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Nursery Habitat and Diet of Juvenile *Centropomus* Species in Puerto Rico Estuaries

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The distribution of the early stages of five species of *Centropomus* was studied in Puerto Rico and varied among the estuarine areas sampled. Based on the collection of 4,710 juvenile snook, the study showed that the most abundant species (standard length < 50 mm) collected in river systems was *C. parallelus* (81%); in contrast, *C. undecimalis* (62%) and *C. ensiferus* (35%) were more abundant in lagoon systems. Colonization peaks of the three most abundant species showed broad overlapping: from June to Nov. for *C. undecimalis*, from July to Dec. for *C. ensiferus*, and from April to Nov. for *C. parallelus*. Preferred nursery habitats were turbid, calm waters in the vicinity of shelter (mangrove roots, grass, or water hyacinths). The physical parameter range of juvenile snook habitat was relatively broad: salinity from 0 to 30 ppt temperature from 24 to 35 C, and anoxic to well-oxygenated water. Condition factors of two size classes of snook (less than 100 mm and between 100 and 300 mm in standard length) showed no significant differences between river and lagoon systems or between seasons. Food habits were significantly different between species during the early stages (standard length < 100 mm), but this difference was resolved when river and lagoon samples were studied separately. In the river system, *C. undecimalis* and *C. ensiferus* preyed primarily upon shrimp, whereas in the lagoon they fed mainly on fish.

The genus *Centropomus* (Perciformes), commonly known as snook, consists of 12 species confined to the tropics and subtropics of South and North Americas. Rivas (1986) described six species in Pacific and six in Atlantic waters, none of which occurs in both oceans. Among the Atlantic species, *C. poeyi* Chavez (Mexican snook) has a very limited distribution in Mexico. The other five, *C. undecimalis* (Bloch) (common snook), *C. ensiferus* Poey (swordspine snook), *C. parallelus* Poey (fat snook), *C. pectinatus* Poey (tarpon snook), and *C. mexicans* Bocourt (large-scale fat snook), are distributed between latitudes 30°N to 30°S. *Centropomus undecimalis* has the largest range, from north Florida (U.S.A.) to Brazil. *Centropomus* distribution is partly explained because they are stenothermic and do not survive at temperatures below 15 C (Shafland and Foote, 1983). Moreover, they are euryhaline, diadromous, estuarine-dependent, and not found in islands deprived of permanent streams (Rivas, 1986). They are also related to areas with mangroves (Rivas, 1986) and seagrass beds (Gilmore et al., 1983). Snook are known to spawn near shore, close to estuaries. After hatching, larvae drift with the currents inshore and colonize shallow and protected estuarine areas (Lasserre and Toffart, 1977; Gilmore et al., 1983; McMichael et al., 1989).

Four snook species were reported in Puerto Rico (Erdman, 1974), the most southern island of the Greater Antilles. The fifth species, *C. mexicanus*, has not been reported in the island, except by Rivas (1986), in which *C. mexicanus* was plotted on the map of Puerto Rico but no reference could be found in the text. *Centropomus undecimalis* is the largest (Table 1) and the most valuable species for recreational fishery, but all species are actively exploited by commercial fishermen throughout the year. None have been studied on the island until recently, and most studies done on this genus concern the biology or fishery management of *C. undecimalis* in Florida. With the exception of the taxonomic work done by Rivas (1986), virtually no information exists on the other four species.

The present study objectives are to 1) describe juvenile snook relative abundance in space and time and 2) define their nursery habitat preference and suitability.

Materials and Methods

Puerto Rico is located between 18°31′N and 17°55′N latitude and 65°37′W and 67°17′W longitude and is the easternmost and smallest island of the Greater Antilles.

Air temperature is almost constant throughout the year (25 ± 3 C), whereas precipitation accounts for a marked but irregular seasonality. Most rain falls from May through Nov. (wet season), and the driest period extends from

TABLE 1. Snook species characteristics from literature.[a]

			Cu	Cpl	Cpc	Cmx	Ce	Reference
Maximum length	SL (cm)		101.0	58.0	39.7	34.5	27.0	Rivas, 1986
First maturation								
Venezuela	TL (cm)	Female	44.1	27.0				Carvajal, 1975
		Male	36.0	28.0				
Mexico	SL (cm)	Female	38.8	15.0	29.7			Chavez, 1963
		Male	34.3	15.4	26.1			
Florida (U.S.A.)	FL (cm)	Female	40.0					Marshall, 1958
		Male	40.0					
Brazil	SL (cm)	Female		16.0				Radasewsky, 1976
		Male		24.0				
Brazil	SL (cm)	Female		30.0				Della-Patrona, 1984
		Male		23.0				

[a] Cu, *Centropomus undecimalis*; Cpl, *C. parallelus*; Cpc, *C. pectinatus*; Cmx, *C. mexicanus*; and Ce, *C. ensiferus*. SL, standard length; TL, total length; FL, fork length.

Dec. to April (dry season). These seasonal changes produce profound habitat modifications: whole systems (river or lagoon) can be temporarily cut off from the sea, substantial morphologic changes of the coastline occur with flooding conditions, and vegetation can invade or be flushed out with drainage water (e.g., water hyacinths in freshwater systems).

