification and sample size appear to be directly related (Table I-30). Unfortunately, there is no way of evaluating how unequal sample size or the geographical inconsistencies in the data affected this analysis. If the comparisons made against year one are

discounted, however, significant differences between years two and three remain and indicate a high level of temporal variation in diet composition.

A second source of error was one of possible seasonal variation in diet composition. Food selection among larval fishes has been shown to vary directly with the relative abundance of prey (Ivlev 1961; Sherman and Honey 1970; Rajasilta and Vuorinen 1983), and in light of the typically strong seasonal component to the abundance and distribution of the plankton community, seasonal differences in availability and utilization undoubtedly existed within the three years. Combining data from two different months from a single winter in order to provide an adequate sample size for discriminant analysis (i.e., December and February) obliterated that seasonal variation. Also, seasonal differences in light penetration in the water accompany changes in the abundance of specific plankters that are related to their density and pigment composition (e.g., Dabrowski and Jewson 1984). Under different ambient light intensities and spectral regimes, the fishes would be expected to feed differently. If the relatively high level of nutritional condition exhibited by larvae collected during year three was indicative of an abundant food supply, then the potential for selective feeding by the larvae was probably high. Unfortunately, no such data of nutritional conditions exist for years one and two, and, therefore, it is difficult to evaluate the feeding conditions of the larvae or this potential source of error.

Finally, when food abundance is high, feeding conditions are good and food selection is strong, then characteristics associated with the prey organisms that determine conspicuousness and reactive distance probably become the most important determinants of food selection (e.g., prey color and size, and swimming ability). Those determinants are in turn affected by environmental conditions, such as turbidity and the spectral quality and level of ambient light. These factors are quite variable on both spatial and temporal scales and the observed interannual differences in diet composition may therefore reflect that variability. Chapter two of this study includes a discussion of

the possible role of prey color in the feeding behavior of spot larvae. The role of swimming ability remains untested in the laboratory.

Food Selection and Prey Size and Shape

Size selective predation has been demonstrated among the larvae of many species of fishes (e.g., Shelbourne 1962; Sherman and Honey 1971; Checkley 1982), and it is not surprising that flexion-postflexion spot and Atlantic croaker larvae ate larger prey than did smaller preflexion larvae (Table I-18). If larvae optimize the cost-benefit parameters of feeding, then optimal foraging theory (OFT) predicts that they should eat the largest prey available to them and thereby maximize their caloric intake with respect to the cost of prey capture (Checkley 1982; Rajasilta and Vuorinen 1983). As Hunter (1981) pointed out, size selective predation may be necessary for normal growth of the larvae. As larvae grow, they diversify their diets by adding larger prey, while continuing to feed on smaller prey. This behavior provides larvae with alternative food items when the abundance of any one food item becomes too low to contribute effectively to the diet. It also provides larvae a means of continually improving the nutritional quality of their diet and generally increases the energy yield per prey organism ingested.

Within the theoretical context of OFT, certain factors associated with the environment (turbidity, time of day, distribution and abundance of prey), the prey organism (size, shape, color, and swimming ability) and the predator (size, swimming ability and nutritional condition) operate together to determine the menu of the predator. This restriction of diet is accomplished, in effect, by determining which prey organisms are available and which are not (i.e., conspicuous, detectable, vulnerable and ingestable). Those factors that affect relative availability are undoubtedly responsible for the observed deviations from the predictions of size selective predation made by the optimal foraging paradigm (e.g., Zaret and Kerfoot 1975; Checkley 1982; Laroche 1982; Rajasilta and Vuorinen 1983). The single factor which physically restricts which prey are

ingested and which are not is the size of the buccal cavity of the larva. Because most fish larvae swallow their prey whole, head-first and with the appendages and setae of the prey folded against the body of the latter, the critical dimension of a potential prey item should be the width (Blaxter (1965; Hunter 1981; Laroche 1982) or height of the prey (i.e., as a reflection of its cross-sectional area). It is therefore somewhat surprising that prey length, width and height all contributed equally to the variation in diet composition of the the four larval groups (Table I-21, Fig. I-5), as well as to food selection (Table I-23, Fig. I-6). Prey width was not the single most important effector of food selection, as has often been suggested in the literature. The relatively high proportion of variation in diet composition explained by the first principal component for all four larval groups indicated that overall prey size was, by far, the most important determinant of diet composition and food selection. That result in itself supports the prediction of size-dependent predation made by OFT. Furthermore, except for preflexion Atlantic croaker larvae, all the larvae ate prey that were, on average, larger in all respects than those available in the ambient plankton (Fig. I-6). Overall prey size, however, is a component of prey shape and therefore, the feeding behavior of the larvae must not be solely determined by prey width or limitations imposed on the larvae by the dimensions of the buccal cavity. In addition, only among preflexion spot larvae was prey width of secondary importance compared to overall prey size. Among the other three larval groups, prey height and length explained a larger proportion of the variation in diet composition and food selection, suggesting that prey shape, and not any single measurement of prey size, is an important determinant of diet composition and food selection among these larvae.

The literature is devoid of any work investigating the role of prey shape in food selection among larval fishes; consequently, the ecological significance of these findings is somewhat unclear. The results do suggest that visual considerations such as the apparent size or conspicuousness of the prey may play a more important role than any

single dimension of prey size in food selection by larval fishes. From a behavioral perspective, the overall size and shape of the profile, may determine whether or not a particular prey organism is pursued, because it affects the reactive distance (RD) for that prey. The shape of the visual profile probably determines how effectively the larva forms a repertoire of search images and that, in turn, must affect future recognition of the prey and food selection. The choice to pursue and strike at a particular prey organism is determined by the RD for the prey, and is made long before the mechanics of ingestion become a significant determinant of successful feeding. In fact, larvae may learn what prey sizes they are able to ingest with increased feeding experience.

On average, prey that appear to the larvae to be larger in profile should be consumed with greater frequency than prey that appear smaller. That is a fundamental prediction of the apparent size model (ASM) of O'Brien et al. (1976) and the greatest stimulus model (GSM) of Wetterer and Bishop (1985), two models that attempt to explain prey selection by visually foraging planktivorous fishes with regard to the size of the prey. The GSM predicts that the predator will always pursue the prey organism that affords the greatest visual stimulus (Wetterer and Bishop 1985), and the predictions of both models are identical under conditions where RD is directly proportional to prey length. That is not always true, however, and the role of prey shape, among other factors, in determining apparent prey size has been proposed (Wetterer and Bishop [1985] and references therein). Unlike the ASM, the GSM can accommodate instances in which RD is not directly proportional to prey length and seems to be a more appropriate model for the observed feeding patterns of spot and Atlantic croaker with respect to prey shape. Functionally, the most striking drawback to the GSM under those conditions is that it requires specific knowledge about the reactive distance of each prey organism. That requirement is unrealistic under all but the most controlled of laboratory conditions.

Finally, differences in the importance of length, width and height in the second and third principal components existed between the four larval groups (Table I-21) and the ambient plankton (Table I-23). Except for flexion-postflexion Atlantic croaker larvae, however, those differences were not significant because they did not clarify differences in diet composition (Fig I-5) or food selection (Fig. I-6) between the larval groups. Those larvae did eat prey that were "flatter" than those that were available or were eaten by the other larval groups. The probable relationship between these secondary factors related to prey shape and reactive distance notwithstanding, it is unclear what specific ecological consequence, if any, those differences had for flexion-postflexion croaker larvae.

SUMMARY

The purpose of this study was to investigate patterns of nutritional condition, diet composition, and the trophic relationships between preflexion and flexion-postflexion larval spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*).

The nutritional condition of both developmental stages of spot was determined to be high, with no larvae classified as starving. The absence of starving larvae indicated either an inability to collect them at sea or an abundance of food resources in the study area at the time of collection. The analysis of starvation, which was based on the morphometrics of the larvae, demonstrated significant interspecific differences in the shapes of the two species. This was somewhat surprising because except for minor differences in pigmentation, spot and Atlantic croaker larvae are visually indistinguishable. It is probable that differences in body shape result in differential swimming abilities between the two species, and may, therefore, ultimately affect the feeding behavior and diet composition of the larvae.

The two species of larvae demonstrated a convergence in diet with age, an unexpected result in light of the morphological, behavioral and ecological interspecific divergence that occurs with growth. In spite of dietary convergence, the degree of food selection (i.e., trophic specialization) in both species increased with age, with larvae adding larger prey to their diets as they grew. Because nutritional condition was high, the food supply was probably not limiting and in spite of the large degree of dietary overlap between the species, it is unlikely that intra- or interspecific competition were important determinants of diet composition.

The larvae fed predominantly on all life stages of copepods, as well as other crustaceans. Larvae of both species selectively fed upon the copepods *Oithona* spp. and

Paracalanus spp., while they demonstrated negative selection for the copepod *Acartia tonsa*. Preflexion larvae of both species demonstrated very similar patterns of food selection, whereas no such similarity was apparent among flexion-postflexion larvae. These results were difficult to reconcile with the results obtained from the analysis of dietary overlap, which showed a convergence in diet with age. Apparently, differential food selection by the two species of larvae was not strong enough to overcome whatever factors were responsible for enhancing overall dietary convergence.

The degree and patterns of food selection among the larvae of both species exhibited a large degree of intra- and interannual variation, indicating that feeding behavior among the larvae is plastic. Those differences were probably determined by spatiotemporal differences in the relative abundance of prey as well as differences in environmental conditions, such as turbidity and small scale ocean currents. Larvae always feed selectively among the available prey, suggesting that larvae are able to modify their feeding strategy in response to changes in their immediate environment.

Among the myriad of factors that have been suggested as important determinants of diet composition and food selection among marine fish larvae, overall prey size and prey shape appear to be particularly important among spot and Atlantic croaker. Larvae generally ate prey that were, on average, larger in all respects than were available in the plankton. The actual relationship between prey shape and feeding behavior may be dependent on the visual profile the prey organism presents to the predator, and ultimately on the resulting reactive distance for the prey.

CHAPTER TWO

FOOD ITEM COLOR AND FEEDING INCIDENCE OF SPOT LARVAE, *LEIOSTOMUS XANTHURUS* LACEPÈDE (PISCES: SCIAENIDAE)

CHAPTER TWO

ABSTRACT

FOOD ITEM COLOR AND FEEDING INCIDENCE OF SPOT LARVAE, *LEIOSTOMUS XANTHURUS* LACEPÈDE (PISCES: SCIAENIDAE)

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The feeding incidence of three age classes of larval spot, *Leiostomus xanthurus*, on the rotifer *Brachionus plicatilis* was investigated in the laboratory under six different spectral regimes. Red, yellow, green and blue plastic filters with broadly overlapping spectral signatures were used to render prey those colors. Feeding incidence was also measured under white light conditions (control) at an irradiance equal to the colored filters ($\approx$3.0 μmol $\cdot$ m^{-2} $\cdot$ sec^{-1}) and at an ambient laboratory irradiance level six times greater than the control. Significant ($P < 0.001$, ANOVA) sources of variation were attributed to age, spectral regime and an interaction term. The incidence of feeding was different for the three age classes. Feeding incidence increased with age in all but the red spectral regime. This increase was attributed to increased visual and swimming abilities, previous feeding experience and gut capacity. Two-to-three week old larvae did not demonstrate a higher feeding incidence in any treatment when compared to the control. Seven and ten week old larvae demonstrated a higher feeding incidence in the yellow and green spectral regimes when compared to the other regimes. It was hypothesized that those larvae possessed two pigments of different maximal absorption that were matched to typical background spacelight in nature, facilitated contrast vision and in higher feeding incidence. Differences in feeding incidence between the age classes indicated that the ability to perceive contrast visual abilities increased with age.

