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John H. Finucane
National Marine Fisheries Service

Churchill B. Grimes
National Marine Fisheries Service

Steven P. Naughton
National Marine Fisheries Service

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DIETS OF YOUNG KING AND SPANISH MACKEREL OFF THE SOUTHEAST UNITED STATES

By
John H. Finucane
Churchill B. Grimes
and
Steven P. Naughton

Southeast Fisheries Center
National Marine Fisheries Service, NOAA
Panama City Laboratory
3500 Delwood Beach Road
Panama City, FL 32408-7499

ABSTRACT: The diet of larval and post-larval (n = 95 and 307), and juvenile (n = 489 and 508) king (*Scomberomorus cavalla*) and Spanish mackerel (*S. maculatus*) from the Gulf of Mexico and southeastern Atlantic coastal waters of the U.S. consisted principally of fishes. Carangids, clupeids, and engraulids occurred in 23, 7 and 9% of larval and post-larval king mackerel stomachs and in 20, 40 and 7% of larval and post-larval Spanish mackerel stomachs, respectively. Sciaenids were also common in king mackerel, occurring in 21% of the stomachs. Prey fishes included the genera *Cynoscion*, *Caranx*, and *Anchoa*, and the species *Opisthonema oglinum*. Invertebrates, principally small crustaceans and nudibranch larvae, occurred infrequently in the diets of both species, but more so in Spanish mackerel than king mackerel.

The dominant prey items for juvenile mackerels from the Atlantic were engraulids, clupeids, balistids, and squids, collectively accounting for 73.3% by volume of the diet of king mackerel and 88.8% of Spanish mackerel. More invertebrates occurred in the diet of juvenile Spanish mackerel than king mackerel, but they accounted for a smaller volume, *i.e.*, 2.1% as compared to 5.4% for the Atlantic fish. Chi-square tests indicated significant differences between the diets of juvenile mackerel from the Gulf of Mexico and the Atlantic coast.

[Keywords: *diets; king mackerel; Spanish mackerel*]

King mackerel (*Scomberomorus cavalla*) and Spanish mackerel (*S. maculatus*) are widely distributed throughout the western Atlantic and the Gulf of Mexico. King mackerel occur from the Gulf of Maine to Brazil, while Spanish mackerel range from Cape Cod to Yucatan, Mexico with centers of abundance off Florida (Collette and Nauen 1983). Both species support important commercial and recreational fisheries in the southeastern United States and Mexico.

The diet and feeding ecology of larval and juvenile mackerels are poorly known. Naughton and Saloman (1981) reported on the stomach contents of juvenile king mackerel and Spanish mackerel from Cape Canaveral, Florida and Galveston Bay, Texas. Jenkins *et al.* (1984) studied the food habits of three species of *Scomberomorus* larvae from the waters off the Great Barrier Reef in Australia. Hunter and Kimbrell (1980) briefly described the foods of Pacific mackerel, *Scomber japonicus*, and Last (1980) and Peterson and Ausubel (1984) presented the diet of Atlantic mackerel, *Scomber scombrus*, from the west-central North Sea and U.S. Middle Atlantic waters, respectively.

Knowledge of the feeding ecology of young mackerels is necessary to understand the role of diet and food availability in regulating growth, survival, and ultimate recruitment. In addition, knowledge of the diets of young king and

Spanish mackerel will be useful in understanding trophic interactions of mackerel and their associated species. In this paper we present the results of our diet studies on larval and juvenile king and Spanish mackerel from the Gulf of Mexico and southeastern Atlantic coastal waters of the U.S.

METHODS

Larvae and post-larvae were obtained from ichthyoplankton samples collected in U.S. coastal waters of the Gulf of Mexico and Atlantic Ocean during the spring, summer, and fall of 1985 and 1986 (Fig. 1). Most fish were captured in 10 minute surface tows using (1 × 2 m) neuston nets with 0.505 and 0.947 mm mesh and 60 cm bongo nets with 0.333 mm mesh. Larvae were preserved in 10% formalin during 1985 and in 95% ethanol (to allow aging of otoliths) during 1986.

Juvenile mackerels were collected in commercial shrimp trawls from 1985-1987, and some fish were caught in almadrabas (trap nets) near Veracruz, Mexico in 1983. Trawl caught fish were frozen, and trap caught juveniles were preserved in 10% formalin.

