

TROPHIC ONTOGENY OF THE LEOPARD SEAROBIN, *PRIONOTUS SCITULUS* (PISCES: TRIGLIDAE)

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ABSTRACT

Ontogenetic feeding changes of the leopard searobin, *Prionotus scitulus*, from Tampa Bay, Fla., showed a shift from planktonic and epifaunal prey in small fish to infaunal prey in larger fish. Smaller fish utilized larval crustaceans, nauplians, brachyurans, cumaceans, copepods, and gammarid amphipods while larger fish showed increasing reliance on the lancelet, *Branchiostoma floridae*.

Biomass and linear dimensions of prey increased exponentially with fish size for larger fish, but were relatively constant for small fish. Relative prey biomass was lowest for intermediate-sized *P. scitulus* (65-95 mm) and increased for both large and small predators so that small individuals were most similar to very large fish in terms of relative prey size.

The switch to larger prey was preceded by rapid increases in mouth size and intestinal length, and was followed by attainment of minimum reproductive size and greater body weight per unit length.

Spatial and trophic partitioning appear quite efficient in reducing potential intraspecific competition.

Our present understanding of energy resource partitioning among metazoans is based primarily on food analyses. However, the study of trophic relationships among fishes is frequently complicated by indeterminate growth and the cooccurrence of several size classes of a species at a single locality.

A significant degree of prey variability of fishes may be due to size related changes. For instance, Darnell (1958) and Carr and Adams (1973) demonstrated changes in food habits with increasing size for numerous juvenile marine fishes, and Northcote (1954), Ivlev (1961), Keast and Webb (1966), Wong and Ward (1972), and others have shown a close relationship between morphology (in particular mouth size and shape) and prey kind or size. Such results indicate that inter- and intraspecific partitioning of energy resources in fish biofacies vary with fish size.

This study examines ontogenetic changes in trophic biology of the leopard searobin, *Prionotus scitulus* Jordan and Gilbert, a common nearshore benthic fish in the eastern Gulf of Mexico. Morphological and developmental attributes of jaw size, intestinal length, growth, reproduction, and distribution are evaluated in relationship to trophic changes and to intraspecific resource partitioning.

MATERIALS AND METHODS

I collected *P. scitulus* from three locations in Tampa Bay, Fla. (Figure 1). Numbers of fish collected and inclusive dates for each station were: Station 1, 489 specimens, July 1972-July 1973; Station 2, 838 specimens, August 1972-July 1973; Station 3, 690 specimens, April 1972-July 1973.

I examined stomachs from 650 specimens of *P. scitulus* from Station 3, collected monthly from April 1972 to May 1973. I also identified stomach contents of fish from August 1972 collections from

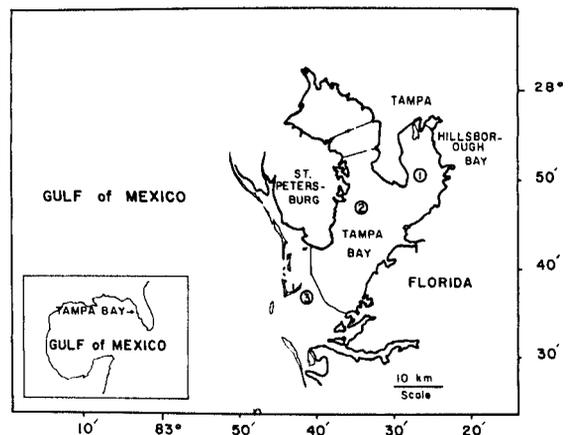


FIGURE 1.—Collection localities of *Prionotus scitulus* in Tampa Bay, Fla., 1972-73.

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Station 2 ($N = 22$) and November and July collections from Station 1 ($N = 122$). A total of 469 stomachs (72%) from all stations contained food items. April and May collections at Station 3 were made during the day; all other collections were from 1 to 5 h after sunset which was near the end of the greatest diel feeding activity. Ross (1977) demonstrated that searobins from the West Florida Shelf, including *P. scitulus*, had their greatest feeding activity during the day, but retained full stomachs through midnight.