Since juvenile snook are known to be estuarine-dependent, four estuarine systems were sampled, including two rivers and two lagoons for comparison purposes (Fig. 1).

Site 1—Añasco River (ANA) is a large river (6 m wide, 3.5 m deep) receiving several irrigation canals. Its drainage basin is 360 km^2 and its average discharge is 8.8 m^3/sec (Curtis et al., 1991). The river is annually invaded by water hyacinths during spring months.

Site 2—Corazones Lagoon (COR) is a 0.5 km^2 saltwater lagoon surrounded by 8.3 km^2 of black and red mangroves. This lagoon is closed to the sea most of the year, but opens during flooding season.

Site 3—Guanajibo River (GUA) is characterized by a narrow (3 m) and deep (4.5 m) section. Its drainage basin is 311 km^2 and its average discharge is 6 m^3/sec. Like Añasco River, Guanajibo is regularly invaded by water hyacinths, and its mouth is completely obstructed by trees, bamboo trunks, and other debris at the end of the dry season.

Site 4—Boquerón system (BOQ) is composed of different wetland areas: Rincon Lagoon (7.5 km^2 and 0.75 m of average depth) is open to the sea by a deep canal. It receives, through its drainage channel, a continuous freshwater input from adjacent fields or, occasionally, from an impoundment when gates overflow. The surrounding vegetation is composed mostly of red mangrove. The impounded area (17 km^2) used as bird refuge, is filled with freshwater. Vegetation is composed primarily of red mangrove and cattail. The backwater area (about 7 km^2) is characterized by shallow waters (0.5 m deep) and salinity comprised from fresh to hypersaline depending on season. The vegetation, from thick red mangrove near the lagoon, becomes more sparse and composed of black mangrove as it reaches dry areas.

From May 1992 to Dec. 1994, collections of snook were made monthly in the four systems. Several sampling techniques were used depending on the collection site (Fig. 1). A small bag seine (8 m length, 1.3 m height, 1.5 mm square mesh) was used for beaches, small pools, creeks, and mud flats ranging from 50 to 150 cm deep (black circles). As a standard effort, sites were seined three times. Trap nets (aisle: 7 m long, 3 mm square mesh; bag: 3 m long, three hoops built with funnels) were set 3 hr during flood tide, blocking small creeks or canals (black triangles). Short-panel gill nets (3–6 m long; 12, 25, and 50 mm square mesh) were deployed in front of the trap nets to prevent entrance of predators. In addition to monthly collection, exploratory sampling (white circles and triangles) was used to determine the presence of snook. This sampling consisted of rotenone poisoning in mangrove roots and canals (2 g of 5% powdered rotenone in 1 m^3 of water), cast netting (radius = 1.5, 2.1, or 2.4 m) in open water, and seining along mangrove banks (white circles). In exploratory sites (white triangles), experimental