INTRODUCTION

Although past studies have described the diets and trophic relationships of larval fishes and have often demonstrated that they feed selectively, these studies have fallen short of determining what factors affect selectivity and in what order of importance they do so (see Turner [1984] for an extensive taxonomic review of this literature). Prey selection is a complex phenomenon directly dependent upon a number of physiological limitations and behavioral patterns of both the forager and the prey, as well as upon stochastic environmental conditions that affect the temporal and spatial limits of the interaction. Such interactions have been described as a cycle of sequential events: encounter, attack (pursuit), capture, and ingestion (Werner and Hall 1974; Drenner et al. 1978; Wright et al. 1983), with an interplay among behavior, physiology and environment that determines the success of either predator or prey (see Durbin [1979] for a review of the feeding biology of planktivorous fishes).

Vision and Feeding

Larval fishes are predominantly photopic visual predators, relying exclusively on cone-containing simplex retinae to detect prey (Blaxter 1968a, 1968b, 1975; Blaxter and Staines 1970; Blaxter 1975 ; Sandy and Blaxter 1980; Blaxter 1986). The actual spectral sensitivity of larval fishes, however, is poorly understood. Diet selection and feeding success may be dependent on several visually-related factors, such as the size (O'Brien et al. 1976), shape, color (Vinyard and O'Brien 1976) and elusiveness of the prey, as well as the ambient light intensity and turbidity (Dabrowski and Jewson 1983; Boehlert and Morgan 1985). Characteristics associated with the appearance of the prey are particularly important during early feeding experiences or with novel prey. This is because

these factors may enable the predator to establish a search image of the prey (Checkley 1982), as well as to reinforce prey recognition with increased experience (Ware 1971). Larvae may then become accustomed to, and imprinted upon, particular food items (Lasker and Zweifel 1978) or to generalized visual images of these items. Novel food items that visually resemble familiar ones may be selected over visually unfamiliar items. The work of several authors has implied that previous feeding experience can affect pursuit and ingestion rates and ultimately increase the reactive distance (RD) of different food items (see below for a discussion of RD). Ware (1971) demonstrated that adult rainbow trout (*Salmo gairdneri*) modify their feeding behavior when they encounter novel prey and are able to develop new search images for specific prey items. In general, feeding performance improved with experience and deteriorated when fish were deprived of experience for 90 days. He also reported that the effects of experience on the feeding behavior of fish was poorly documented. I am unaware of any similar work that addresses the question of search images and feeding experience in larval fishes.

It is curious that most teleost larvae rely exclusively on vision for feeding, considering the developmental state of other sensory systems. Although many teleosts possess laterosensory neuromasts at the time of, or just after, hatching (O'Connell 1981; Blaxter 1986, 1987), there is no evidence to suggest that larvae use the acousticolateralis system or any other nonvisual sensory system in prey detection and capture. Blaxter (1986) however, stated that many species of larval fishes respond to hydrodynamic stimuli and that free neuromasts are probably responsible for that sensitivity. In laboratory feeding experiments with larval plaice (*Pleuronectes platessa*), conducted at different light intensities, Blaxter (1968a) discovered a residual level of feeding in the dark by *P. platessa* larvae and attributed it to "some other sense." The nearly complete reliance by larvae on visual cues during foraging is evidenced by the fact that most larvae collected either during crepuscular periods or at night, contain little or no food in their guts. This suggests that they feed only when light levels are above some threshold neces-

sary for visual detection of prey. Without a scotopic visual capability, that threshold is considerably higher for larvae than juvenile and adult fishes that possess a duplex retina (Blaxter 1975). There are some notable exceptions to this generalization. For example, the sole (*Solea solea*) and several mesopelagic species are known to feed in the dark (Blaxter 1969a, 1969b). Copepods generate distinctive currents and turbulent water flow around their bodies when feeding and swimming (Gauld 1966; Strickler 1982), and it is surprising that fish larvae do not use that information to detect such prey. Very little is know about the thigmotactic sensitivity of larval fishes, and the turbulent zones associated with copepod activity may not provide stimuli on a spatial scale coincident with the sensitivity of the acousticolateralis (for a review of copepod feeding and the resulting turbulent zones, see Strickler [1982]).

Although vision is clearly of principal importance in prey detection, most marine fish larvae that have been studied inhabit the photic zone and typically do not develop rods or retinomotor pigment until the time of metamorphosis (e.g., anchovy, herring and sole), after which they are more active in dim light (Blaxter 1968a, 1968b; Blaxter and Staines 1970; Blaxter 1975; Sandy and Blaxter 1980; Hunter 1981; O'Connell 1981; Guma'a 1982; Neave 1984). In a histological study of retinal development in two flatfishes, Neave (1984) found that plaice larvae (*Pleuronectes platessa*) exhibited migration of retinomotor pigment at hatching, while turbot larvae (*Scopthalmus maximus*) did not show that activity until just before metamorphosis. *P. platessa* showed cone migration and rod development at metamorphosis, but *S. maximus* demonstrated no cone migration, although rod formation also commenced at metamorphosis. Retinomotor pigments are contained in rod cells and retinal epithelial tissue (i.e., rhodopsin and porphyropsin), and retinomotor activity refers to the movement of the rods, cones and retinal epithelial pigment in response to changes in light intensity (Neave 1984). Visual cell and pigment migration is thought to protect rod cells from damage by bright light. Guma'a (1982) reported similar results for larval perch (*Perca flavescens*), with retinomotor activity and

rod development commencing just after metamorphosis. Both species had pure cone retinae at hatching. In newly hatched goldfish (*Carassius auratus*), Johns (1982) determined that the outer nuclear layer of the larval retina contained only a single layer of cells that apparently differentiated into a single row of cones within a few days after hatching. Immature rods and their outer segments were found in the outer nuclear layer of the eye, vitread to the cones (Sandy and Blaxter 1980), and were presumed to be nonfunctional. Raymond (1985, formerly Johns) also determined that three cone types were present in the larval goldfish retina within two days of hatching, but Stell (1972) described five types of cone cells in *C. auratus*, while Stell and Hárosi (1976) reported six distinct varieties! In another study, which described the appearance, development and identification of photoreceptors in the zebrafish (*Brachydanio rerio*), Branchek and BreMiller (1984) reported a full photoreceptor compliment in 12 day old larvae that included rods as well as four types of cones. That timing is in contradistinction to retinal development of the marine fish larvae investigated by Blaxter and his coworkers (see above), in which retinal pigment migration and rod development were delayed until metamorphosis. Retinal pigment and visual cell migration in *B. rerio* was completed eight days postfertilization, even before rods could be identified in the retina (Branchek and BreMiller 1984). In a companion study, Branchek (1984) reported a functional divergence of rods and cones at two weeks postfertilization. Although she was able to demonstrate that cone cells and their synaptic specializations were functional at this early age, she did not address the specific question of spectral sensitivity. In a study of the functional development of visual pathways in larval sardines (*Sardinops caerulea*), Schwassmann (1965) described very rapid development of the lens and retina within the first two days after hatching, although optic nerve fibers and connection to the optic tectum were not observed histologically until three days posthatching. These results prompted Blaxter (1975) to suggest that because only approximately 40 nerve fibers compose the optic nerve at that age, first feeding larvae may only be capable of coarse

perception of movement and have relatively low sensitivity to, and poor resolving powers at, low light levels (Blaxter 1969a, 1969b, 1975). There is confusion regarding the characterization and identification of specific cone types, and it is now accepted practice to base such descriptions on the position, size and morphology of the photoreceptor (e.g., see Stell [1972]). There still remains a degree of subjectivity in designating new cone types (Loew and Lythgoe 1978), which prompted Branchek and BreMiller (1984) to state that the exact timing of specific events in the development of the retina in fishes is undoubtedly species-specific and appears correlated with the physiobehavioral development characteristic of each species.

Interspecific differences in the timing of development and composition of the fish retina have an ecological basis (Ali and Wagner 1975; Loew and Lythgoe 1978). For instance, it has long been known that freshwater and marine fishes generally possess different visual pigments in their rods, the former possessing the purple photolabile pigment porphyropsin and the latter possessing the red photolabile pigment rhodopsin, common to most other vertebrates (e.g., Wald 1937, 1939). Euryhaline and diadromous fishes typically possess mixtures of these two pigments (McFarland and Munz 1975; Hemilä et al. 1976; Loew and Lythgoe 1978) in proportions that may change seasonally (Allen et al. 1982). Loew and Lythgoe (1978) related habitat type and the spectral quality of ambient water to the visual pigments of 18 species of littoral and coastal fishes. They found that double and twin cones contained a visual pigment that roughly matched the background spacelight of the habitats from which the fish were collected, whereas single cones contained a visual pigment with an absorption offset from background light (e.g., see McFarland and Munz 1975; Hemilä et al. 1976). This pattern of pigment sensitivity is thought to maximize visual contrast and sensitivity to both reflective and nonreflective surfaces and necessitates the possession of at least two cone types.

Other changes in the retina take place with growth. The density of cones in the retina decreases during growth because of retinal stretching (Blaxter 1975; Johns 1981;

Guma'a 1982; Breck and Gitter 1983), as does the distance between cones measured in minutes of visual angle (the angle made by the image on the eye). This results in an ontogenetic increase in visual resolution (Hairston and Li 1982). In studying retinal development in larval perch (*Perca flavescens*), Guma'a (1982) found that cone density decreased, but that the number of cones increased, with age. He also demonstrated that visual acuity increased exponentially with retinal growth and attributed that finding more to increased focal length of the lens (see also Blaxter [1975]) than to actual cone number. As Johns (1981) pointed out, visual acuity is dependent on the optical resolving power of the eye, as well as retinal detector and processor efficiency. Because the retinae of larger fish possess more cones (Blaxter 1975), acuity and sensitivity should improve with age, even though cone density decreases. In at least one species, increased in visual capabilities with growth may be related to seasonal changes in the spectral quality and irradiance of the water. Dabrowski and Jewson (1984) determined that maximum feeding thresholds for larval and juvenile pollan (*Coregonus pollan*) were in the green waveband (490-595 nm) and that seasonal deterioration in the maximum depth of light penetration and changes in the spectral quality of the water offset the improving visual capabilities of the larvae.

In addition, visual acuity is not equal in all directions because binocular vision is restricted to that part of the visual field directly in front of the fish (for those fish with laterally located eyes). Observations made of the swimming behavior of larval fishes during feeding have suggested that binocular vision is necessary for successful prey capture (Durbin 1979). Neuroanatomical evidence (see Li et al. [1985]), as well as behavioral studies, support this theory (e.g., Blaxter 1968a, 1968b, 1969a; Hairston and Li 1982; Schmidt and O'Brien 1982), but the electrophysiological work of Johns (1981) suggests otherwise. Although more retinal cells are present in the eyes of older fish, a larger eye produces a larger retinal image as the receptive field increases in surface area and, consequently, the number of cells responsible for a given point of visual space remains

approximately the same. Why then are bigger fish able to detect and capture smaller prey (that subtend much smaller visual angles on the retinae) than smaller fish? Increased acuity at all light levels must be enhanced by the development and growth of a duplex retina and scotopic vision.