Collection depths averaged 5, 5, and 7 m, respectively, for Stations 1-3. Sampling gear was a 3.6-m otter trawl with 2.5-cm stretched mesh and a 0.5-cm cod end liner. Upon capture I injected all specimens intraperitoneally with 10% Formalin.² Fish were fixed for 2 wk in 10% Formalin and then washed and transferred to 40% isopropanol for storage.

I sorted prey by taxa from each 10-mm size class of fish and measured a random sample ($n \leq 25$) of each prey kind to the nearest 0.1 mm along the axis of greatest dimension. The level of prey identification used in comparisons of size groups was the lowest taxon which was regularly identifiable for each prey kind. Since polychaetes were generally fragmented, they were not measured. Mean number of prey per fish was based only on fish which contained food items.

I used a volume displacement technique to measure food items $>0.05 \text{ cm}^3$ and a squash technique, modified from Hellowell and Abel (1971), to measure volume of food items $<0.05 \text{ cm}^3$ (Ross 1974). To establish minimum sample sizes for description of the ration I used the criterion t , obtained by plotting cumulative trophic diversity (H_k) against cumulative stomachs examined (k). Actual numbers of stomachs (k) varied between samples but had a lower limit of 17. The value of k was greater when specimens varied more in date or location of capture. Trophic diversity was determined by the Brillouin information function (H) according to Pielou (1966) and Hurtubia (1973). A horizontal asymptote, beginning at t , indicated a sufficient sample size so that examination of stomachs in excess of t would not yield an increase in trophic diversity.

To compare trophic differences of size groups of *P. scitulus* I used an unweighted pair group, arithmetic average (UPGMA) cluster analysis

(Sneath and Sokal 1973) based on a Czechanowski similarity matrix (Bray and Curtis 1957). All linear regressions were based on the Berkson case of a model I regression (Sokal and Rohlf 1969).

All fish lengths reported are standard length (SL), measured to the nearest 0.1 mm. Mouth width was measured externally between the posterior maxillary processes with the mouth fully closed. Internal mouth width was not routinely measured because of difficulty in working with preserved specimens. However, there was no difference between external mouth width with the mouth fully closed and internal mouth width with the mouth fully opened on 36 specimens favorable to such a comparison (two-tailed paired $t = 1.88$; $P > 0.05$). Measurement of mouth length followed Hubbs and Lagler (1958).

To measure intestinal length I cut the hindgut distally at the anus and freed the intestine from the investing mesentery. Length (to the nearest millimeter) was measured from the stomach with the intestine fully extended, but not stretched.

Wet weights of *P. scitulus* were taken to the nearest 0.1 g after removing stomach contents and blotting the specimens with absorbent paper. Ovaries and testes were removed, blotted, and weighed to the nearest 0.001 g. To compare levels of gonadal activity I used a gonadosomatic index ($GSI = (\text{gonad weight}/\text{somatic weight}) \times 100$).

RESULTS

Food Habits

The dominant prey of *P. scitulus* based on percent occurrence and percent volume was the lancelet, *Branchiostoma floridae*, which composed 61% of the food volume and occurred in 60% of the fish examined (Table 1). Numerically, cumaceans were dominant, making up 40% of the total number of prey. On the basis of percent number, volume, and occurrence, the ration of *P. scitulus* was composed primarily of lancelets, polychaetes, natantians, brachyurans, gammarid amphipods, cumaceans, pelecypods, copepods, and larval crustaceans. Ninety percent of the number of prey items and volume of prey items were accounted for by 6 and 7, respectively, of the 22 major food categories.