In the laboratory larval and post-larval mackerel were measured to 0.1 mm standard length (SL) using a dissecting microscope at 20 to 60 × magnification and an ocular micrometer; juveniles were measured to the nearest mm fork length (FL) with a millimeter scale. The stomach and intestine of each fish were dissected and the food items teased out with fine probes. Food items in the mouth were

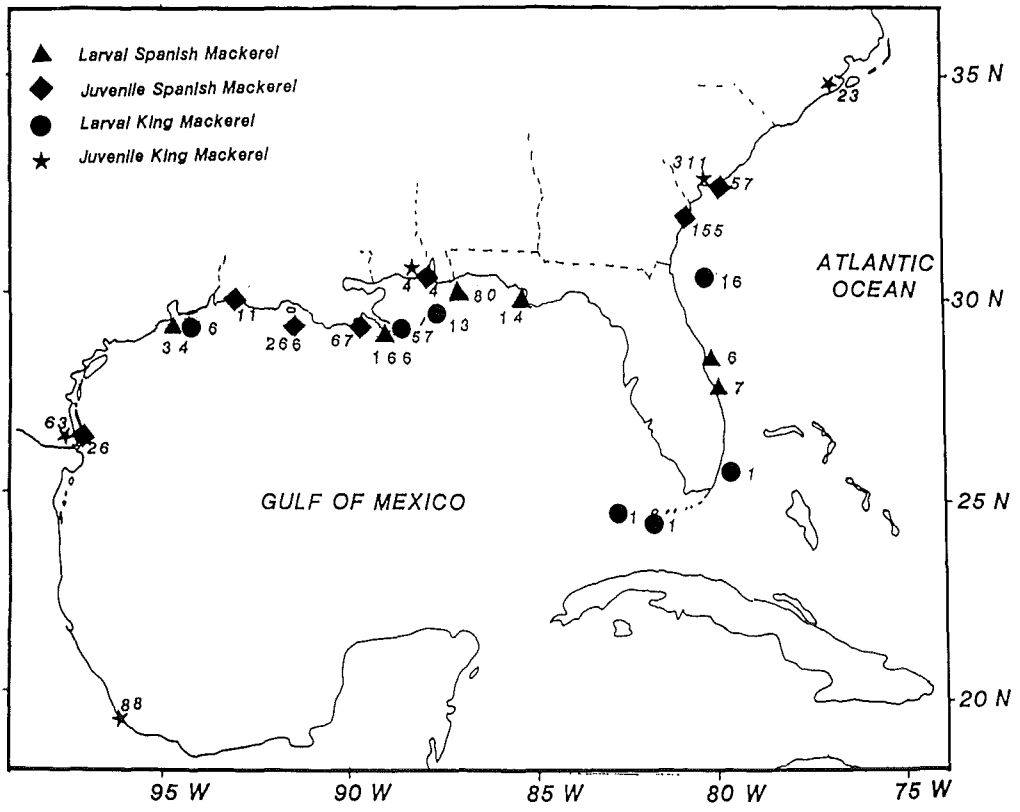

Figure 1. Collection sites and sample sizes of larval and juvenile king and Spanish mackerel from the Gulf of Mexico and U.S. south Atlantic. Larval sample sizes include post-larval fish.

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not included in the diet data because they were probably eaten while the fish were in the cod-end of the net.

For quantitative analysis of larval and post-larval food all prey items were counted and identified to the most precise taxonomic level possible. Percentage by number and frequency of occurrence were calculated for consistently recognizable taxonomic categories. Food items for juveniles were identified, counted, and displacement volumes measured in a partially water filled graduated cylinder. Chi-square statistics were used to make spatial comparisions of diets of juveniles when there were at least two food categories that cooccurred in fish from areas being compared (Windell and Bowen 1978).

To measure mutual resource use by the two scombrid species and the extent of diet similarity for each species among areas we calculated diet overlap according to Horn's (1966) modification of Morisita's Index (1959). The coefficient (C_λ) measures overlap between species j and k:

$$C_\lambda = \frac{2\left(\sum_{i=1}^{s} P_{ij}P_{ik}\right)}{\sum_{i=1}^{s} P_{ij}^2 + \sum_{i=1}^{s} P_{ik}^2},$$

where P_i^2 is the relative frequency (larvae and post-larvae) or numerical proportion (juveniles) of prey category i in species j and k, and s is the number of prey categories in the diet spectrum. For calculations of diet overlap (similarity) among areas for each species, j and k represented the Gulf of Mexico and south Atlantic Ocean areas. C_λ varies from 0, when there is no overlap between the diets of species or areas j and k, to 1, when all prey categories are in equal proportions.