Other than the behavioral work of Blaxter (1968a, 1968b, 1969a) on herring (*Clupea harengus*) and flatfishes (*Pleuronectes platessa* and *Solea solea*), I am unaware of any work that has investigated the spectral sensitivity of larval fish or the relationship between color vision and feeding. Blaxter (1968a, 1968b, 1969a) demonstrated that both herring and plaice larvae were maximally sensitive to yellow-green light (550-600 nm) and exhibited varying degrees of sensitivity at all wavelengths between 400-650 nm, suggesting that those larval fishes were able to detect all the colors in the spectrum of visible light to some degree. Blaxter (1975) suspected that different populations of cones were involved in the detection of colored light, with maximal sensitivity at wavelengths unlike that of more typical rhodopsin-bearing rods common to most teleost eyes. He did not elaborate on what sorts of cones or visual pigments were responsible for that broad sensitivity to colored light, but he was intrigued that larval fishes could survive with visual equipment substantially inferior to that of adults. The detection of a particular color of visible light by the retina requires that the retina possess a specific cone that contains a visual pigment that absorbs light of a certain wavelength. The fact remains that it is unknown whether larval fishes are capable of color vision, but because many adult fishes have good color vision (Hárosi and Hashimoto 1983) and because most larvae possess the neurophysiological anatomy necessary for spectral sensitivity (Schwassmann 1965), it is likely that larval fishes see color.

The Role of Reactive Distance

The basic underlying concept of all visual predation studies of planktivorous fishes, as well as of models that attempt to explain size selective feeding patterns (see

below) is that of reactive distance (RD). That is the maximum distance from the eyes of the fish at which a particular prey item can be visually detected and is better described as a reactive volume surrounding the fish. The shape of that volume is determined, in part, by the position of the eyes on the fish's head and is relatively larger in those fishes that have laterally placed eyes (Durbin 1979). RD has been defined behaviorally by Confer and Blades (1975) as the distance at which different species and sizes of zooplankton elicit pursuit behavior on the part of the predator. RD is dependent on the size (Confer and Blades 1975; Vinyard and O'Brien 1976; Confer et al. 1978; Kerfoot 1980; Schmidt and O'Brien 1981; Breck and Gitter 1983), color (Kerfoot 1980), conspicuousness (Kerfoot 1980; Dendrinos et al. 1984), and location of the prey in three-dimensional space (Luecke and O'Brien 1981). RD is also dependent on the size, age and taxon of the predator (Breck and Gitter 1982; Schmidt and O'Brien 1982; Mills et al. 1986), ambient light level (Vinyard and O'Brien 1976; Confer et al. 1978; Schmidt and O'Brien 1982; Mills et al. 1986), and turbidity (Ware 1971; Vinyard and O'Brien 1976; Eggers 1977; Gardner 1981; Boehlert and Morgan 1985; Breitburg 1988). Larger prey project larger images on the retina, thereby stimulating more photoreceptors, resulting in a more highly resolved signal being sent to the brain (Durbin 1979). The RD for a particular prey item determines its encounter probability with the predator, as well as the number of prey items simultaneously seen by the predator. In turn, those factors determine what prey choices are available to the predator at any single time and thus presumably affect food selectivity. The duration that a particular prey item remains in the visual field also appears to be important in determining detection and capture success (Govoni et al. 1986a). Prey location, with respect to the reactive distance of that prey, may be the most important phase in the predation sequence because of the inherent difficulties of prey detection in the pelagic environment (O'Brien 1979).

Food Item Color and Feeding

It has been suggested that the color of food organisms may be an important factor affecting food selection in fish larvae (Teska and Behmer 1981; Stoecker and Govoni 1984; Govoni et al. 1986a). Kerfoot (1980) has stated that pigmentation and not size is the most important factor influencing prey conspicuousness and therefore is of ultimate importance in determining the selective feeding patterns of the juvenile and adult planktivorous fishes. In fact, such a relationship between color of prey and diet of predator is probably a complex one. In nature, reflectivity, contrast with background spacelight, iridescence and pattern may all affect the conspicuousness of the prey and recognition by fish larvae, and their behavioral resultant, selectivity. Without regard to actual pigment color, it has been demonstrated that juvenile and adult planktivorous fishes show a preference for pigmented prey (Brooks and Dodson 1965; Mellors 1975; Zaret and Kerfoot 1975; Confer et al. 1978; Kettle and O'Brien 1978; Kerfoot 1980; Byron 1982; Schmidt and O'Brien 1982). It is believed that this is because the presence of pigmentation renders the prey more conspicuous than unpigmented prey (Zaret and Kerfoot 1975; Kerfoot 1980; Dendrinos et al. 1984), thereby increasing the RD of the prey (Ware 1971; Confer and Blades 1975; Schmidt and O'Brien 1982). The result is that prey conspicuousness determines both prey encounter and predator attack probabilities. In a laboratory study investigating feeding selectivity of larval and juvenile Dover sole *(Solea solea)*, Dendrinos et al. (1984) found highly significant differences in feeding efficiency among larvae fed nauplii of *Artemia* sp. stained with five different nontoxic food colorings. Their results suggested a possible spectral order of feeding-preference (black, red, pink, blue, yellow and an unstained control, respectively), but their experimental design and statistical application permitted only a cursory analysis of contrast perception and conspicuousness, and not of color-dependent food selection.

Conspicuousness is difficult and complex to analyze, for it depends on shape, physical appearance (e.g., armature, appendages and sensory structures), color and swimming movement of the prey organism. In making the general comparison between selection based on the presence or absence of pigmentation, the question of color selectivity of predators for prey items that are pigmented is not addressed. Ginetz and Larkin (1973) demonstrated that adult rainbow trout (*Salmo gairdneri*) possess an acute ability to distinguish different colors and prefer food items of a particular color (their own eggs) under specific light intensities. Variation in ambient light intensities resulted in differences in the order of preference for certain colors, and the authors attributed much of this selection to contrast with background light, although actual prey color also was important. As Govoni et al. (1986a) pointed out, many of the zooplanktonic prey organisms, particularly the harpacticoid and cyclopoid copepods typically eaten by larval fishes, contain carotenoid pigments that reflect yellow, orange and red light. To date, preference for these food items has been measured with regard to unpigmented plankters and not plankters of different colors (e.g., blue and green). It is generally accepted that the lack of pigmentation in most zooplankton inhabiting the photic zone is an adaptation to predation pressure. Copepods are not able to synthesize carotenoid compounds which are instead obtained by eating algae that contain these pigments or by eating zooplankton that have eaten such algae (Hairston 1979). Although there is still disagreement about the adaptive significance of pigmentation in zooplankton (see Hairston [1979] and Byron [1982] for discussions of pigmentation in zooplankton), plankters from coastal waters that possess yellow or orange pigment may be camouflaged against their background spacelight. As Govoni et al. (1986a) pointed out, estuarine coastal waters are maximally transparent to yellow and orange light and must therefore result in background light of those colors. Color detection in fishes may have originated to enhance contrast vision (McFarland and Munz 1975), and fishes may maximize their contrast vision by possessing visual pigments which are maximally sensitive to their back-

ground spacelight. The conspicuousness of a plankter would therefore be a function of how well matched its own color is with that of the background. It is therefore not surprising that larval fishes have demonstrated their greatest sensitivity of yellow and orange light (see Blaxter [1975]).

Research on larval spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*; Govoni et al. [1986a]), larval lake whitefish (*Coregonus clupeaformis*; Teska and Behmer [1981]) and juvenile and adult rainbow trout (*Salmo gairdneri*; Byron [1982]) has demonstrated that planktivorous fishes actively select yellow or orange prey items over those that appear transparent. This is probably because many, although not all, pigmented and thus conspicuous prey items are indeed yellow (i.e., carotenoid-bearing). Among pigmented plankton, feeding preference by planktivorous fishes may reflect the relative abundance of yellow and orange plankters in the environment and not a preference for them. As of yet, this has not been determined because selection has been measured in relation to the presence or absence of pigment, but not to pigment color.

Study Objective

The objective of this study was to determine the effect of the color of prey on feeding incidence by three age classes of larval spot, *Leiostomus xanthurus* Lacepède.

MATERIALS AND METHODS

The relationship between food item color and feeding behavior was investigated for three different age classes of spot larvae, *Leiostomus xanthurus*, under six different spectral regimes. Two to three week old and seven week old laboratory-reared larvae (rearing procedure followed Hettler and Powell 1981) were maintained in the laboratory in 57 cm diameter × 54 cm deep cylindrical black-sided containers and fed a daily diet of the rotifer, *Brachionus plicatilis* (mean water temperature of 23.5°C and mean salinity of 34‰). Older larvae ($\overline{SL}$ = 16.26±1.40 mm, N = 126, of a probable age of 75 d [see: Warlen and Chester 1985]) were collected on an incoming tide in Gallant Channel, Beaufort, North Carolina, maintained as described above, but fed nauplier and adult *Artemia salina* and wild plankton (mainly calanoid copepods) in addition to *B. plicatilis*. These larvae were acclimated to laboratory conditions (mean water temperature of 19°C, mean salinity of 35‰ and a 12 hour dark/light photoperiod) for at least 24 hours prior to experimentation. The length of that acclimation period ensured that the larvae had empty guts and were hungry. One hour crepuscular periods were simulated by turning overhead lights on (0700 h) and off (1800 h) one hour prior to main laboratory lights (0600-1900 h). All light sources in this study consisted of banks of 40 W sunlight simulating Vita-lites (Luxor Lighting Products, Inc., New York, N.Y.).

The experimental design consisted of two banks of six 14 cm deep × 34.5 cm diameter black cylindrical containers (tophats) each containing 2.4 L of tap water. The total light irradiance, measured as photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$, was determined for each tophat with a LI-COR, Inc. (Lincoln, NE) model LI-1000 datalogger and an LI-192S SA-type cosine quantum radiation sensor at a depth of one centimeter in filtered seawater with a specific spectral filter (see below) placed on top of the tophat. Be-

cause lighting conditions varied somewhat along each bank of tophats, it was necessary to adjust the total irradiance within each tophat with respect to the specific filter used in the various treatments. The tophat-filter combination with the lowest irradiance was determined and all other tophat-filter combinations were equilibrated to that value with neutral density filters (Table II-1). The following spectral filters were utilized: medium red (#823), medium lemon (#806), medium green (#874) and medium blue (#863) (Edmund Scientific Co., Barrington, NJ). It was necessary to add four neutral density filters to the yellow filter in order to further reduce its irradiance to that of the other filters. A Biospherical Instruments, Inc. (San Diego, CA) model MER-1000 scanning radiometer (λ = 410-694 nm) was used to obtain plots of spectral transmission for each filter (Fig. II-1). This was done by measuring irradiance through a 4 × 4 cm sheet of each spectral filter illuminated with a single bank of four 40 W Vita-lites. Spectral irradiance (measured in $\mu W \cdot cm^{-2} \cdot nm^{-1}$ or quanta $\cdot cm^{-2} \cdot sec^{-1} \cdot nm^{-1}$) and total irradiance (measured in quanta $\cdot cm^{-2} \cdot sec^{-1} \cdot nm^{-1}$) were converted to photon flux density ($\mu mol \cdot cm^{-2} \cdot s^{-1}$) following Lüning (1981). Quantum irradiance, a measure of the radiant energy incident upon a unit area per unit time, was measured instead of the more commonly used measures of intensity or illuminance (klux or foot-candles) because irradiance is more meaningful in ecological terms, particularly with respect to photosynthesis (Lüning 1981) and the photochemistry of vision. Also, light intensity is a property of a light source and not the light incident on, or reflected by, an object (Ramus 1985). Values of intensity (klux) were also calculated for comparison with those reported in the literature.