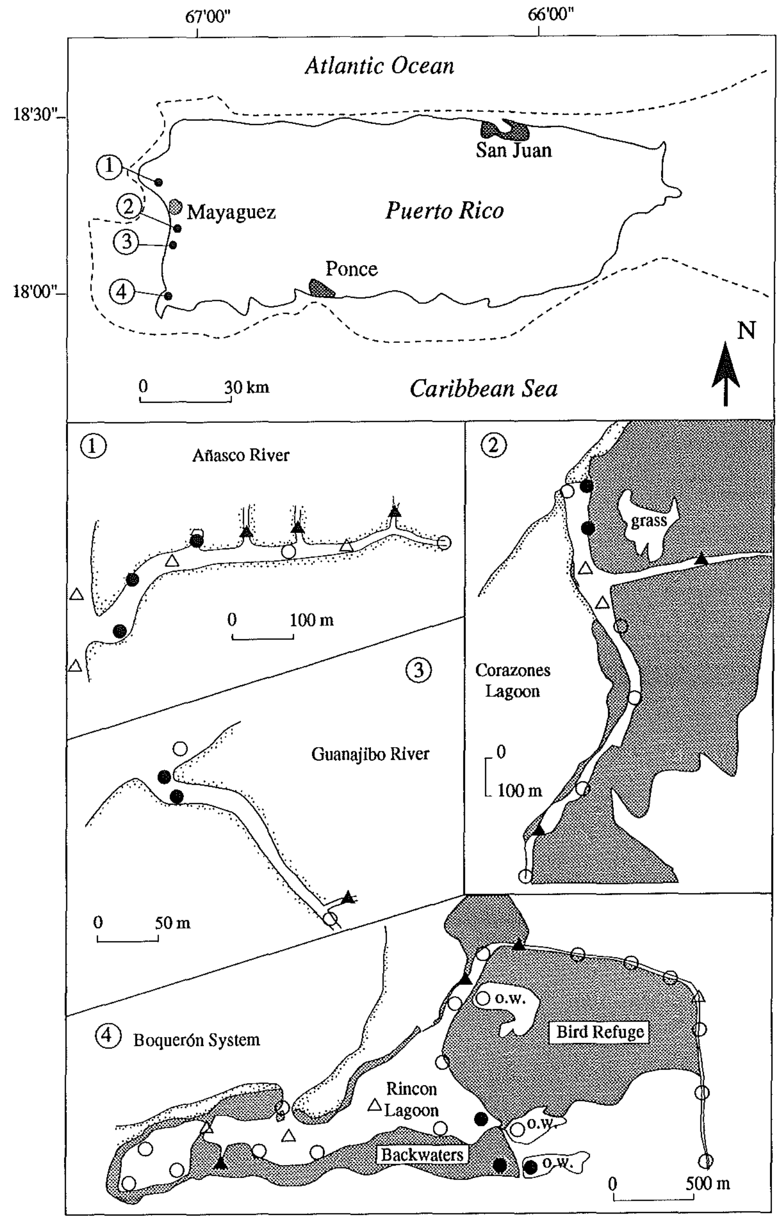

Fig. 1. Location of collection sites in western Puerto Rico: (1) Añasco River, (2) Corazones Lagoon, (3) Guanajibo River, and (4) Boquerón System. The dashed line represents the limit of the continental shelf. White symbols represent exploratory collection sites; black symbols represent monthly survey collection sites. Circles represent collection made by active sampling (seine, cast net, rotenone poisoning) and triangles represent collection made by passive sampling gear (trap net, gill net).

gill nets (30-m long net composed of three panels of 12, 25, and 50 mm square mesh) were also deployed seaward of river mouths or in lagoons. Only snook caught in the monthly survey were used in the data analyses.

Water depth, water clarity (Secchi), temperature, pH, dissolved oxygen, and salinity where measured concurrently during fish sampling to characterize habitat type. Means of these physical parameters were compared using a Student's t-test to define the preferred habitat of a given species.

Collected fish were either released in the field (about 40%) or put immediately on ice and kept frozen before processing. Released fish were measured in standard (SL) and total

TABLE 2. Relative abundance of snook species in two lagoons (Boquerón and Corazones) and two rivers (Añasco and Guanajibo) of Puerto Rico (1992–94 samples combined).[a]

	C. undecimalis		*C. ensiferus*		*C. parallelus*		*C. mexicanus*		*C. pectinatus*	
	n	%	n	%	n	%	n	%	n	%
Boquerón	1,323	61.4	732	34.0	57	2.6	32	1.5	9	0.4
Corazones	314	37.8	493	59.3	15	1.8	7	0.8	2	0.2
Guanajibo	60	40.0	1	0.7	86	57.3	3	2.0	0	0.0
Añasco	186	11.8	299	19.0	954	60.5	112	7.1	25	1.6
Total	1,883	40.0	1,525	32.4	1,112	23.6	154	3.3	36	0.8

[a] Chi square = 2,563; $P < 0.0001$; n = 4,710.

length (TL) to the nearest millimeter. Fish processed at the laboratory were also measured to the nearest millimeter, then weighed to the nearest 0.01 g. Length given in this article will be standard unless stated otherwise.

Snook species, for individuals larger than 100 mm were identified according to the systematic review of Rivas (1986). For early juvenile snook, this key is no longer applicable, and a new key based on meristic ratios and pigmentation was built (in preparation for publication). A few individuals were identified using allozyme electrophoresis analysis, following the procedure described by Bert (1986).

Condition factor (C) was calculated using the formula: $C = W/W_{est} \cdot 100$, where W = wet weight (g), and W_{est} is the estimated weight calculated from the weight–length relationship ($W = aL^b$). Only fish measured at the laboratory were used in this analysis and grouped in two size classes (SL < 100 mm or 100 ≤ SL < 300 mm). Condition factors were compared between systems (lagoon/river) and between seasons (wet/dry) using a two-way ANOVA.

Stomach contents were examined and grouped into the following categories: fish, shrimp, crab, insect, zooplankton, or detritus. Only snook captured with a seine were included in this analysis to avoid stomach spoiling in passive gear such as trap nets or gill nets. Prey category occurrence (number of times a prey category was found) was used to identify juvenile snook diet. To identify onthogenetic shifts in diet, snook juveniles were categorized in 10 size class groups of 30-mm increments. For each species, prey category occurrence was analyzed using a clustering method [centroid method with a squared Euclidean distance, Sokal and Michener (1958)]. Prey category occurrences were compared among snook species at given size classes using a chi-square test. Because food habit may be a function of habitat resources, prey category occurrences among two snook species (*C. undecimalis* and *C. ensiferus*) were compared within the same estuarine system (e.g., Guanajibo and Añasco combined for rivers; Corazones and Boquerón combined for lagoons) (chi-square test).

RESULTS

During 1992–94 sampling, 4,710 snook juveniles were collected: 40% *C. undecimalis*, 32% *C. ensiferus*, 24% *C. parallelus*, 3% *C. mexicanus*, and <1% *C. pectinatus* (Table 2). *Centropomus mexicanus* was positively confirmed as a different species from *C. parallelus* with the allozyme electrophoresis analysis.