The sum of P over S prey categories for a species equals the probability that any two categories selected at random will be the same category. Thus, the reciprocal,

$$B = 1/\sum_{i=1}^{s} p_i^2,$$

measures diet breadth or diversity (Levins 1968). If all categories are in equal proportions, B equals the total number of categories in the diet array, S. Therefore, S determines the maximum value of B. We computed B for each species in each area as scaled and unscaled values. Unscaled values incorporate two contributions to breadth (diversity): richness (S) and evenness of the distribution of amounts among the S categories. Values were scaled as B/S between 0, the most uneven distribution possible, and 1 representing the most even distribution possible among S categories. C_λ, B and B/S have been applied to fish diet studies by Bray and Ebeling (1975). Cailliet and Barry (1978) evaluated the performance of C_λ and several other food array overlap measures and concluded that all indices lead to similar conclusions about the degree of overlap. However, they noted differences among indices in sensitivities to species richness and evenness, the influence of dominant and rare species, the amount of diet overlap and the inequality of prey arrays. For all calculations prey categories were the most precise taxon consistently recognizable (*i.e.*, fish families, and among invertebrates, squid, gastropods, etc.).

RESULTS

Larval and post-larval specimens of Spanish mackerel used in the dietary analysis were larger than king mackerel. Spanish mackerel were 2.8 to 22.0 mm SL, $\bar{x}$ = 10 mm SL; king mackerel were

2.9 to 13.2 mm SL, $\bar{X}$ = 6.5 mm SL. However, the size range of juveniles was similar for both species (Spanish mackerel were 9-42 cm FL, $\bar{X}$ = 15.5; king mackerel were 9-42 cm FL, $\bar{X}$ = 23.5) (Fig. 2).

Analysis of the diet of larvae and post-larvae of 95 king mackerel and 307 Spanish mackerel showed that both species were principally piscivorous (Table 1). Fishes occurred in all of the king and Spanish mackerel stomachs. Carangids, clupeids, and engraulids occurred frequently in both species; the sciaenids occurred frequently only in king mackerel stomachs. King mackerel consumed a greater variety of fishes than Spanish mackerel (Table 1). Fishes that were identified in the diet were the genera *Cynoscion, Caranx*, and *Anchoa*, and the species *Opisthonema oglinum*. Invertebrates, principally small crustaceans and nudibranch larvae, occurred infrequently in the diets of both species, with Spanish mackerel consuming a wider variety. The most frequently occurring invertebrate category, nudibranch larvae, was present in only 2.0% of Spanish mackerel guts (Table 1).

We also characterized the diet of larvae and post-larvae using the measures of diet breadth (diversity) and overlap. Diet breadth (diversity, B) measures indicated that the diet of king mackerel larvae and post-larvae was more diverse and more evenly distributed among categories (B/S) than for Spanish mackerel (Table 2). Diet overlap (C_λ) between larval and post-larval king and Spanish mackerel was surprisingly small (0.50) for such morphologically similar species,