Seven 11.5 cm diameter × 7.5 cm deep black-sided cups were placed in each tophat and arranged hexagonally with one cup in the middle. A black background was chosen to minimize shadow and reflection, and to maximize contrast of the prey inside the cups. Enough tap water was added to each tophat to completely surround the cups and moderate the water temperature within each cup. Each cup was filled with 400 mL

of filtered seawater (mean temperature of 20°C and mean salinity of 32‰). A single larva was transferred from a rearing container to each cup with a wide-bore pipette. Larvae were allowed at least 17 hours to dark adapt under these conditions before a trial was begun. Larvae that died during this period were replaced with similarly acclimated larvae (in their own cups) prior to each trial. A trial commenced at 1000 h on the day following acclimation, resulting in three hours of light adaptation prior to experimentation. To begin a trial, one milliliter of filtered seawater containing 400±30 *Brachionus plicatilis* was injected into each cup in the same order in which the larvae were introduced. This resulted in an initial food density of one rotifer per milliliter. A single one milliliter aliquot of inoculum was archived after all the cups in a trial were injected, for future verification of aliquot contents and concentration. One of four spectral filters measuring 36.5 cm in diameter, was immediately placed on the tophat just after inoculation. A series of four neutral density filters, roughly equilibrated to the total irradiance within each tophat with the spectral filters ($\approx 3\ \mu mol \cdot m^{-2} \cdot s^{-1}$), was placed on the fifth tophat. This series of neutral density filters effected a change only in total irradiance and not in the spectral quality of the light, and served as a control by allowing larvae to feed under white light conditions (Table II-1). A sixth tophat at the ambient laboratory irradiance level (roughly six times that of the control) provided a second control and permitted the evaluation of feeding incidence at the total irradiance level. A single neutral density filter was added to one of these two tophats in order to equilibrate its total irradiance to its replicate in the other bank (Table II-1).

Quantum irradiance and illuminance varied little between the filtered tophats, excepting the ambient spectral regime, which had a six-fold greater irradiance (Table II-1). Each spectral filter exhibited a distinctive spectral irradiance signature and a wide range of wavelengths at which maximum irradiance occurred (Fig. II-1). There was considerable overlap of wavebands of total irradiance between several of the spectral filters. The green and yellow filters showed a broad band of overlap from 450-550 nm, whereas

the yellow and red filters showed a somewhat narrower band of overlap from 600-695 nm. Transmission of broad wavebands was characteristic of all the filters. For example, the blue filter exhibited two peaks of irradiance from 450-485 nm and from 695 nm, while the yellow filter showed peak irradiance from 550-695 nm. Exhibiting peak absorbance and irradiance over broadly overlapping wavebands are inherent characteristics of acetate-film (gelatin) filters and must be considered in behavioral studies that attempt to demonstrate or make inferences regarding color-mediated behavior (J.H.S. Blaxter, pers. comm.).

Larvae were allowed to feed for three hours (until 1300 h) under these conditions, corresponding to the approximate gut retention time of these larvae (Govoni et al. 1982). They were then removed from the cups in the order in which they were isolated and were sacrificed on frozen 5% buffered (mono/dibasic sodium phosphate) formalin to inhibit regurgitation and defecation of the gut contents. This was done three times for each age class, resulting in a sample size of 21 larvae per treatment.

Gut contents were examined microscopically by dissection of the gastrointestinal tract (fore-, mid- and hindgut; Govoni et al. 1986b), and the total number of adult *Brachionus plicatilis* ingested were counted. Guts often contained *B. plicatilis* eggs as well as loricae which were probably consumed while attached to adult females and released in the gut upon digestion, rather than having been eaten separately. Consequently, they were not counted in the analysis. The assumption of incidental release upon digestion of the loricae was supported by the fact that no eggs were found in the representative aliquots preserved during each trial, suggesting that the adult rotifers were not releasing eggs at the time of each trial. A two-way analysis of variance of $\log_{10}(X+1)$ transformed data was used to demonstrate differences in feeding incidence between each age class and spectral regime (Table II-2).

All statistical analyses were run under the VM/XA-CMS operating system (release 2) on an IBM 3090-180 using the SAS (version 5.18) statistical package (SAS Institute, Cary, NC).

RESULTS

All three age classes of larvae exhibited remarkably similar patterns of feeding incidence with respect to spectral regime (Fig II-2). When feeding incidence was compared between age classes for each spectral regime, the mean number of prey eaten by the larvae increased with the age of the larvae (Table II-3, Fig. II-2). That general trend was true for all but the red spectral regime, in which only minor differences in feeding incidence existed. All three age classes were most similar in the number of prey eaten in the red and blue spectral regimes, with feeding incidence among these regimes being the lowest of all. No larva ever consumed all the rotifers in its respective cup and mean feeding incidence was never zero in a treatment.

Relatively large standard deviations were calculated for the mean number of prey eaten in each treatment and were attributed to the relatively small sample size utilized in each treatment group.

Feeding incidence within all three age classes was highest in yellow colored light. Both seven and 10 week old larvae showed greater feeding incidence in the yellow and green spectral regimes than they did in the neutral (control) regime. The 10 week old age class also demonstrated a greater level of feeding incidence in the ambient spectral regime, which had a six-fold greater irradiance level, than the control. The 2-3 week old age class did not demonstrate higher feeding incidence in any spectral regime when compared to the control and the general order of feeding incidence for these larvae was neutral, yellow, red, ambient, green and blue. For seven-week-old larvae, the order of feeding incidence was yellow, green, ambient, neutral, red and blue, and for the 10 week old larvae it was yellow, ambient, green, neutral, blue and red.

When the feeding incidence by three age classes of spot larvae on the rotifer, *Brachionus plicatilis*, was compared among the six spectral regimes with a two-way analysis of variance, highly significant ($P < 0.001$) sources of variation were attributed to age class, spectral regime and an interaction term (Table II-2). The significance of the interaction term indicated that the exact patterns of feeding incidence, with respect to the color of the prey, were not the same among the three age classes. Because of the significant interaction term, separate range tests could not be used to evaluate specific differences in the means (Sokal and Rolf 1981; Underwood 1981).

TABLE II-1.—Quantum irradiance and illuminance[1] values measured as photon flux density ($\mu mol \cdot m^{-2} \cdot s^{-1}$) and klux, in two banks of aquaria used in laboratory feeding experiments of spot (*Leiostomus xanthurus*) larvae. Measurements were made with an SA-type cosine quantum radiation sensor at a depth of one centimeter in filtered seawater.

	Quantum irradiance and illuminance			
	Bank A		Bank B	
Light regime	($\mu mol \cdot m^{-2} \cdot s^{-1}$)	(klux)	($\mu mol \cdot m^{-2} \cdot s^{-1}$)	(klux)
Red	3.30	0.28	3.01	0.25
Yellow[2]	3.36	0.28	3.55	0.30
Green	3.11	0.26	3.02	0.25
Blue	3.13	0.26	2.90	0.24
Neutral density[2]	3.16	0.26	2.97	0.24
Ambient	18.90*	1.58	18.60**	1.40

[1]Under fluorescent lights, irradiance is converted to illuminance by the formula: Quanta (=μmol) = klux × 12 (LI-COR, Inc. 1985, Publ. No. 8510-15).

[2]These regimes included four neutral density filters used to approximately equilibrate the irradiance of each spectral filter and served as a control group.

*This tophat had the lowest initial irradiance value and served as the basis for equilibrating all tophat-filter combinations.

**This tophat included one neutral density filter to equilibrate its irradiance with the ambient tophat in Bank A.

TABLE II-2.–Results of a of a two-way analysis of variance of the $\log_{10}(X+1)$ transformed number of prey items (*Brachionus plicatilis*) ingested by three age classes of spot larvae (*Leiostomus xanthurus*) in feeding experiments conducted under six different spectral regimes[1].

Source	SS	df	*F*	*P*
Age class	16.121	2	90.53	<0.001
Spectral regime	10.174	5	22.86	<0.001
Age × Spectral regime	5.407	10	5.41	<0.001

[1]*N* = 3 trials/treatment × 7 fish/trial = 21 fish/treatment.

TABLE II-3.–Mean number (± S.D.) of prey items (*Brachionus plicatilis*) eaten by three age classes of spot larvae in laboratory feeding experiments conducted under six different spectral regimes.

Spectral regime	Mean (±*SD*) number ingested by each age class		
	2-3 wk old	7 wk old	10 wk old
Red	6.19±3.09	6.48±2.82	7.00±6.00
Yellow	6.81±3.60	11.47±4.29	38.52±18.41
Green	3.57±3.47	9.48±4.08	20.19±11.43
Blue	2.29±2.57	4.00±3.41	9.71±7.42
Neutral (control)	6.95±5.58	7.43±3.75	17.05±12.62
Ambient	3.95±3.12	7.81±3.22	21.00±10.68

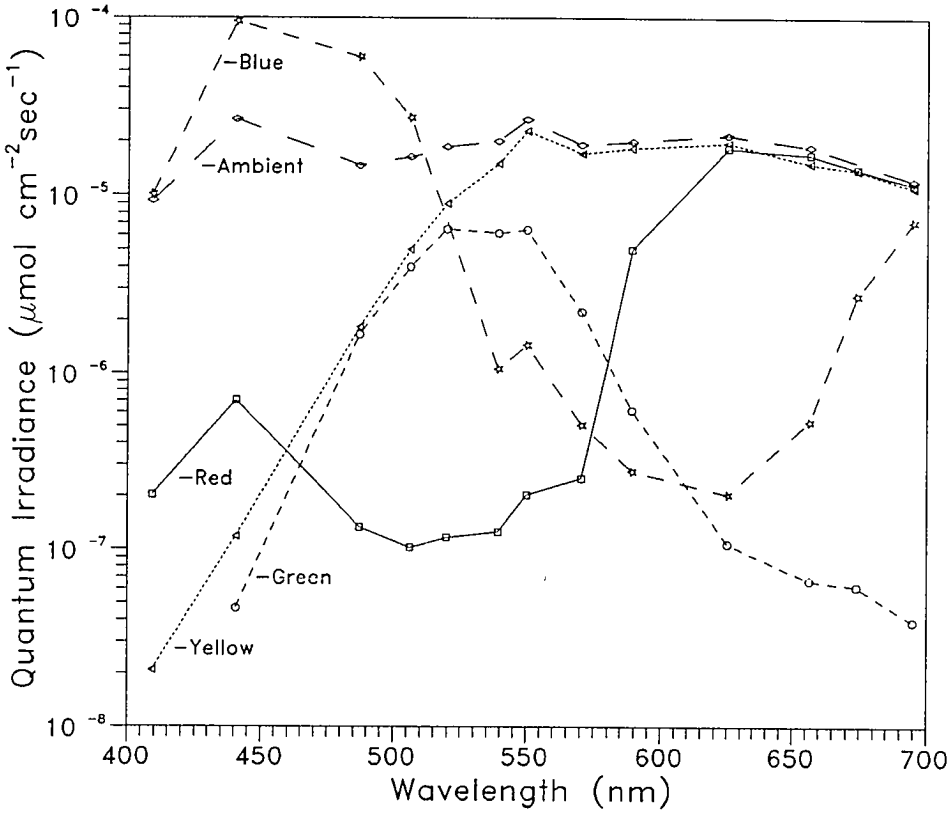

FIGURE II-1.–Quantum irradiance (photon flux density) versus wavelength plotted for each spectral filter.