Relative abundance of snook species caught in the four sampling systems is shown in Table 2. Since all snook had similar shape and presumably the same behavior, there was no reason to suspect different selectivity among snook species for a given sampling method. Assuming that sampling bias was similar for the different species of snook, a comparison between their relative abundance was processed. Relative abundance among the systems was significantly different ($P < 0.0001$, n = 4,710, chi-square = 2,563).

Species distribution was analyzed by size class in Boquerón Lagoon and Añasco River systems where sufficient data were collected (Table 3). For size class <50 mm, *C. undecimalis* was more abundant in Boquerón (62% of the snook catch), whereas *C. parallelus* was more abundant in Añasco (81%). Between 50 to 150 mm, the ranks remained in Boquerón but changed in Añasco—*C. ensiferus* representing 56%. For SL ≥ 150 mm, a similar distribution was observed between snook species in Boquerón, whereas in Añasco, *C. undecimalis* composed most of the sample (47%).

Bimonthly frequencies of *C. undecimalis*, *C. ensiferus*, and *C. parallelus* observed in 1992, 1993, and 1994 are presented in Figure 2. Data from river and lagoon were combined and months pooled in pairs for clarity of the graphs. According to our sampling, snook (any species) arrived at the nursery ground as small

TABLE 3. Relative abundance of snook species, separated in three size classes (SL in mm), observed in two systems (Boquerón Lagoon, BOQ; Añasco River, ANA) (1992–94 samples combined).

	C. undecimalis		*C. ensiferus*		*C. parallelus*		*C. mexicanus*		*C. pectinatus*	
	n	%	n	%	n	%	n	%	n	%
BOQ										
SL < 50	1,024	62.2	569	34.5	36	2.2	18	1.1	0	0.0
50 ≤ SL < 150	240	70.0	86	25.1	9	2.6	8	2.3	0	0.0
SL ≥ 150	59	36.2	77	47.2	12	7.4	6	3.7	9	5.5
ANA										
SL < 50	50	5.1	37	3.7	805	81.3	81	8.2	17	1.7
50 ≤ SL < 150	43	11.1	217	56.1	106	27.4	13	3.4	8	2.1
SL ≥ 150	93	46.7	45	22.6	43	21.6	18	9.0	0	0.0

as 7 mm SL. The period of higher colonization for *C. undecimalis* lasted from June to Nov. and from April to Nov. for *C. parallelus*. For *C. ensiferus*, the colonization period occurred from July to Dec. in 1992 and 1994 but lasted only from May to Aug. in 1993.

Exploratory sampling in rivers generally found juvenile snook at the mouth and in adjacent irrigation canals close to floating or overhanging vegetation (water hyacinth, bamboo, or dead trees). All five species were found at the mouth, whereas only *C. parallelus* was