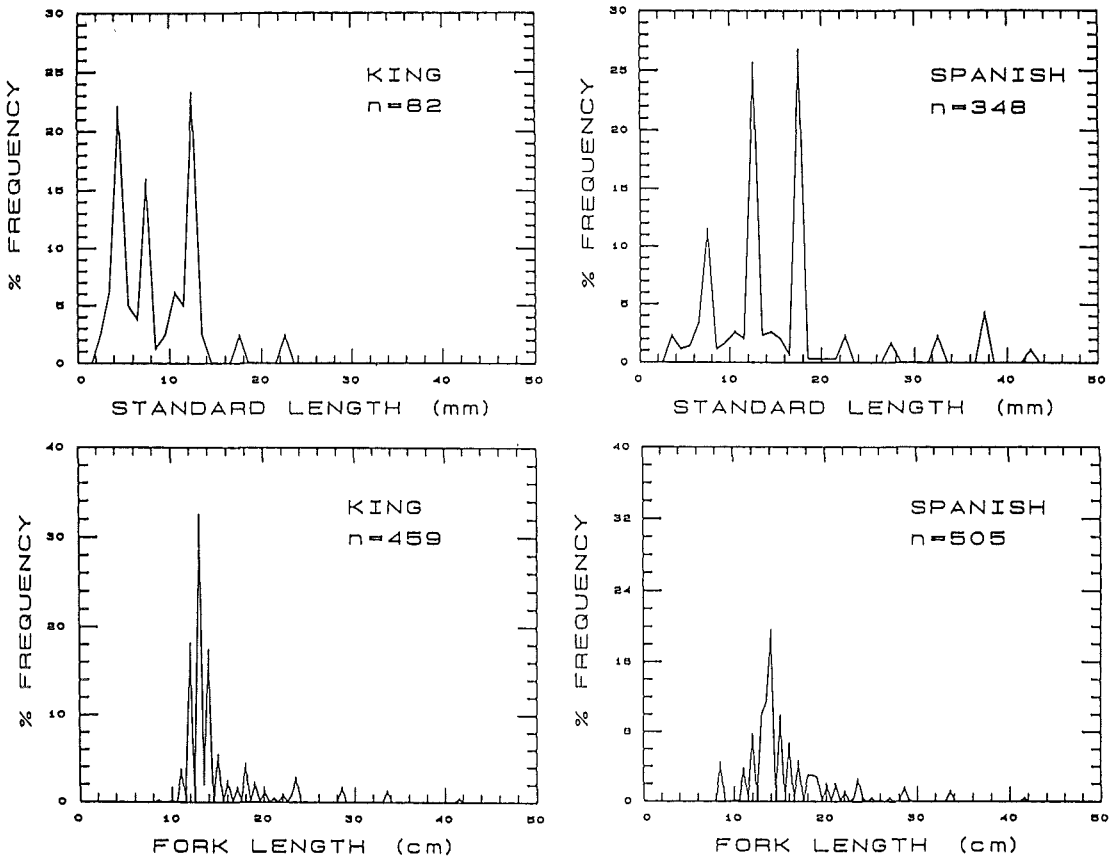

Figure 2. Length frequency distributions of larval and post-larval (upper polygon) and juvenile (lower polygon) king and Spanish mackerel.

Table 1. Frequency of occurrence of foods in the diets of larval and post-larval king and Spanish mackerel.

King Mackerel	Frequency	%
Fish with food	90	
Fish with empty stomachs	5	
Fishes		
Unidentified	42	46.7
Carangids	21	23.3
Sciaenids	19	21.1
Engraulids	8	8.9
Clupeids	6	6.7
Hemiramphids	2	2.2
Bothids	1	1.1
Callionymids	1	1.1
Myctophids	1	1.1
Scombrids	1	1.1
Syngnathids	1	1.1
Invertebrates		
Decapods	1	1.1
Spanish Mackerel	**Frequency**	**%**
Fish with food	245	
Fish with empty stomachs	62	
Fishes		
Unidentified	107	43.7
Clupeids	98	40.0
Carangids	49	20.0
Engraulids	16	6.5
Myctophids	2	0.8
Bothids	1	0.4
Tetraodontids	1	0.4
Fish eggs	1	0.4
Invertebrates		
Nudibranch larvae	5	2.0
Amphipods	3	1.2
Penaeids	2	0.8
Euphausiids	1	0.4

presumably because king mackerel ate fewer invertebrate prey and a wider variety of fishes than Spanish mackerel.

The diets of 489 juvenile Spanish mackerel and 508 juvenile king mackerel also consisted primarily of fish. The dominant prey catgories according to volume, number and frequency of occurrence were engraulids (primarily *Anchoa*) followed by clupeids, squids, and balistids (Tables 3 and 4). As in larvae and post-larvae (but samples were only from the Gulf of Mexico), invertebrates were more important in the diet of juvenile Spanish mackerel than king mackerel in the U.S. south Atlantic (Table 3).

Because juvenile samples were more numerous and collected over a wider area than larval and post-larval samples, we were able to compare the diets of juvenile king and Spanish mackerel from the Gulf of Mexico and Atlantic coast. Identifiable prey in 178 (11-73 cm FL) juvenile king mackerel from the Atlantic coast (Table 3) consisted mainly of engraulids (58.0% by number), clupeids (1.0% by number) and squid (3.1% by number). These prey groups were also present in the diet of 66 juvenile king mackerel (10-38 cm FL) from the Gulf of Mexico, but in different proportions (21.4%, 4.3% and 7.1% by number, respectively); gerreids, labrids and synodontids also occurred in low numbers in samples from the Gulf of Mexico (Table 4). Chi-square contingency tests indicated significant differences between the Gulf of Mexico and Atlantic coast for the testable prey categories Clupeidae, Engraulidae, and squid ($X^2 = 16.7$, $df = 2$, $X^2_{0.001} = 13.81$).