I examined seasonal feeding patterns of *P. scitulus* from Station 3, using fish 100 mm or larger to eliminate effects of fish size. *Branchiostoma floridae* occurred in over 50% of the fish in 8 of the

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Food items utilized by *Prionotus scitulus* collected between April 1972 and May 1973 at three stations in Tampa Bay, Fla. Based on 469 specimens containing food items.

Prey category	Percent occurrence	Number		Volume		Prey category	Percent occurrence	Number		Volume	
		no.	%	cm ³	%			no.	%	cm ³	%
Teleostei:						Penaeidae	8.4	99	0.50	2.42	3.68
Sciaenidae	0.2	1	0.01	0.06	0.09	<i>Lucifer faxoni</i>	1.3	13	0.07	0.02	0.03
<i>Prionotus scitulus</i>	0.4	2	0.01	0.15	0.23	Unidentified shrimp	17.4	111	0.60	1.18	1.80
All fishes	2.3	11	0.06	0.81	1.24	Natantian larvae	0.4	2	0.01	(¹)	
Amphioxii:						All shrimps	42.4	304	1.70	5.12	7.79
<i>Branchiostoma floridae</i>	59.5	1,171	6.50	39.77	60.49	Amphipoda:					
Hemichordata:						Gammaridea	56.1	4,615	25.6	2.44	3.71
Enteropneusta	0.6	3	0.01	0.02	0.03	Caprellidea	3.9	67	0.04	0.02	0.03
Echinodermata:						Isopoda	13.1	87	0.50	0.19	0.29
Ophiuræ	0.4	2	0.01	0.06	0.09	Cumacea	38.3	7,287	40.40	1.45	2.21
Brachyura:						Mysidacea	7.7	119	0.70	0.14	0.21
Portunidae	3.0	25	0.01	0.40	0.61	Leptostraca:					
Xanthidae	3.6	42	0.20	1.27	1.93	<i>Nebalia</i>	0.8	4	0.02	0.08	0.12
Grapsidae	0.9	35	0.20	0.58	0.88	Copepoda	12.8	2,882	16.00	0.12	0.18
Pinnotheridae	7.4	127	0.70	0.75	1.14	Ostracoda	8.8	83	0.50	0.07	0.11
Oxyrhyncha	0.2	1	0.01	0.01	0.02	Unidentified crustacea	5.1	363	2.00	0.03	0.05
Unidentified crabs	13.9	138	0.80	1.56	2.37	Acarina:					
Brachyuran megalops	8.4	140	0.80	0.11	0.17	Hydracarina	0.4	2	0.01	(¹)	
All crabs	44.6	507	2.82	4.70	7.13	Pycnogonida	0.2	1	0.01	(¹)	
Anomura:						Annelida:					
<i>Euceramus praelongus</i>	9.4	71	0.40	0.58	0.88	Polychaeta	36.2	(²)		9.11	13.86
Paguridae	0.4	2	0.01	0.12	0.18	Mollusca:					
Natantia:						Pelecypoda	22.1	356	2.00	0.78	1.19
<i>Leptochela serratorbita</i>	4.9	45	0.20	0.79	1.21	Gastropoda	4.9	52	0.30	0.13	0.20
Palaemonidae	2.4	11	0.06	0.05	0.08	Brachiopoda	0.2	1	0.01	0.01	0.02
Alpheidae	0.6	11	0.06	0.21	0.32	Cnidaria	0.9	6	0.03	0.02	0.03
Proceppidae	1.7	8	0.04	0.43	0.65	Totals		17,992		65.75	
Hippolytidae	0.4	4	0.02	0.02	0.03						

¹Only a trace amount of food present.²An accurate count of individuals was not possible.

13 mo examined, dropping between 30 and 40% in September, January, and May. Number, volume, and percent occurrence for *B. floridae* all showed major peaks in utilization between June and August, and October and December 1972. Polychaetes were irregular in percent occurrence, but the data suggest a peak in spring and summer, while natantians and brachyurans showed increases in percent occurrence in the spring and fall. Amphipods, cumaceans, mysids, and pelecypods showed strong spring peaks in importance.