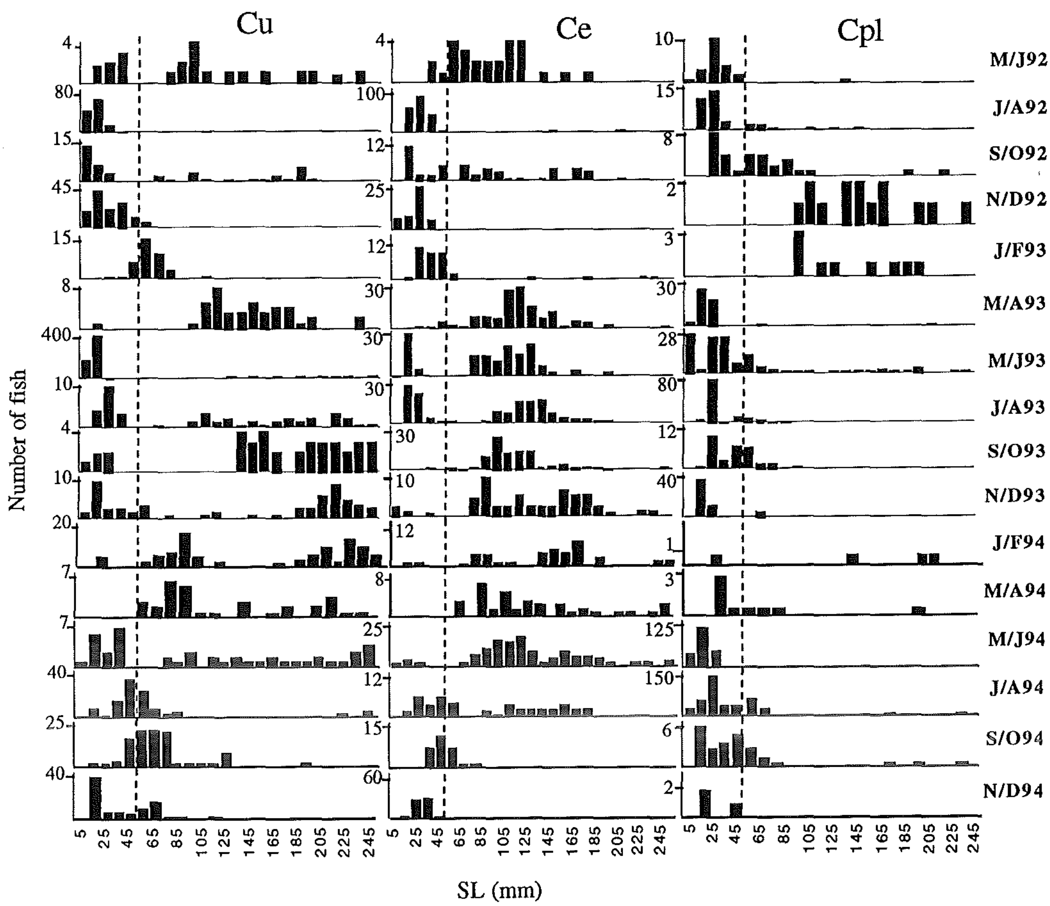

Fig. 2. Pooled bimonthly size frequencies of snook species observed from May 1992 to Dec. 1994 from Puerto Rico (dashed lines give the 50-mm size limit). Cu, *C. undecimalis*; Ce, *C. ensiferus*; Cpl, *C. parallelus*.

TABLE 4. Habitat description for snook juveniles < 50 mm SL.[a]

	Species	n	$\bar{x}$	SD	Range
Depth (cm)	Cu	500	76	142.0	17–175
	Ce	380	91	106.0	25–175
	Cpl	350	93	87.0	17–125
Secchi (cm)	Cu	500	34.5	70.0	10–125
	Ce	380	53	76.6	10–125
	Cpl	350	34.3	69.5	10–96
Temperature (C)	Cu	500	28	11.0	23–35.5
	Ce	380	27	4.8	23–35.3
	Cpl	350	26.5	4.8	24–33
Salinity (ppt)	Cu	500	10	30.6	0–34.2
	Ce	380	10	19.0	0–28.2
	Cpl	350	1.2	15.6	0–34.2
D.O. (% saturation)	Cu	500	41	156.0	3–160
	Ce	380	28.5	57.0	5–160
	Cpl	350	62	62.0	5.5–87

[a] Cu, *Centropomus undecimalis*; Cpl, *C. parallelus*; Cpc, *C. pectinatus*; Cmx, *C. mexicanus*; and Ce, *C. ensiferus*. SD, standard deviation; D.O., dissolved oxygen (percentage of saturation).

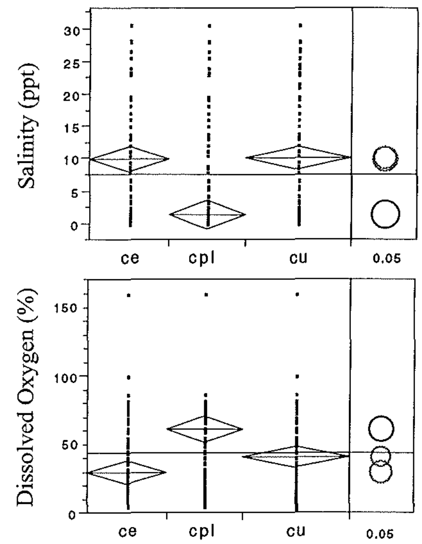

Fig. 3. Preferred habitat features of snook species: distribution, mean (horizontal bar), and 95% confidence interval (diamond) of salinity and dissolved oxygen observed for *C. ensiferus* (Ce), *C. parallelus* (Cpl), and *C. undecimalis* (Cu). Student's t-test is significant if circles are separate.

found upriver, well above the limit of the saltwater wedge. In lagoons, juvenile snook usually were found in some type of refuge: shallow waters, mangrove roots, small channels, or backwater areas. Rarely did exploratory sampling reveal the presence of juveniles in open waters or at the mouth of the lagoon.

Physical parameters of depth, Secchi, temperature, salinity, and dissolved oxygen where early juveniles were caught (500 *C. undecimalis*, 380 *C. ensiferus*, and 350 *C. parallelus*) are summarized in Table 4. All three species had parameter ranges rather broad and similar: salinity from 0 to 28–30 ppt; dissolved oxygen from anoxic to well-oxygenated habitat, and temperature from 24 to 35° C. These data showed that snook early juveniles have a high tolerance to varying habitats.

The results of a Student's t-test relating physical parameters to the preferred habitat of a species are presented in Figures 3 and 4. *Centropomus parallelus* habitat was characterized by low salinity and high dissolved oxygen (mean significantly different than two other species, $P < 0.05$). This result was expected since they were found primarily in rivers. *Centropomus ensiferus* was found in water significantly clearer (Secchi) than for two other species ($P < 0.05$) and with lower dissolved oxygen, even though it was not significantly different than that of *C. undecimalis*. For *C. undecimalis*, only the temperature was higher than for the two others ($P < 0.05$); this species did not show any other preferences.