The results for juvenile Spanish mackerel were similar. Identifiable prey from 155 Atlantic coast fish (11-29 cm FL) included mainly engraulids (54.9% by number), and a few balistids (1.2% by number) while 91 Gulf of Mexico juveniles

Table 2. Diet breadth (diversity, B) and evenness of food amounts among prey categories (B/S). B and B/S were calculated using relative frequency of occurrence of prey categories for larvae and post-larvae, and relative number for juveniles.

	Larvae and post-larvae		South Atlantic Ocean juveniles		Gulf of Mexico juveniles	
	B	B/S	B	B/S	B	B/S
King mackerel	8.89	0.81	2.08	0.51	2.32	0.33
Spanish mackerel	4.87	0.44	2.31	0.33	3.59	0.89

Table 3. Diet of juvenile king and Spanish mackerel from the U.S. south Atlantic. N = 178 king mackerel stomachs with food and 155 Spanish mackerel stomachs with food.

KING MACKEREL						
	Volume		Number		Freq. of Occurrence	
Food Item	(ml.)	%	No.	%	Freq.	%
Fishes	113.1	94.6	189	96.9	178	100.0
Unidentified	31.8	26.6	74	37.9	74	41.6
Engraulidae	78.5	65.6	113	58.0	107	60.1
Anchoa sp.	67.3	56.3	82	42.1	78	43.8
Cludpeidae	2.8	2.3	2	1.0	2	1.1
Invertebrates						
Squid	6.5	5.4	6	3.1	6	3.4
SPANISH MACKEREL						
	Volume		Number		Freq. of Occurrence	
Food Item	(ml)	%	No.	%	Freq.	%
Fishes	95.7	97.9	155	89.6	155	100.0
Unidentified	9.4	9.6	61	35.3	61	39.4
Engraulidae	83.5	85.4	95	54.9	95	61.3
Anchoa	63.5	64.9	69	39.9	69	44.5
Balistidae	2.8	2.8	2	1.2	2	1.3
Invertebrates sp.	2.1	2.1	18	10.4	18	11.6
Squid	0.6	0.6	2	1.2	2	1.3
Gastropoda	0.8	0.8	1	0.6	1	0.6
Shrimp	0.5	0.5	1	0.6	1	0.6
Nematoda	0.2	0.2	14	8.1	14	9.0

(7-42 cm FL) consumed more engraulids (74.3% by number) than the Atlantic fish, and also clupeids and labrids (10.6 and 0.9% by number, respectively) (Tables 3 and 4); the differences were not testable using Chi-square.

We also compared diet breadth (diversity) and overlap of mackerels collected in the Gulf of Mexico and along the Atlantic coast. Diet breadth (diversity, B) was higher for juveniles of both species from the Gulf of Mexico, however there was no consistent pattern for evenness (B/S) of the distribution of foods among categories for the two species and areas (Table 2). Diet overlap between the two species was greater for south Atlantic Ocean ($C_\lambda = 0.99$) than for the Gulf of Mexico ($C_\lambda = 0.53$) juveniles.

Although numerical proportions of the diet of both species were significantly different between the two areas studied, diet overlap calculations showed that the diet of juvenile Spanish mackerel was more similar (*i.e.*, had greater overlap) between the Gulf of Mexico and south Atlantic Ocean than the diet of juvenile king mackerel ($C_\lambda = 0.94$ for Spanish mackerel and 0.65 for king mackerel).

DISCUSSION

King and Spanish mackerel are principally piscivorous throughout life, beginning at a very small size and young age. Our results show that both species consumed mostly fish as larvae and post-larvae (2.8-22 mm SL), and juveniles (9-42 cm FL). The estimated age of the smallest larva (2.8 mm SL) was 3 days (DeVries *et al.* 1990). *Scomberomorus* spp. larvae over the Great Barrier Reef in Australia also fed almost exclusively on fish larvae (Jenkins *et al.* 1984). Saloman and Naughton (1983a and 1983b) and

Table 4. Diet of juvenile king and Spanish mackerel from the Gulf of Mexico. N = 61 king mackerel stomachs with food and 91 Spanish mackerel with food.