Nine size groups of *P. scitulus* (21-40, 41-60, 61-80, 81-90, 91-100, 101-110, 111-120, 121-130, 131-140) reached stabilized horizontal asymptotes of cumulative trophic diversity versus cumulative stomachs examined. The analyses of size changes in feeding are based on these groups.

The percent occurrence of lancelets and polychaetes increased with increasing fish size, while gammarid amphipods decreased (Table 2). Brachyurans, cumaceans, copepods, larval crustaceans, pelecypods, and ostracods increased in percent occurrence for searobins up to 80-100 mm,

TABLE 2.—Percentage of prey occurrence for size groups (millimeters standard length) of *Prionotus scitulus* from Tampa Bay, Fla., 1972-73. Only prey categories with an overall occurrence of 1% or greater were included.

Prey category	21-40	41-60	61-80	81-90	91-100	101-110	111-120	121-130	131-140
Teleostei	0	5.3	4.6	5.9	0	3.7	2.9	0	3.7
<i>Branchiostoma floridae</i>	4.0	21.1	22.7	29.4	63.0	69.1	64.5	70.6	70.3
Brachyura	8.0	20.1	45.5	64.7	25.9	37.0	30.4	29.4	22.2
Natantia	20.0	26.3	13.6	17.6	11.1	29.6	34.1	32.4	48.2
Anomura	4.0	5.3	0	5.9	11.1	11.1	10.9	9.8	7.4
Gammaridea	88.0	89.5	54.5	52.9	48.1	51.9	59.4	48.0	48.2
Caprellidea	8.0	0	4.6	0	0	2.5	8.7	2.0	3.7
Isopoda	0	15.8	9.1	5.9	18.5	8.6	17.4	8.8	25.9
Cumacea	36.0	78.9	72.7	52.9	74.1	51.9	25.4	21.6	25.9
Mysidacea	8.0	10.3	0	0	25.9	17.3	5.8	1.0	7.4
Copepoda	8.0	26.3	63.6	41.2	37.0	9.9	3.6	4.9	7.4
Ostracoda	16.0	20.1	22.7	41.2	14.8	7.4	3.6	2.9	7.4
Crustacean larvae	4.0	21.1	54.6	23.5	3.7	2.5	0	0	0
Polychaeta	0	5.3	9.1	23.5	25.9	30.9	47.1	44.1	62.9
Pelecypoda	4.0	0	45.5	29.4	25.9	21.0	21.7	23.5	22.2
Gastropoda	0	0	18.2	11.8	7.4	2.5	5.8	2.0	7.4
No. of fish examined	25	19	22	25	27	81	138	102	27

and then decreased for larger fish. Other prey categories either did not show regular trends or remained relatively constant in occurrence between size classes. The percent number of prey showed similar trends with increasing fish size. Crustacean larvae, copepods, gammarid amphipods, and cumaceans were of greater importance to small fish, while larger fish (100-140 mm) utilized more lancelets and pelecypods.

The volumetric importance of *Branchiostoma* to the 41- to 60-mm size group resulted from one fish capturing a single large lancelet. Volumetrically, the diet of *P. scitulus* 80 mm and larger was dominated by lancelets and polychaetes, while cumaceans, copepods, and natantians (especially larval forms) were of greater importance to small fish (Figure 2). Branchyurans showed a more uniform pattern of distribution among size groups.