Condition factors (C) were calculated for

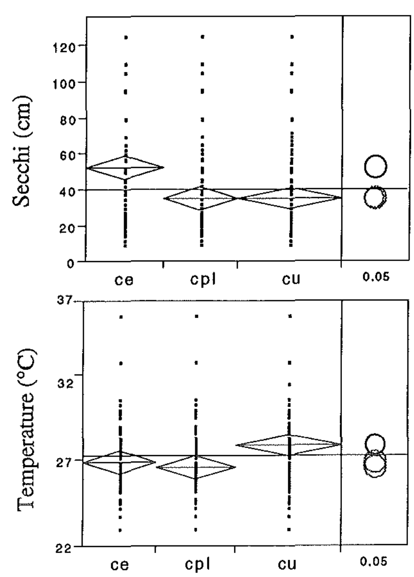

Fig. 4. Preferred habitat features of snook species: distribution, mean (horizontal bar), and 95% confidence interval (diamond) of Secchi and temperature observed for *C. ensiferus*, *C. parallelus*, and *C. undecimalis*. Student's t-test is significant if circles are separate.

TABLE 5. Condition factor (C) comparisons among systems (river/lagoon) and seasons (wet/dry), for *C. undecimalis* (Cu), *C. ensiferus* (Ce), and *C. parallelus* (Cpl) in two size classes (SL < 100 mm and 100 ≤ SL < 300 mm) (two-way ANOVA).[a]

		CU (n = 274)		Ce (n = 274)		Cpl (n = 96)	
SL < 100 mm	df	F	*P*	F	*P*	F	*P*
System	1	2.34	0.13	1.59	0.21	0.08	0.78
Season	1	1.28	0.26	0.22	0.64	2.40	0.12
		CU (n = 220)		Ce (n = 289)		Cpl (n = 64)	
100 ≤ SL < 300 mm	df	F	*P*	F	*P*	F	*P*
System	1	2.86	0.09	0.02	0.89	0.60	0.44
Season	1	2.50	0.12	0.67	0.41	1.41	0.24

[a] $P > 0.05$ shows no significant effect in the model.

fish < 100 mm (SL) and fish from 100 to 300 mm (SL). Comparisons between river and lagoon systems and between seasons, through a two-way ANOVA, provided the results presented in Table 5. The analysis concludes that for both size classes neither system nor season has an effect on the condition factor of snook ($P > 0.05$).

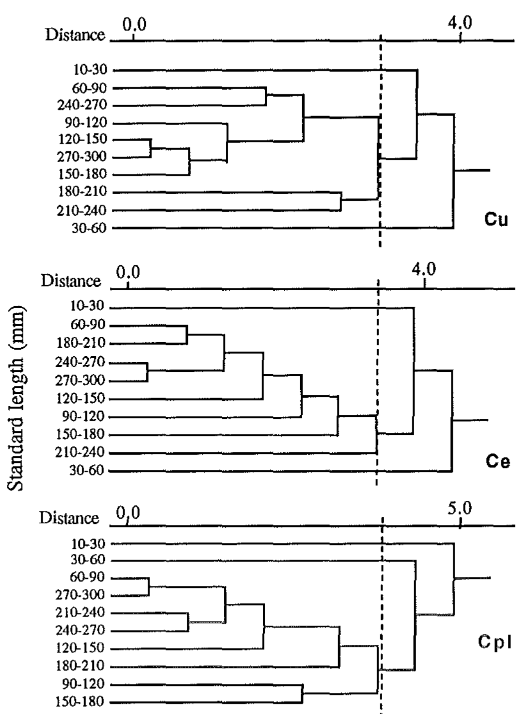

Fig. 5. Size class clustering results based on prey category frequency of occurrence. Snook standard length observations were first pooled in 10 classes of 30-mm intervals. The dashed line represents when the first two size classes split from the rest of the size classes (see text for further explanation).

Food habits were studied for snook juveniles (SL < 300 mm). Among 439 *C. undecimalis,* 444 *C. ensiferus,* and 171 *C. parallelus* stomachs examined, empty stomachs represented 39%, 47%, and 28%, respectively.

The results from clustering analyses of prey composition among snook species are given in Figure 5. In all the snook species studied, major change in diets occurred at size classes 10–30 mm and 30–60 mm. At 10–30 mm, *C. undecimalis* and *C. ensiferus* were mainly planktivorous. At 30–60 mm, most individuals of these two species started to diversify their diet by including fish and shrimp, and at 60 mm they ceased to consume zooplankton. At 10–30 mm, *C. parallelus* consumed a variety of prey taxa, with shrimp already being regular prey.

Small *C. undecimalis* and *C. ensiferus* of 12.5 and 17 mm (respectively) ate shrimp, and later fish, at 20 and 29 mm (respectively). *Centropomus parallelus* ate shrimp as small as 11 mm and fish at 15 mm. The upper limit for planktivory was 59 mm for *C. undecimalis,* 48 mm for *C. ensiferus,* and 28 mm for *C. parallelus.* Later, they all switched to fish and shrimp, occasionally consuming crabs, mollusks or insects.