KING MACKEREL						
	Volume		Number		Freq. of Occurrence	
Food Item	(ml.)	%	No.	%	Freq.	%
Fishes	90.7	89.3	65	92.8	61	92.4
Unidentified	49.1	48.3	43	61.4	43	65.2
Clupeidae	14.5	14.3	3	4.3	3	4.5
Gerridae						
Eucinostomus sp.	12.5	12.3	2	2.9	2	3.0
Engraulidae	11.0	10.8	15	21.4	11	16.7
Anchoa sp.	2.6	2.6	3	4.3	1	1.5
Labridae	1.8	1.8	1	1.4	1	1.5
Synodontidae	1.8	1.8	1	1.4	1	1.5
Invertebrates						
Squid	10.9	10.7	5	7.1	5	7.8
SPANISH MACKEREL						
	Volume		Number		Freq. of Occurrence	
Food Item	(ml.)	%	No.	%	Freq.	%
Fishes	83.6	100.0	113	100.0	91	100.0
Unidentified	21.1	25.2	52	46.0	51	56.0
Clupeidae	27.7	31.0	12	10.6	9	9.9
Harengula sp.	1.8	2.2	1	0.9	1	1.1
Engraulidae	32.1	40.6	49	74.3	30	33.0
Anchoa sp.	29.5	35.3	35	30.9	18	19.8
Labridae	2.7	3.2	1	0.9	1	1.1

Naughton and Saloman (1981) reported mainly fishes in the diet of juvenile and adult king and Spanish mackerel from the Gulf of Mexico and Atlantic coast, and DeVane (1978) did also for adult king mackerel from North Carolina. The larvae, post-larvae, and juveniles of both species consumed mainly schooling prey (*e.g.*, clupeids, engraulids, carangids and squid) that inhabit the same pelagic realm that they inhabit. Spanish mackerel larvae and juveniles apparently eat more invertebrate prey than king mackerel. Juveniles of both species consumed a more diverse prey assemblage (*i.e.*, greater diet breadth, B) in the Gulf of Mexico, probably because juveniles are able to feed on a wider taxonomic array of prey than in the Atlantic Ocean. Similary, diet overlap (C_λ) among species was lower in the Gulf of Mexico, perhaps because in the Gulf of Mexico mackerels were able to utilize a wider variety of prey available in the Gulf of Mexico as compared to the U.S. south Atlantic.

The high rate of piscivory for *Scomberomorus* species is apparently not the case for species of the confamilial genus *Scomber*. Peterson and Ausubel (1984) reported phytoplankton remains in stomachs of the smallest *Scomber scombrus* (3.5-4.4 mm TL) from Long Island Sound, New York. Larvae >4.4 mm TL contained mostly larval copepods (nauplii and copepodites), while fish >6.0-6.4 mm TL ate some adult copepods; larvae >6.4-10.1 mm TL also contained mostly larval and adult copepods, but also other *S. scombrus* larvae. Last (1980) gave similar diet results for North Sea *S. scombrus*, but reported no piscivory. Pacific mackerel, *Scomber japonicus*, evidently have a similar diet; stomachs of larvae 3-16 mm SL contained mostly copepod larval stages, a few cladocerans, oikopleurans, gastropods, invertebrate eggs, diatoms

and one fish larva (Hunter and Kimbrell 1980).

Apparently, confamilial larval tunas are also not piscivorous to the extent that *Scomberomorus* larvae are. Young and Davis (in press) reported mostly adult and larval copepods in diets of *Thunnus maccoyi* (2.7-9.8 mm SL) from the Indian Ocean. Copepod nauplii were found mostly in larvae <5 mm SL, and fish only in larger larvae (>7 mm SL for *T. maccoyi* and >5.5 mm SL for *K. pelamis*).

Limitations in the data make it difficult to interpret diet similarities and/or differences among species. Many of the larvae, post-larvae and juveniles reported on here came from different samples, therefore it is not possible to rigorously determine if diet differences reflect active resource partitioning or differences in prey availability. Larval and post-larval king mackerel and Spanish mackerel have been relatively rare in ichthyoplankton collections (Grimes *et al.* 1990; Collins and Stender 1987). The same is true for juvenile king mackerel (Grimes *et al.* 1990; Collins and Wenner 1988).

Because larvae and post-larvae feed primarily on other fishes, hydrographic phenomena that concentrate ichthyoplankton can create enhanced feeding opportunities for young mackerels. For example, hydrodynamic convergence at the Mississippi River plume front in winter and late summer accumulates ichthyoplankton up to several orders of magnitude higher at the front than in adjacent non-frontal areas (Govoni *et al.* 1989; Grimes and Finucane in press). Thermal fronts associated with the Loop Current boundary also accumulate ichthyoplankton (Richards *et al.* 1988). Enhanced feeding opportunities in these microhabitats for piscivores like young mackerels could lead to enhanced growth, survival, and recruitment.

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