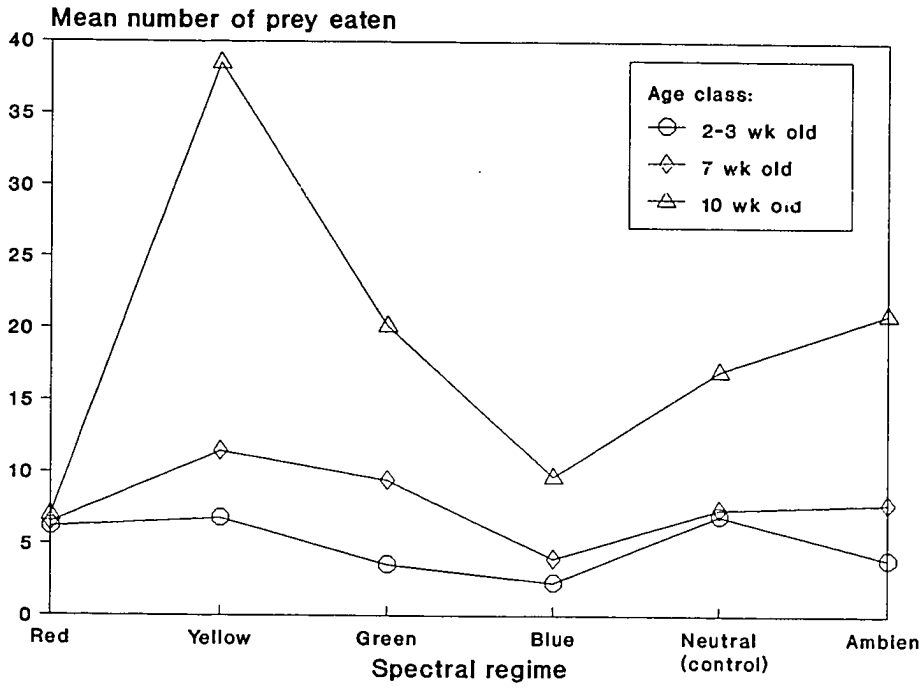

FIGURE II-2.–Mean number (N = 21) of prey items (*Brachionus plicatilis*) eaten by spot larvae of three different age classes in laboratory feeding experiments conducted under six different light regimes.

DISCUSSION

In all but the red spectral regime, feeding incidence by larval spot for *Brachionus plicatilis* increased with age. Differences in feeding incidence between the three age classes may be explained by differences in visual ability, swimming performance, previous feeding experience and differential gut capacities of the larvae. It is not possible to determine the significance of any one of these factors, but differential gut capacities and satiation, as evidenced by differences in gut fullness among the three age classes at the end of each trial, were probably the primary determinants of age-specific differences in feeding incidence among the larvae. It is unclear why there were only minor differences in feeding incidence in the red spectral regime between the three age classes. Perhaps all three age classes shared an equally poor sensitivity to red light (see below for a more specific discussion of spectral sensitivity).

Only minor differences in feeding incidence by the 2-3 week old larvae were evident between the spectral regimes. Although feeding incidence in the yellow and red spectral regimes was nearly equal to the neutral regime (control), feeding incidence in every regime was below that of the control (Table II-3, Fig. II-2). These larvae generally had full guts at the end of each trial, and their state of satiation may have affected the number of prey they consumed. Consequently, by the time each trial was completed, any differences in feeding incidence between the spectral regimes that may have existed during that trial, were lost because larvae in each of the regimes had reached satiation. For this reason, no conclusions regarding the role of prey color in feeding incidence can can be made from these larvae.

Larvae in both the seven and 10 week old age classes demonstrated their greatest feeding incidence for yellow-colored prey when compared with the other spectral

regimes (Table II-3, Fig. II-2). These results are in agreement with those reported for plaice (*Pleuronectes platessa*) and herring (*Clupea harengus*) by Blaxter (1968a, 1968b), where larvae were maximally sensitive to yellow and green light (550 - 600 nm). They are not, however, in agreement with results reported for Dover sole (*Solea solea*) by Dendrinos et al. (1984), whereas a preference for black and red colored prey (*Artemia*) against an unspecified background color was displayed. If spot larvae possessed spectral sensitivity similar to that of *P. platessa* and *C. harengus*, it is not surprising that feeding incidence was highest in the yellow spectral regime. The yellow filter, with its broad-banded (i.e., 550 - 700 nm) irradiance signature (Fig. II-1), provided larvae with a large spectral array in which to feed, and therefore, an excellent potential for maximum feeding incidence. Consequently, yellow colored-prey would have been more strongly contrasted against a black background and therefore more conspicuous than the other colors.

Both these age classes of larvae demonstrated their second highest level of feeding incidence in the green spectral regime. The green filter exhibited peak irradiance from 520 - 550 nm, and except for the ambient light regime, had the greatest degree of overlap with the 550 - 600 nm waveband of the yellow filter of any spectral filter. That broad band of overlap may explain why feeding incidence was second highest in the green regime. Spectral sensitivity must decrease as the wavelength of light shifts away from the bandwidth of maximum sensitivity. Because the green filter had its maximum irradiance just below the yellow filter, prey in this regime were not as well contrasted as were prey in yellow light, and feeding incidence was therefore lower. The idea that feeding incidence was related to the proximity of a spectral regime's peak irradiance to the 550 - 600 nm bandwidth, is further supported by the fact that feeding incidence among these larvae was lowest in the red and blue spectral regimes. Both of those spectral regimes exhibited peak irradiance well above and below the 550 - 600 nm bandwidth, resulting in prey being poorly contrasted against the background. Also, although the

ambient regime exhibited almost the same level of irradiance as the yellow filter at wavelengths > 550 nm, prey in this regime would not have appeared colored to the larvae (*Brachionus* is transparent) and, consequently, feeding incidence was lower than in either the yellow or green spectral regimes. Larvae in this regime perhaps relied on some other visually related phenomenon, such as movement perception, to detect the prey.

Total irradiance levels and the spectral quality of light in estuarine and coastal waters is variable and changes daily, seasonally and in response to phytoplankton abundance and suspended and dissolved material. The quantity and quality of light also changes with depth (Ramus 1985), as must the visibility of prey organisms (Govoni and Chester 1990). Background spacelight, as well as downwelling and upwelling light, all have their own spectral qualities, with the latter being more nearly monochromatic (Munz and McFarland 1975; Ramus 1985). Spot larvae feed by positioning themselves in roughly the same horizontal plane as their prey, and therefore background spacelight and downwelling light are important factors in the visual detection of prey.

Coastal waters inhabited by spot larvae are maximally absorbent to red and violet light. Contrarily, these waters are maximally transparent to yellow and orange light (Govoni et al. 1986a and references therein), and therefore background spacelight is yellow-orange. Prey organisms must exhibit varying degrees of contrast and conspicuousness as photic conditions in their environment change, and at one time or another most of the prey encountered must be visible to the larvae. Under optimal conditions, in which a particular prey organism is well contrasted against the background and has a relatively large reactive distance, larvae should have little trouble in detecting them. Under suboptimal conditions, in which prey are more closely matched with the color of their background spacelight, larvae must rely on perception of movement in order to see prey, or perhaps possess visual adaptations that enable the predator to enhance contrast of prey in spite of the apparent camouflage of the prey. In fact, it

would be evolutionarily advantageous for the larvae to detect all prey organisms regardless of their state of camouflage.

Spot larvae preferentially feed on yellow-pigmented plankton, such as the calanoid copepod *Oncaea venusta*, pteropods and the rotifer *Stenosemella* sp. (Govoni et al. 1986a; Govoni and Chester 1990; chapter I of this study). These prey organisms should be poorly contrasted against the predominantly yellow background of their environment, and larvae either feed on these prey at times when background spacelight is not yellow-orange or they possess some other means of visually detecting these prey. Considering the relatively large numbers and consistent role that these plankters play in their diet (see chapter I), the latter is a more likely explanation.

Munz and McFarland (1975) suggested that color vision in fishes evolved to enhance contrast vision and that contrast vision of reflective objects is enhanced by possessing at least two visual pigments, one matched in its photosensitivity to background spacelight and the other offset from the first pigment. The offset pigment maximizes contrast against a monochromatic background because it is less sensitive to background space and closer to the object being viewed. As the total spectral environment becomes more nearly monochromatic, such as during crepuscular periods and with depth, offsetting becomes a less effective means of enhancing contrast (Munz and McFarland 1975). A dual-pigment system would provide a means of distinguishing prey under many different photic conditions, particularly given that most prey probably only rarely match their background. If this paradigm holds true for spot larvae, then they should at least be dichromatic. In the present study, spot larvae demonstrated their maximum sensitivity to yellow light, while being secondarily sensitive to green light. Green light, although attenuated to a greater extent than yellow and orange, is prevalent in the coastal photic marine environment. In fact, estuarine water is often green because of ambient phytoplankton, and Govoni and Chester (1990) reported maximally transmitted wavelengths ≈ 500 nm at one meter in May 1989 in continental shelf waters adjacent to the

Mississippi River. In the present study, feeding incidence was highest for the seven and 10 week old larvae in the yellow and green spectral regimes because the larvae possessed visual pigments that were sensitive to these wavelengths. In the photic environment of marine coastal waters, those pigments would provide effective contrast vision under varying spectral conditions. The spectral quality and transparency of water is known to have a strong seasonal component that is associated with the density and type of plankters in the water (e.g., Dabrowski and Jewson 1984), and possessing a dual pigment would facilitate contrast vision as the seasonal changes manifest themselves. In the laboratory, however, larvae showed their highest feeding incidence for yellow and green-colored prey against a black background for the very reason that they possessed visual pigments that were maximally sensitive to those wavelengths. The relatively low feeding incidence observed in the red and blue spectral regimes may have been because the larvae lacked photopigments that were at once sensitive to these wavelengths and optimally offset from them. The fact that the relationship between age and feeding incidence was most pronounced in the yellow, green and ambient spectral regimes, indicates that the contrast visual capabilities of the larvae and the development of a match-mismatch pigment pair improve with age.

SUMMARY

This study was not designed to address the question of color vision in larval fishes. The purpose of this study was to investigate the possible role of the color of prey on feeding incidence by larval spot, *Leiostomus xanthurus*. The larvae in this study demonstrated differential incidences of feeding for differently colored prey, which may either have been due to functional color vision capabilities in the larvae or, more probably, to the effects of contrast with background spacelight. This study demonstrated that the age of the larvae was a significant determinant of the role of prey color on feeding incidence.

Even if larval fish cannot distinguish different colors, the results of the present study and past work by Blaxter (1975) and Dendrinos et al. (1984) suggests that larvae are capable to some degree of distinguishing differences in prey items of different colors, and that certain colors (i.e., yellow and green) can result in significantly different patterns of feeding incidence. It is hypothesized that a dual-pigment visual system that enhanced contrast vision in the larvae was responsible for the higher feeding incidence observed for seven and 10 week old larvae in the yellow and green spectral regimes, and that such as system has specific ecological significance to the larvae.

LITERATURE CITED

Abrams, P. 1980. Some comments on measuring niche overlap. Ecology 61(1):44-49.

Alden, R.W. III, R.C. Dahiya, and R.J. Young, Jr. 1982. A method for the enumeration of zooplankton subsamples. J. Exp. Mar. Biol. Ecol. 59(2-3):185-206.