At SL < 30 mm, snook species did not show the same food habits (chi-square = 53, $P < 0.0001$); *C. parallelus* ate mainly fish and shrimp (n = 54), whereas *C. undecimalis* (n = 56) and *C. ensiferus* (n = 22) fed primarily on plankton. For snook 30–60 mm SL, the difference in food habits decreased, but was still significantly different (chi-square = 39, $P < 0.05$; *C. undecimalis* n = 35, *C. ensiferus* n = 58, and *C. parallelus* n = 41). *Centropomus parallelus,* in this size range, had shrimp as the most frequent food item. After 60 mm, differences continued to decrease between snook food habits, but still remained significantly different (chi-square = 16, $P < 0.05$; *C. undecimalis* n = 160,

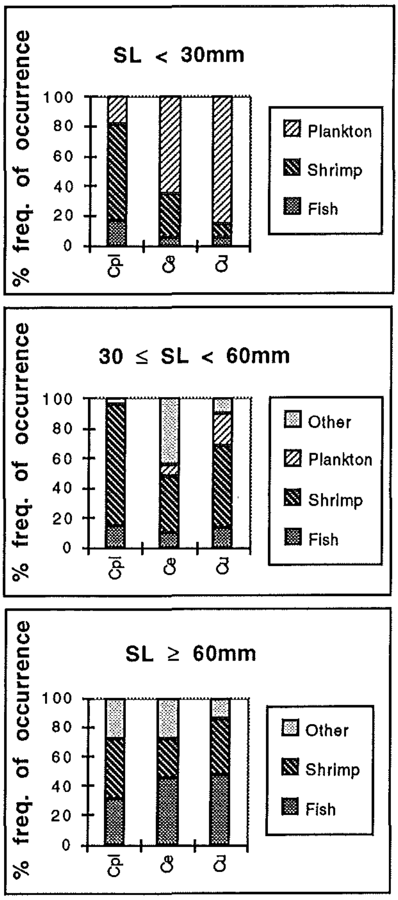

Fig. 6. Food habits (% frequency of occurrence) of *C. undecimalis, C. ensiferus,* and *C. parallelus* for individuals of three size ranges.

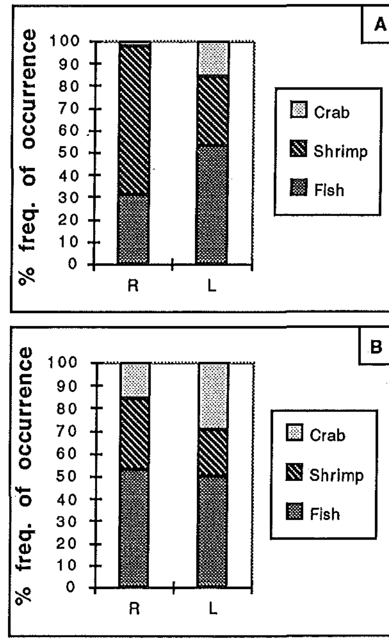

Fig. 7. Food habits (% frequency of occurrence) of *C. undecimalis* (A) and *C. ensiferus* (B) collected in either river (Añasco and Guanajibo—R) or lagoon (Corazones and Boquerón—L).

C. ensiferus n = 155, and *C. parallelus* n = 28). To illustrate food composition of the three size classes of snook, prey occurrences, expressed as percentages, are shown in Figure 6.

Stomach contents were compared between two snook species (size range 60–300 mm) collected in rivers (*C. undecimalis* = 46, *C. ensiferus* = 32) and in lagoons (*C. undecimalis* = 134, *C. ensiferus* = 123). *Centropomus parallelus* was not compared because not enough data were available for this analysis. The dominant prey item found in stomachs of snook captured in lagoons was fish (Fig. 7). When comparing the two species' diet, no significant difference was found (chi-square = 5.8, $P > 0.05$). In rivers, the main food item was shrimp, and a comparison between *C. undecimalis* and *C. ensiferus* also showed no significant difference (chi-square = 4.7, $P > 0.05$).

Discussion

Although four snook species were previously reported for Puerto Rico (Erdman, 1974; Martin and Patus, 1984), a fifth species, *C. mexicanus,* was confirmed during this study. Three species were abundant (*C. undecimalis, C. ensiferus,* and *C. parallelus*), while *C. pectinatus* remained extremely rare. In Florida, four snook species are reported, but one is most abundant (*C. undecimalis*), probably because Florida is the northern limit of the other three species. In Mexico, four species coexist: *C. undecimalis, C. parallelus, C. pectinatus,* and *C. poeyi* (Chavez, 1963), but only *C. undecimalis* and *C. poeyi* are relatively abundant (Chavez, 1963; Fuentes, 1973; Carvajal, 1975). In Brazil, the same snook species that occur in Puerto Rico are represented, but only *C. undecimalis* and *C. parallelus* are believed to be common (Vasconcelos Filho and Braga Galiza, 1980). In contrast, *C. undecimalis,* although abundant, represented only 40% of all the snook captured in our study. Being the largest snook species, *C. undecimalis* is probably more affected by reduced habitat and overfishing than the other, smaller species. In Puerto Rico, 50% of the mangrove habitat has been lost during the 1940s to 1970s (Lugo, 1988), and the level of fishing mortality upon adult snook is consistently intense (Nieves-Figueroa, 1987).

That 32% of our samples is composed of *C. ensiferus* is revealing since this species is not widely known. *Centropomus ensiferus* has been previously reported in ichthyological check lists (Puyo, 1949; Cervigon, 1966; Austin, 1971; Erdman, 1974; Castro-Aguirre, 1978; Rivas, 1986), but never studied in depth. Since *C. ensiferus* is the smallest snook species in Puerto Rico, finding it in abundance further reinforces the hypothesis that large *Centropomus* individuals are overfished in Puerto Rico. *Centropomus ensiferus* probably is less targeted by commercial fishermen, who regularly employ large-mesh (75 mm) gillnets.