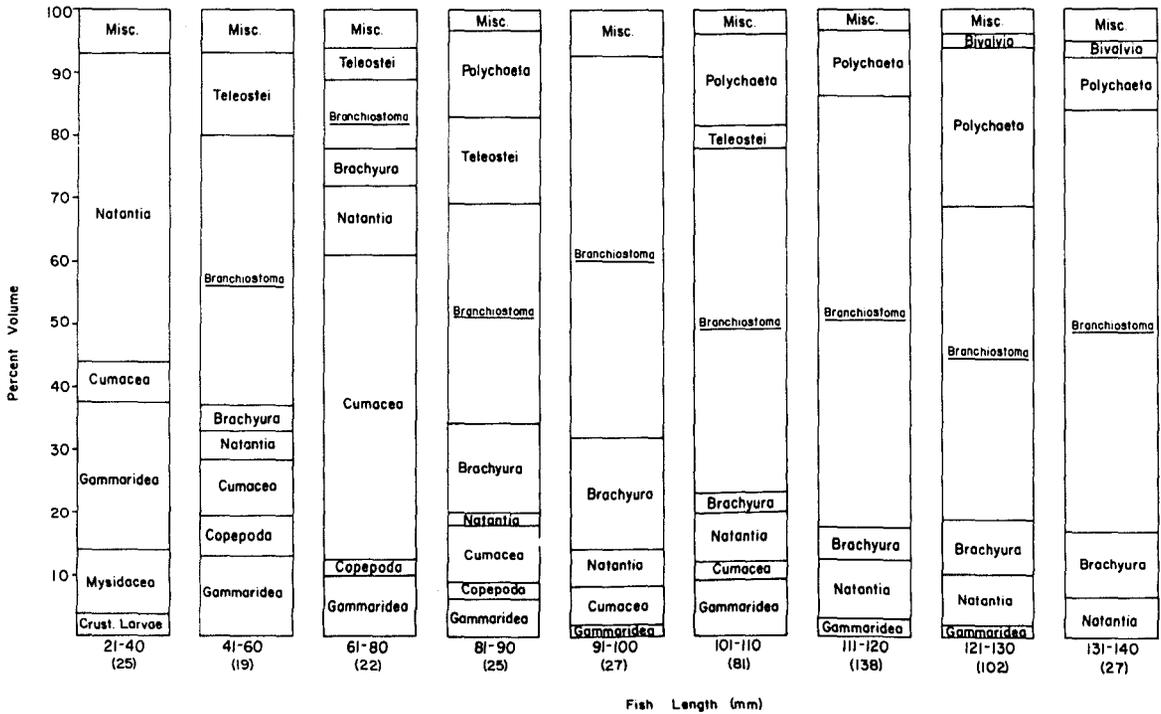
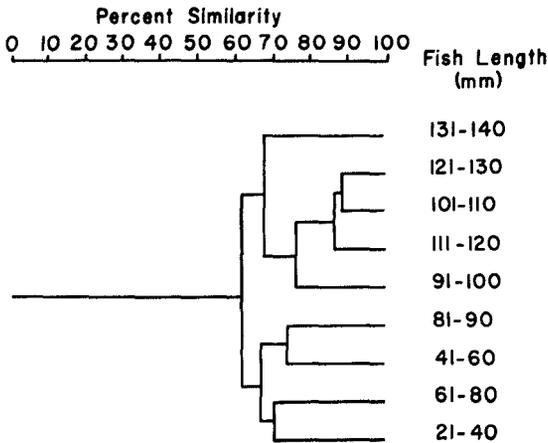


FIGURE 2.—Changes in the percent volume of major prey categories for size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73.



Trophic relationships among size groups were summarized by cluster analysis based on the percent occurrence of prey (Figure 3). Fish smaller than 81-90 mm and larger than 91-100 mm formed two major divisions, linking at 77% similarity. The lower similarity between size classes of smaller size bins compared with larger size classes is indicative of the more rapid changes in trophic ontogeny occurring between small individuals.

FIGURE 3.—Cluster analysis (UPGMA; unweighted pair group, arithmetic average) of prey similarity between size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73. Similarity was determined from percent occurrence of prey categories.