Ali, M.A., and H.-J. Wagner. 1975. Visual pigments: phylogeny and ecology. *In* M.A. Ali (editor), Vision in fishes: new approaches in research, p. 427-443. Plenum Press, Inc., New York. 836 p.

Allen, D.M., E.R. Loew, and W.N. McFarland. 1982. Seasonal changes in the amount of visual pigment in the retinae of fish. Can. J. Zool. 60(3):281-287.

Al-Yamani, F.Y. 1988. Distributional ecology of zooplankton and fish larvae (spot, croaker, menhaden) in the northern Gulf of Mexico. Ph.D. dissertation, The University of Miami, Coral Gables, Florida, 421 p.

Arthur, D.K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74(3):517-530.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-1971. NOAA Tech. Rept. NMFS SSRF-671, 103 p.

Balon, E.K. 1984. Reflections on some decisive events in the early life-history of fishes. Trans. Am. Fish. Soc. 113(2):178-185.

Bams, R.A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24(5):1117-1153.

Batty, R.S. 1984. Development of swimming movements and musculature of larval herring (*Clupea harengus*). J. Exp. Biol. 110:217-229.

Beers, J.R., and G.L. Stewart. 1967. Micro-zooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board Can. 24(10):2053-2068.

Beers, J.R., and G.L. Stewart. 1969. Micro-zooplankton and its abundance relative to the larger zooplankton and other seston components. Mar. Biol. (Berl.) 4(10):182-189.

Beverton, R.J.H. 1962. Long-term dynamics of certain North Sea fish populations. *In* E.D. LeCren and M.W. Holdgate (editors), The exploitation of natural animal populations, p. 242-264. John Wiley and Sons, Inc., New York, 399 p.

Beyer, J.E. 1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana 1:65-91.

Beyer, J.E. 1989. Recruitment stability and survival—simple size-specific theory with examples from the early life dynamics of marine fish. Dana 7:45-147.

Birdsong, R.S., H.G. Marshall, R.W. Alden, III, and R.M. Ewing. 1989. Lower Chesapeake Bay mainstem plankton monitoring program for 1987-1988. Final report to the Virginia State Water Control Board. 152 p.

Blaxter, J.H.S. 1965. The feeding of herring larvae and their ecology in relation to feeding. CalCOFI Rep. X:79-88.

Blaxter, J.H.S. 1968a. Light intensity, vision, and feeding in young plaice. J. Exp. Mar. Biol. Ecol. 2(3):293-307.

Blaxter, J.H.S. 1968b. Visual thresholds and spectral sensitivity of herring larvae. J. Exp. Biol. 48(1):39-53.

Blaxter, J.H.S. 1969a. Visual thresholds and spectral sensitivity of flatfish larvae. J. Exp. Biol. 51(1):221-230.

Blaxter, J.H.S. 1969b. Development: eggs and larvae. *In* W.S. Hoar and D.J. Randall (editors), Fish physiology, Volume III: reproduction and growth, bioluminescence, pigments, and poisons, p. 177-252. Academic Press, New York, 485 p.

Blaxter, J.H.S. 1975. The eyes of larval fish. *In* M.A. Ali (editor), Vision in fishes: new approaches in research, p. 427-443. Plenum Press, New York, 836 p.

Blaxter, J.H.S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115(1):98-114.

Blaxter, J.H.S. 1987. Structure and development of the lateral line. Biol. Rev. 62(4):471-514.

Blaxter, J.H.S., and M. Staines. 1970. Pure-cone retinae and retinomotor responses in larval teleosts. J. Mar. Biol. Ass. U.K. 50(2):449-460.

Boehlert, G.W., and J.B. Morgan. 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*. Hydrobiol. 123(2):161-170.

Branchek, T. 1984. The development of photoreceptors in the zebrafish, *Brachydanio rerio*. II. Function. J. Comp. Neurol. 224:116-122.

Branchek, T., and R. BreMiller. 1984. The development of photoreceptors in the zebrafish, *Brachydanio rerio*. II. Structure. J. Comp. Neurol. 224:107-115.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and food supply. *In* S.D. Gerking (editor), The biological basis of freshwater fish production, p. 113-131. Blackwell Scientific Publications, Oxford.

Breck, J.E., and M.J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (*Lepomis machrochirus*) sunfish. Can. J. Fish. Aquat. Sci. 40(2):162-167.

Breitburg, D.L. 1988. Effects of turbidity on prey consumption by striped bass larvae. Trans. Am. Fish. Soc. 117(1):72-77.

Brodeur, R.D., and W.G. Pearcy. 1984. Food habits and dietary overlap of some shelf rockfishes (Genus *Sebastes*) from the northeastern Pacific Ocean. Fish. Bull., U.S. 82(2):269-293.

Brooks, J.L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17(3):273-291.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science, N.Y. 150(3692):28-35.

Brown, B.W., Jr., and M. Hollander. 1977. Biostatistics: a biomedical introduction. John Wiley and Sons, N.Y. 456 p.

Butler, S.M., and J.R. Bence. 1984. A diet model for planktivores that follow density-dependent rules for prey selection. Ecology 65(6):1885-1894.

Byron, E.R. 1982. The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. Ecology 63(6):1871-1886.

Carnes, B.A., and N.A. Slade. 1982. Some comments on niche analysis in canonical space. Ecology 63(4):888-893.

Checkley, D.M. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Mar. Ecol. Prog. Ser. 9(3): 245-253.

Chesson, J. 1978. Measuring preference in selective predation. Ecology 59(2): 211-215.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64(5):1297-1304.

Chia, F.S., J. Buckland-Nicks, and C.M. Young. 1984. Locomotion of marine invertebrate larvae: a review. Can. J. Zool. 62(7):1205-1222.

Coates-Markle, L.J. 1982. Larval and pelagic juvenile feeding ecology of three sympatric Scotian Shelf hakes (Pisces: Gadoidei). M.S. thesis, The University of Guelph, Guelph, Ontario, 219 p.

Confer, J.L., and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20(4):571-579.

Confer, J.L., G.L. Howick, M.H. Corzette, S.L. Kramer, S. Fitzgibbon, R. Landesberg. 1978. Visual predation by planktivores. Oikos 31(1):27-37.

Costanza, M.C., and A.A. Afifi. 1979. Comparison of stopping rules in forward stepwise discriminant analysis. J. Am. Stat. A. 74(368):777-785.

Costello, M.J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. J. Fish. Biol. 36(2):261-263.

Courtois, R., and J.J. Dodson. 1986. Régime alimentaire et principaux facteurs influençant l'alimentation des larves de capelan (*Mallotus villosus*), d'éperlan (*Osmerus mordax*) et de hareng (*Clupea harengus harengus*) dans un estuarie partiellement mélangé. Can. J. Fish. Aquat. Sci. 43(5):968-979.

Crecco, V.A., and M.M. Blake. 1983. Feeding ecology of coexisting larvae of American shad and blueback herring in the Connecticut River. Trans. Am. Fish. Soc. 112(4):498-507.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, New York, 278 p.

Cushing, D.H. and J.G.K. Harris. 1973. Stock and recruitment and the problem of density dependence. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164:142-155.

Dabrowski, K.R., and D.H. Jewson. 1984. The influence of light environment on depth of visual feeding by larvae and fry of *Coregonus pollan* (Thompson) in Lough Neagh. J. Fish. Biol. 25(2):173-181.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murray, London.

Dendrinos, P., S. Dewan, and J.P. Thorpe. 1984. Improvement in the feeding efficiency of larval, post larval and juvenile dover sole (*Solea solea* L.) by the use of staining to improve the visibility of *Artemia* used as food. Aquaculture 38(2):137-144.

Desselle, W.J., M.A. Poirrier, J.S. Rogers, and R.C. Cashner. 1978. A discriminant functions analysis of sunfish (*Lepomis*) food habits and feeding niche segregation in the Lake Pontchartrain, Louisiana Estuary. Trans. Am. Fish. Soc. 107(5):713-719.

Drenner, R.W., J.R. Strickeler, and W.J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. 35(10):1370-1373.

Drenner, R.W., and S.R. McComas. 1980. The roles of zooplankton escape ability and fish selectivity in the selective feeding and impact of planktivorous fish. *In* W.C. Kerfoot (editor), Evolution and ecology of zooplankton communities. Special Symposium Volume 3, American Society of Limnology and Oceanography, p. 587-593. University Press of New England, Hanover, New Hampshire, 793 p.

Durbin, A.G. 1979. Food selection by plankton feeding fishes. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p 203-218. Sport Fishing Institute, Washington.

Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58(1):46-59.

Eggers, D.M. 1982. Planktivore preference by prey size. Ecology 63(2):381-390.

Ehrlich, K.F., J.H.S. Blaxter, and R. Pemberton. 1976. Morphological and histological changes during the growth and starvation of herring and plaice larvae. Mar. Biol. (Berl.) 35(2):105-118.

Ellersten, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgård, and V. Øiestad. 1981. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:317-319.

Fabre-Domergue, and E. Biétrix. 1897. La périod critique post larvaire des poissons marins. Bull. Mus. Nat. Hist. Nat. Paris 3:57-58.

Feller, R.J., and V.W. Kaczynski. 1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish. Res. Board Can. 32(8):1419-1429.

Frank, K.T., and W.C. Leggett. 1982. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*), and its application to the match/mismatch hypothesis. Can. J. Fish. Aquat. Sci. 39(5):691-699.

Fruge, D.J. and F.M. Truesdale. 1978. Comparative larval development of *Micropogonias undulatus* and *Leiostomus xanthurus* (Pisces: Sciaenidae) from the northern Gulf of Mexico. Copeia 1978(4):643-648.

Fuiman, L.A. 1986. Burst-swimming performance of larval zebra danios and the effects of diel temperature fluctuations. Trans. Am. Fish. Soc. 115(1):143-148.

Fuiman, L.A., and P.W. Webb. 1988. Ontongeny of routine swimming activity and performance in zebra danios (Teleostei: Cyprinidae). Anim. Behav. 36(Part I): 250-261.

Gardner, M.B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology 62(3):571-578.

Gauld, D.T. 1966. The swimming and feeding of planktonic copepods. *In* Some contemporary studies in marine science, H. Barnes (editor), p. 313-334. George Allen and Unwin Ltd., London, 716 p.

Ginetz, R.M., and P.A. Larkin. 1973. Choice of colors of food items by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 39(2):229-234.

Govoni, J.J. 1980. Morphological, histological, and functional aspects of alimentary canal and associated organ development in larval *Leiostomus xanthurus*. Rev. Can. Biol. 39(2):69-80.

Govoni, J.J. 1981. Alimentary canal development and its relation to the early life-history of spot, *Leiostomus xanthurus*. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:314-315.

Govoni, J.J. 1987. The ontongeny of dentition in *Leiostomus xanthurus*. Copeia 1987(4):1041-1046.

Govoni, J.J., D.S. Peters, and J.V. Merriner. 1982. Carbon assimilation during larval development of the marine teleost *Leiostomus xanthurus*. J. Exp. Mar. Biol. Ecol. 64:287-299.

Govoni, J.J., D.E. Hoss, and A.J. Chester. 1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13(2-3):189-199.

Govoni, J.J., A.J. Chester, D.E. Hoss, and P.B. Other. 1985. An observation of episodic feeding and growth of larval *Leiostomus xanthurus* in the northern Gulf of Mexico. J. Plank. Res. 7(1):137-146.

Govoni, J.J., P.B. Ortner, F. Al-Yamani, and L.C. Hill. 1986a. Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 28(1-2):175-183.