Spatial and Temporal Distribution.—Early juvenile *C. parallelus* (SL < 50 mm) showed a clear preference for freshwater habitat, compared to *C. undecimalis* or *C. ensiferus*, which were more abundant in saltwater lagoon systems. As previously reported, *C. parallelus* was more common in freshwater systems than any other snook species (Rivas, 1986). In larger individuals, the pattern changed, and after *C. undecimalis* reached 250 mm, it could be found in any system. For *C. undecimalis*, the distribution differed from that described by Gilmore et al. (1983). These authors reported that, in Florida, early juvenile *C. undecimalis* (SL $\bar{x}$ = 27.5 mm) occurred mostly in freshwater tributaries, while older juveniles (SL $\bar{x}$ = 67 mm) inhabited marsh habitat for a few weeks and then migrated to seagrass beds (SL $\bar{x}$ = 240 mm). No such pattern was found in our study.

Colonization of the three most abundant snook species overlapped, with a common peak occurring from June to Aug. A period of no colonization was limited to a few months (Jan.–April for *C. undecimalis*, March–April for *C. ensiferus*, Jan.–Feb. for *C. parallelus*) and occurred during the dry season. If high colonization coincided with the rainy season, it coincided also with increased habitat accessibility (connection of lagoon to sea, such as Corazones, or connection of the backwater area in the Boquerón system) and an increase in food resource (e.g., bloom of shrimp larvae in rivers observed in our seine samples).

The broad range of colonization for *C. undecimalis* was described in other works: from Aug. to Oct. in Mexico with a minimum size of 45 mm SL (Chavez, 1963); from April to Jan. on the east coast of Florida when 15–20-mm SL juveniles were recruited into freshwater and brackish habitats (Gilmore et al., 1983; Tucker and Campbell, 1988); and from July to Dec. on the west coast of Florida when colonization of <30-mm SL juveniles were observed (McMichael et al., 1989). Colonization for *C. parallelus* juveniles in Mexico has been reported from June to Nov. (Chavez, 1963), which is very similar to the present study. Unfortunately, no reference on *C. ensiferus* colonization was found for comparison with our findings. Of the three species of snook, *C. ensiferus* exhibited more interannual variability in its colonization pattern, which suggested that it may be more sensitive to environment changes (e.g., interannual climatic variability).

Preferred habitat description.—Previous studies have shown that snook species are tolerant of a wide range of environmental parameters [*C. undecimalis* (Chavez, 1963; Fore and Schmidt, 1973; Gilmore et al., 1983), *C. parallelus* (Della-Patrona, 1984), *C. ensiferus* (Austin, 1971)]. Even though temperature in estuarine waters of Puerto Rico is not limiting for snook distribution and *Centropomus* spp. can stand a wide change in salinity, the spatial distribution was unequal among the species studied. The preferred habitats could be described as well-oxygenated freshwater for *C. parallelus*; low-oxygen and turbid water for *C. ensiferus*, and no real preference for *C. undecimalis.*

Habitat use and benefits.—Stomach content analyses showed that prey composition was different among species at various stages of their lives. *Centropomus undecimalis* and *C. ensiferus* switched from a plankton diet (10–30 mm SL) to a diversified diet of fish, crustaceans, and mollusks (>60 mm SL), with a transitory stage of mixed prey of either plankton, crustaceans, or fish (30–60 mm). *Centropomus parallelus* were found to be the earliest species (as small as 15 mm) to switch from plankton to fish and shrimp. In that regard, these results differ from those of Della-Patrona (1984), who described *C. parallelus* as nonpiscivorous until 120 mm SL. *Centropomus undecimalis* fed on fish at 20 mm SL, which differs from the results of Gilmore et al. (1983) in Florida, where *C. undecimalis* became piscivorous at 11 mm SL (preying upon neonatal *Gambusia affinis*).

The differences in diet among snook species decreased with increased size, when all three species fed upon fish, shrimp, crabs, or insects. A comparison test among species found a significant difference for food items, with the *C. parallelus* diet composed mainly of shrimp. However, this difference disappeared when river and lagoon samples were studied separately.

In the river system, *C. undecimalis* and *C. ensiferus* preyed primarily upon shrimp; while in the lagoon, they fed on fish. *Centropomus undecimalis* in freshwater tributaries of Florida preyed principally upon fish and secondarily on shrimp and microcrustaceans (Gilmore et al., 1983). The similarity in diet among snook species within a system suggest they all fed basically on the most abundant prey item. This is supported by the fact that in rivers most of the by-catch biomass from exploratory sampling was composed of shrimp. Thus, ontogenetic changes in juvenile snook seemed largely related to changes in food abundance within a habitat. Moreover, the condition factors of all snook species studied remained high among the different systems, suggesting that they were able to find sufficient food. As a consequence, it is reasonable to believe that snook species adapt well to different habitats and do not seem to suffer from competition among themselves.

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