The total amount of food ingested, as shown by the mean volume of stomach contents, increased rapidly with increasing fish size; log transformed values of total prey volume varied linearly with fish size over most size classes (Figure 4). The total number of prey per fish also increased rapidly with increasing fish size up to the 60- to 80-mm size class, but then declined markedly for larger size groups (Figure 4). The decline in number of prey ingested occurred somewhat prior to a detectable increase in mean prey size (cf. Figure 5). Searobins smaller than the 90- to 100-mm size group showed an asymptotic relationship of fish length and linear prey size, while prey sizes increased rapidly over the larger size groups. Since linear prey measurements may be misleading, I also examined the average volume (cubic centimeters) of prey items eaten by size classes of *P. scitulus*. Prey volume was calculated from the total sorted food volume from each 10- or 20-mm size class, divided by the total prey number for each size class. Mean prey volume did not increase over small size classes of searobins, but at 90-100 mm it initiated a rapid increase (Figure 6). Consequently, the rapid rise in total stomach volume of the leopard searobin occurred initially through the capture of increasing numbers of small prey, followed (after 90-100 mm) by the capture of fewer, but progressively larger, prey.

Relative prey biomass (mean prey volume/mean wet weight) was initially very high but then de-

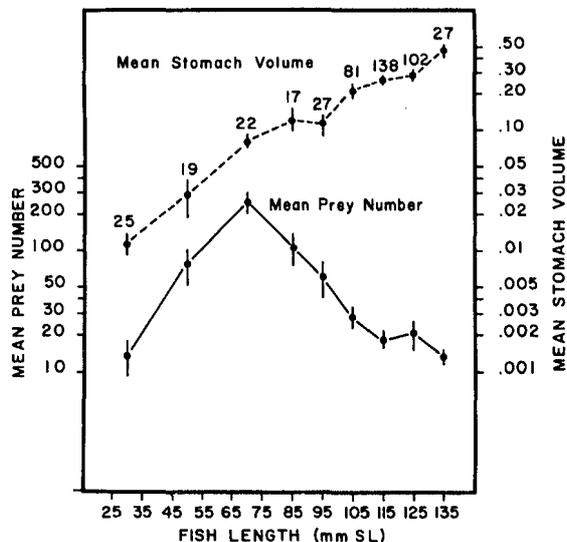


FIGURE 4.—The relationship of mean volume of stomach contents (cubic centimeters) and mean prey number (logarithmic scales) to fish length for *Prionotus scitulus*, Tampa Bay, Fla., 1972-73. The vertical lines indicate 1 SE on either side of the mean, sample sizes are shown above the upper graph.

creased with fish size to the 61- to 70-mm size class, followed by an increase for fish larger than the 90- to 100-mm size class (Figure 6).

Increases in prey size with increasing predator size might occur through shifts in the utilization of progressively larger prey kinds, or through the