Govoni, J.J., G.W. Boehlert, and Y. Watanabe. 1986b. The physiology of digestion in fish larvae. Env. Biol. Fishes 16(1-3):59-77.

Govoni, J.J., and A.J. Chester. 1990. Diet composition of larval *Leiostomus xanthurus* in and about the Mississippi River plume. J. Plank. Res. 12(4):819-830.

Gulland, J.A. 1965. Survival of the youngest stages of fish, and its relation to year-class strength. Spec. Publ. ICNAF 6:363-371.

Guma'a, S.A. 1982. Retinal development and retinomotor responses in perch, *Perca flavescens* L. J. Fish. Biol. 20(5):611-618.

Hairston, N.G., Jr. 1979. The adaptive significance of color polymorphism in two species of *Diaptomus* (Copepoda). Limnol. Oceanogr. 24(1):15-37.

Hairston, N.G., Jr., and K.T. Li. 1982. Fish vision and the detection of planktonic prey. Science, N.Y. 218 (4578):1240-1242.

Hansen, M.J., and D.H. Wahl. 1981. Selection of small *Daphnia pulex* by yellow perch in Oneida Lake, New York. Trans. Am. Fish. Soc. 110(1):64-71.

Hároshi, F.I., and Y. Hashimoto. 1983. Ultraviolet visual pigment in a vertebrate: a tetrachromatic cone system in the dace. Science, N.Y. 222(4626):1021-1-23.

Hemilä, T. Reuter, and K. Virtanen. 1976. The evolution of colour-opponent neurones and colour vision. Vision Res. 16(11):1359-1362.

Hettler, W.F., and A.B. Powell. 1981. Egg and larval fish production at the NMFS Beaufort Laboratory, Beaufort, N.C. USA. Rapp. P-v. Réun. Cons. int. Explor. Mer 178:501-503

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 20:1-228.

Hjort, J. 1926. Fluctuations in year classes of important food fishes. J. Cons. int. Explor. Mer 1(1):5-38.

Houde, E.D. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28(3):395-411

Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. J. Fish. Biol. 35(A):29-38.

Houde, E.D., and R. Schekter. 1978. Simulated food patches and survival of larval bay anchovy, *Anchoa mitchilli* and sea bream, *Archosargus rhomboidalis*. Fish. Bull., U.S. 76(2):483-486.

Houde, E.D., and R. Schekter. 1980. Feeding by marine fish larvae: development and functional response. Env. Biol. Fish. 5(4):315-334.

Houde, E.D., and R. Schekter. 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:441-453.

Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70(3):821-848.

Hunter, J.R. (editor) 1976. Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. NOAA Tech. Rept. NMFS Circ. 395, 5p.

Hunter, J.R. 1981. Feeding ecology and predation in marine fish larvae. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology and relation to fisheries, p. 34-77. Washington Sea Grant, Seattle, Washington, 131 p.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59(1):67-77.

Hyslop, E.J. 1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17(4):411-429.

Ivlev, V.S. (editor) 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, 302 p.

Jenkins, G.P. 1987. Comparative diets, prey selection, and predatory impact of co-occurring larvae of two flounder species. J. Exp. Mar. Biol. Ecol. 110(2):147-170.

Johns, P.R. 1981. Growth of fish retinas. Am. Zool. 21(2):447-458.

Johns, P.R. 1982. The formation of photoreceptors in the growing retinas of larval and adult goldfish. J. Neurosci. 2:179-198.

Johnson, D.H. 1980. The comparison of usage an availability measurements for evaluating resource preference. Ecology 61(1):65-71.

Judkins, D.C., and A. Fleminger. 1972. Comparison of foregut contents of *Sergestes similis* obtained from net collections and albacore stomachs. Fish. Bull., U.S. 70(1):217-223.

Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Mar. Ecol. Prog. Ser. 16(1-2):9-20.

Kerfoot, W.C. 1980. Commentary: transparency, body size, and prey conspicuousness. *In* W.C. Kerfoot (editor), Evolution and ecology of zooplankton communities. Special Symposium Volume 3, American Society of Limnology and Oceanog-

raphy, p. 609-617. University Press of New England, Hanover, New Hampshire, 793 p.

Kettle, D., and W.J. O'Brien. 1978. Vulnerability of arctic zooplankton species to predation by small lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 35(11):1495-1500.

Kirk, R.E. 1982. Experimental design: procedures for the behavioral sciences, second edition. Brooks/Cole Publishing Co., Belmont, California, 911 p.

Kjelson, M.A., D.S. Peters, G.W. Thayer, G.N. Johnson. 1975. The general feeding ecology of postlarval fishes in the Newport River Estuary. Fish. Bull., U.S. 73(1):137-144.

Kohler, C.C., and J.J. Ney. 1982. A comparison of methods for quantitative analysis of feeding selection in fishes. Env. Biol. Fish. 7(4):363-368.

Koslow, J.A., S. Brault, J. Dugas, R.O. Fornier, and P. Hughes. 1985. Condition of larval cod (*Gadus morhua*) off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. Mar. Biol. (Berl.) 86(2):113-121.

Laroche, J.L. 1982. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary. Fish. Bull., U.S. 80(4):827-840.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73(3):453-462.

Lasker, R. 1978a. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212-230.

Lasker, R. 1978b. Ocean variability and its biological effects - regional review - Northeast Pacific. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:168-181.

Lasker, R. 1981a. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California Current: contrasting years 1975 through 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:375-388.

Lasker, R. 1981b. The role of a stable ocean in larval fish survival and subsequent recruitment. *In* R. Lasker (editor), Marine fish larvae: morphology, ecology and relation to fisheries, p. 80-87. Washington Sea Grant Program, Seattle, Washington, 131 p.

Lasker, R., H.M. Feder, G.H. Theilacker, and R.C. May. 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5(4):345-353.

Lasker, R., and J.R. Zweifel. 1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In* J.H. Steele (editor), Spatial patterns in plankton communities, p. 329-354. NATO Conference Services (IV:3). Plenum Publishing Corp., New York, 552 p.

Last, J.M. 1978a. The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Mar. Biol. (Berl.) 45(4):359-368.

Last, J.M. 1978b. The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Mar. Biol. (Berl.) 48(4):377-386.

Last, J.M. 1980. The food of twenty species of fish larvae in the west-central North Sea. Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft No. 60, 44 p.

Laurence, G.C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). J. Fish. Biol. 4(1):73-78.

Laurence, G.C. 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J. Fish. Res. Board Can. 31(8):1415-1419.

Laurence, G.C. 1978. Comparative growth, respiration, and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. (Berl.) 50(1):1-7.

Laurence, G.C., A.S. Smigielski, T.A. Halavik, and B.R. Burns. 1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:304-311.

Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. Oecologia (Berl.) 52(1):22-30.

Li, K.T., J.K. Wetterer, and N.G. Hairston, Jr. 1985. Fish size, visual resolution, and prey selectivity. Ecology 66(6):1729-1735.

Lippson, A.J., and R.L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River Estuary. Martin Marietta Corp., Baltimore, Maryland, 282 p.

Loew, E.R., and J.N. Lythgoe. 1978. The ecology of cone pigments in teleost fishes. Vision Res. 18(6):715-722.

Luecke, C., and W.J. O'Brien. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. Can. J. Fish. Aquat. Sci. 38(10):1264-1270.

Lüning, K. 1981. Light. *In* C.S. Lobban and M.J. Wayne (editors), The biology of seaweeds, p. 327-355. Blackwell Scientific Publications, Oxford, 786 p.

Malhotra, Y.R., and S. Munshi. 1985. First feeding and survival of *Aspidoparia morar* larvae (Cyprinidae). Trans. Am. Fish. Soc. 114(2):286-290.

Manly, B.F.J. 1986. Multivariate statistical methods: a primer. Chapman and Hall, New York, 159 p.

Martin, F.D., D.A. Wright, J.C. Means, and E.M. Setzler-Hamilton. 1985. Importance of food supply to nutritional state of striped bass in the Potomac River Estuary. Trans. Am. Fish. Soc. 114(1):137-145.

Maule, A.G., and H.F. Horton. 1984. Feeding ecology of walleye, *Stizostedion vitreum*, in the mid-Columbia River, with emphasis on the interaction between walleye and juvenile anadromous fishes. Fish. Bull., U.S. 82(2):411-418.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. *In* J.H.S. Blaxter (editor), The early life-history of fish, p. 1-19. Springer-Verlag, New York, 765 p.

McCullough, R.D., and J.G. Stanley. 1981. Feeding niche dimensions in larval rainbow smelt (*Osmerus mordax*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:352-354.

McFarland, W.N. and F.W. Munz. 1975. Part III: The evolution of photopic visual pigments in fishes. Vision Res. 15:1071-1080.

Mellors, W.K. 1975. Selective predation of ephippial *Daphnia* and the resistance of ephippial eggs to digestion. Ecology 56(4):974-980.

Mills, E.L., J.L. Confer, and R.C. Ready. 1984. Prey selectivity by young yellow perch: the influence of capture success, visual acuity, and prey choice. Trans. Am. Fish. Soc. 113(5):579-587.

Mills, E.L., J.L. Confer, and D.W. Ketchmer. 1986. Zooplankton selection by young yellow perch: the influence of light, prey density, and predator size. Trans. Am. Fish. Soc. 115(5):716-725.

Minello, T.J. 1980. The neritic zooplankton of the northwestern Gulf of Mexico. Ph.D. dissertation, Texas A & M University, College Station, Texas, 240 p.

Monteleone, D.M., and W.T. Peterson. 1986. Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. Mar. Ecol Prog. Ser. 30(2-3):133-143.

Munz, F.W., and W.N. McFarland. 1975. Part I: Presumptive cone pigments extracted from tropical marine fishes. Vision. Res. 15:1045-1062.

Neave, D.A. 1984. The development and visual acuity of larval plaice (*Pleuronectes platessa* L.) and turbot (*Scophthalmus maximus* L.). J. Exp. Mar. Biol. Ecol. 78(2):167-175.

O'Brien, W.J. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57(6):1304-1310.

O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67(5):572-581.

O'Brien, W., N.A. Slade, and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57(6):1304-1310.

O'Connell, C.P. 1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the seas as estimated by histological methods. Fish. Bull., U.S. 78(2):475-489.

O'Connell, C.P. 1981. Development of organ systems in the northern anchovy, *Engraulis mordax*, and other teleosts. Am. Zool. 21(2):429-446.

O'Connell, C.P., and L.P. Raymond. 1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

Ortner, P.B., L.C. Hill, and S.R. Cummings. 1989. Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. Cont. Shelf. Res. 9(4):387-402.

Owen, R.W. 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments. J. Mar. Res. 47:197-240.

Paloheimo, J.E. 1979. Indices of food type preference by a predator. J. Fish. Res. Board Can. 36(2):470-473.

Pasch, R.W., and L.H. Lyford, Jr. 1972. The food habits of two species of *Cottus* occupying the same habitat. Trans. Am. Fish. Soc. 101(2):377-381.

Peterman, R.M., M.J. Bradford, N.C.H. Lo, and R.D. Methot. 1988. Contribution of early life history stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45(1):8-16.

Peterson, W.T., and S.J. Ausubel. 1984. Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar. Ecol. Prog. Ser. 17(1-2):65-75.

Powell, A.B., and H.R. Gordy. 1980. Egg and larval development of the spot, *Leiostomus xanthurus* (Sciaenidae). Fish. Bull., U.S. 78(3):701-714.

Powell, A.B., and A.J. Chester. 1985. Morphometric indices of nutritional condition and sensitivity to starvation of spot larvae. Trans. Am. Fish. Soc. 114(3):338-347.

Powell, A.B., A.J. Chester, J.J. Govoni, and S.M. Warlen. (In press). Nutritional condition of spot (*Leiostomus xanthurus*) larvae associated with the Mississippi River plume. Trans. Am. Fish. Soc.

Powles, H., and B.W. Stender. 1978. Taxonomic data on the early life history stages of Sciaenidae of the the South Atlantic Bight of the United States. S.C. Mar. Resour. Cent. Tech. Rep. No. 31, 64 p.

Rajasilta, M., and I. Vuorinen. 1983. A field study of prey selection in planktivorous fish larvae. Oecologia (Berl.) 59(1):65-68.

Ramus, J. 1985. Light. *In* M.M. Littler and D.S. Littler (editors), Ecological field methods: macroalgae, p. 33-51. Cambridge University Press, Cambridge, 617 p.

Raymond, P.A. 1985. Cytodifferentiation of photoreceptors in larval goldfish: delayed maturation of rods. J. Comp. Neurol. 236:90-105.

Roblin, C., and J. Bruslé. 1984. Le régime alimentaire des alevins et juvéniles de loup (*Dicentrarchus labrax* L.) des lagunes littorales du Golfe du Lion (Étangs Roussillonnais, France). Vie Milieu 34(4):195-207.

Sandy, J.M., and J.H.S. Blaxter. 1980. A study of retinal development in larval herring and sole. J. Mar. Biol. Ass. U.K. 60(1):59-71.

SAS Institute. 1985. SAS User's Guide: Statistics. Version 5 Edition. SAS Institute, Cary, N.C. 956 p.

Schmidt, D., and W.J. O'Brien. 1982. Planktivorous feeding ecology of arctic grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. 39(3):475-482.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51(3):408-418.

Schoener, T.W. 1982. The controversy over interspecific competition. Am. Sci. 70(6):586-595.

Schwassmann, H.O. 1965. Functional development and visual pathways in larval sardines and anchovies. CalCOFI Rept. X:64-70.

Scura, E.D., and C.W. Jerde. 1977. Various species of phytoplankton as food for larval northern anchovy *Engraulis mordax*, relative nutritional value of the dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fish. Bull., U.S. 75(3):577-583.

Shelbourne, J.E. 1962. A predator-prey size relationship for plaice larvae feeding on *Oikopleura*. J. Mar. Biol. Ass. U.K. 42(2):243-252.

Sherman, K., and K.A. Honey. 1971. Seasonal variations in the food of larval herring in coastal waters of central Maine. Rapp. P.-v. Réun. Cons. int. Explor. Mer 160:121-124.

Sherman, K., R. Maurer, R. Byron, and J. Green. 1981. Relationship between larval fish communities and zooplankton prey species in an offshore spawning ground. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:289-294.

Sinclair, M., M.J. Tremblay, and P. Bernal. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42(3):602-608.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, second edition. W.H. Freeman and Co., New York, 859 p.

Stell, W.K. 1972. The morphology organization of the vertebrate retina. *In* M.G.F. Fuortes (editor), Handbook of sensory physiology, VII/1B, p. 111-213. Springer-Verlag, Berlin

Stell, W.K., and F.I. Hárosi. 1976. Cone structure and visual pigment content in the retina of the goldfish. Vision Res. 16(6):647-657.

Stoecker, D.K., and J.J. Govoni. 1984. Food selection by young larval gulf menhaden (*Brevoortia patronus*). Mar. Biol. (Berl.) 80(3):299-306.

Strauss, R.E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Trans. Am. Fish. Soc. 108(4):344-352.

Strauss, R.E. 1982. Influence of replicated subsamples and subsample heterogeneity on the linear index of food selection. Trans. Am. Fish. Soc. 111(4):517-522.

Strickler, J.R. 1982. Calanoid copepods, feeding currents, and the role of gravity. Science, N.Y. 218:158-160.

Sumida, B.Y., and H.G. Moser. 1980. Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. CalCOFI Rep., Vol. XXI:161-166.

Taggart, C.T., and W.C. Leggett. 1987. Short-term mortality in post-emergent larval capelin *Mallotus villosus*. II. Importance of predator density, and density-dependence. Mar. Ecol. Prog. Ser. 41(3):219-229.

Teska, J.D., and D.J. Behmer. 1981. Zooplankton preference of larval lake whitefish. Trans. Am. Fish. Soc. 110(3):459-461.

Theilacker, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*. Fish. Bull., U.S. 76(2):403-414.

Turner, J.T. 1984. The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Tech. Rep. NMFS 7, 28 p.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 19:513-605.

Vinyard, G.L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) predation. Can. J. Fish. Aquat. Sci. 37(12):2294-2299.

Vinyard, G.L., and W.J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33(12):2845-2849.

Vlymen, W.J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution and larval behavior. Env. Biol. Fish. 2:211-233

Wald, G. 1937. Visual purple system in fresh-water fishes. Nature 139(3528):1017.

Wald, G. 1939. The porphyropsin visual system. J. Gen. Physiol. 22(3):775-794.

Wallace, R.K., Jr. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110(1):72-76.

Ware, D.M. 1971. Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J. Fish. Res. Board Can. 28(12):1847-1852.

Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32(12):2503-2512.

Warlen, S.M., and A.J. Chester. 1985. Age, growth, and distribution of larval spot, *Leiostomus xanthurus*, off North Carolina. Fish. Bull., U.S. 84(4):587-599.

Webb, P.W., and R.T. Corolla. 1981. Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 79(1):143-150.

Webb, P.W., and D. Weihs. 1986. Functional locomotory morphology of early life-history stages of fishes. Trans. Am. Fish. Soc. 115(1):115-127

Werner, E.E., and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55(5):1042-1052.

Werner, R.G., and J.H.S. Blaxter. 1981. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:405-408.

Wetterer, J.K., and C.J. Bishop. 1985. Planktivore prey selection: the reactive field volume model vs. the apparent size model. Ecology 66(2):457-464.

Wiebe, P.H., S.H. Boyd, and S.H. Winget. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34(3): 313-326.

Wright, D.I., W.J. O'Brien, and C. Luecke. 1983. A new estimate of zooplankton retention by gill rakers and its ecological significance. Trans. Am. Fish. Soc. 112(5):638-646.

Wroblewski, J.S. 1984. Formulation of growth and mortality of larval northern anchovy in a turbulent feeding environment. Mar. Ecol. Prog. Ser. 20(1-2): 13-22.

Wroblewski, J.S., J.G. Richman, and G.L. Mellor. 1989. Optimal wind conditions for the survival of larval northern anchovy, *Engraulis mordax*: a modeling investigation. Fish. Bull., U.S. 87(3):387-395.

Zaret, T.M., and A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52(2):337-342.

Zaret, T.M. and W.C. Kerfoot. 1975. Fish predation on *Bosmina longirostris*: body size selection versus visibility selection. Ecology 56(1):232-237.

VITA

I was born on Tuesday, March 18, 1958, in New Hyde Park, on Long Island, New York, that wonderful suburban landscape. To my good fortune a somewhat precocious childhood and early academic boredom did not inhibit me from pursing my interests in science and nature. I am amazed I was able to survive the myopia and inflexibility of my primary schooling. It was confining and unimaginative. What a horror to be at the disposal of an uncreative system designed to perpetuate mediocrity. I am grateful that I have always had the love and support of my nuclear family, because without them, I would have perished.

I have always wanted to be a scientist. There was never any doubt in my mind what I would do with my life. Science is possibly the noblest, most intellectually satisfying pursuit one can have. It is an exquisite tool used to perceive things in our complex *Umvelt* that are otherwise unintelligible. The study of life has brought me great pleasure. So many unanswered questions! Only one who has used the scientific method can fully understand and appreciate the elegant beauty of problem solving.

In June 1980, I completed a mediocre performance in Tallahassee, Florida, for my Baccalaureate degree in Biological Science at Florida State University. My only regret is that I did not apply myself with more vigor and diligence. I owe much to my advisor, William Herrnkind. Through my own independent study under his guidance and as a student at the F.S.U Marine Laboratory, he gave me my first exposure to true scientific investigation and to the wonders of behavioral ecology.

I then moved back to New York to take my Master of Science degree in Environmental Studies at C.W. Post College of Long Island University in Brookville, which I was awarded in May 1984. Hard work, persistence and poor guidance, those four years. I am particularly grateful to my friend and colleague, Jon Greenlaw, for his assistance and guidance during those difficult years. An abridged version of my thesis won the 1984 annual Beta Beta Beta honor society (Kappa Epsilon chapter) award for best graduate student research paper.

Finally, or so I believed, I entered my terminal degree program in August 1983 at Old Dominion University in Norfolk, Virginia, as a University Fellow. I served as a teaching assistant, research assistant, biological illustrator and department computer consultant. Teaching gave me my greatest pleasure while a student at O.D.U because I have always felt I made a contribution to the lives of my students and that many of them understood that fact. I am fortunate my friend and advisor, Ray Birdsong, gave me the space, time and financial support to do what I wanted, otherwise my development as a competent scientist would have been incomplete. I will be awarded my Doctorate in Ecological Sciences in December of 1990. What a long and difficult road it has been.

I have decided to continue my studies on another taxon far more difficult to understand. As a whole, they will ultimately be the destruction of the planet and the doom of mankind. In August of 1990, I entered the Case Western Reserve University School of Medicine in Cleveland, Ohio, and ultimately, I will become a physician.

BIBLIOGRAPHY

Original Research and Publications:

Peterson, D.E. 1984. Sensitivity to hydrodynamic stimuli and predator detection in the North American sand lance, *Ammodytes americanus* (Pisces: Ammodytidae). M.S. Thesis, Long Island University, Brookville, New York. 104 pp.

Matta, J.F., and D.E. Peterson. 1985. The larvae of six nearctic *Hydroporus* of the subgenus *Neoporus* (Coleoptera: Dytiscidae). Proc. Acad. Nat. Sci. Phila. 137:53-60.

Matta, J.F., and D.E. Peterson. 1987. The larvae of two North American diving beetles of the genus *Acilius* (Coleoptera: Dytiscidae). Proc. Entomol. Soc. Wash. 89(3):440-443.

Unpublished Technical Reports:

Birdsong, R.S., D.E. Peterson, and D.W. Byrd. 1987. A survey of alosine fish occurrence and spawning utilization of the Crump/Pollard Creek System and the adjacent Pamunkey River in Hanover County, Virginia. Final Report of Research to Black and Veatch, Inc., Rockville, Maryland. 18 p.

Poster Contributions:

Peterson, D.E., R.S. Birdsong, R.W. Alden, R.M. Ewing, and D.W. Byrd. 1988. Spatial and temporal patterns of zooplankton abundance in the lower Chesapeake Bay tributaries. Annual meeting of The Atlantic Estuarine Research Society, Hampton, Virginia.

Papers Presented at Professional Meetings:

Peterson, D.E., R.S. Birdsong, R.W. Alden, III. 1988. Spatial and temporal patterns of zooplankton abundance in the lower Chesapeake Bay tributaries. Virginia Academy of Sciences. Abstract published in Virginia. J. Sci. 39(2):121.

Professional Societies:

American Society of Ichthyologists and Herpetologists
Virginia Academy of Science
American Fisheries Society
Early Life History Section, AFS

Honor Societies

Phi Kappa Phi, Scholastic Honor Society
Sigma Xi, Scientific Research Society
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