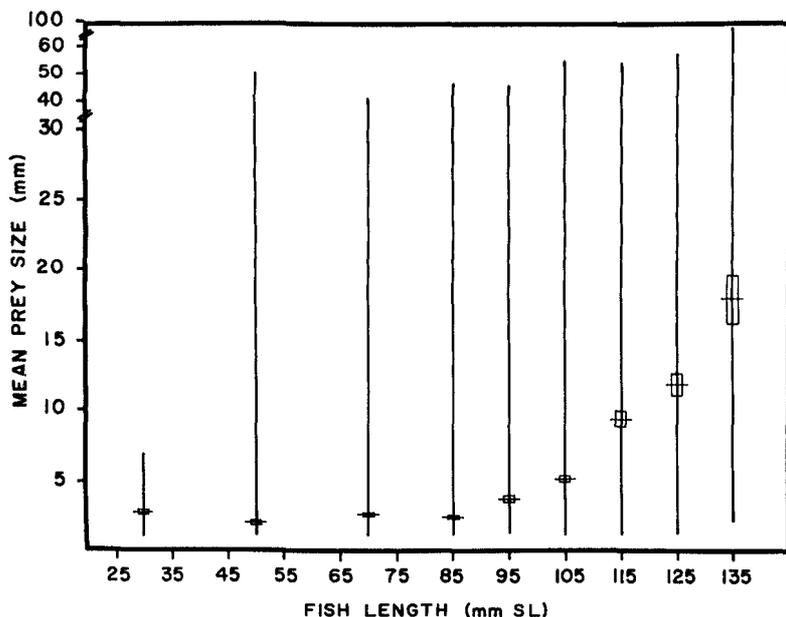


FIGURE 5.—Mean prey length versus standard length groups of *Prionotus scitulus* from Tampa Bay, Fla. Vertical lines are ranges; cross-bars and open rectangles are $\bar{x} \pm 2$ SE.

Morphology and Growth

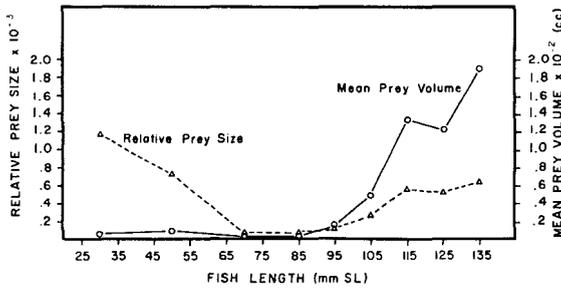


FIGURE 6.—Mean prey volume (cubic centimeters) and relative prey size (\bar{x} prey volume/ \bar{x} wet fish weight) for size classes of *Prionotus scitulus*, Tampa Bay, Fla., 1972-73.

selection of larger sized individuals within a single prey kind. Only one prey item, *B. floridae*, exhibited a broad enough size range to meaningfully test for differences between fish sizes. The mean size of lancelets, however, did increase with increasing fish size ($P < 0.001$) (Figure 7), but the rate of increase was quite low compared with the overall increase in mean prey size (cf. Figure 5).

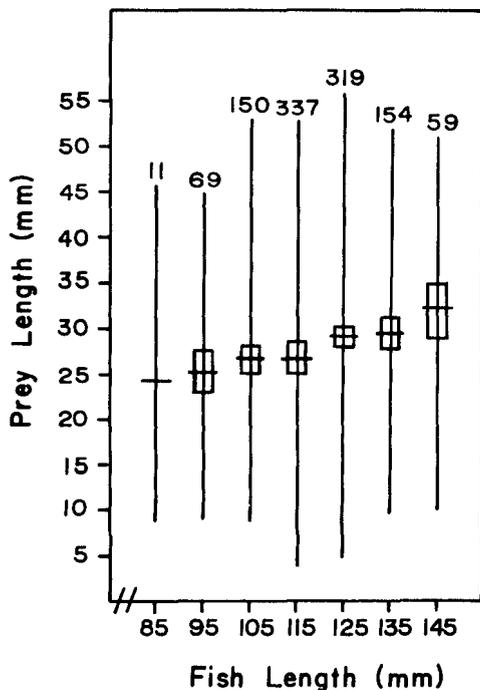


FIGURE 7.—The relationship between lengths of the dominant prey, *Branchiostoma floridae*, and its predator, *Prionotus scitulus*. See Figure 5 for explanation of symbols.

Trophic changes showed a critical size interval between approximately 60 and 100 mm, within which the mean prey number decreased, and after which the mean prey volume, length, and relative volume increased. These trophic changes suggested the presence of certain morphological or developmental correlates, of which I examined jaw size, intestinal length, and growth.

Ontogenetic changes in mouth size were expressed by relative jaw width and relative jaw length. Juvenile leopard searobins showed proportionately greater mouth widths and lengths compared with adults, but plots of both relative jaw length and relative jaw width versus SL showed considerably lower slopes by approximately 75 mm (Figure 8). Proportionate mouth length continued to decrease with increasing fish size for fish > 75 mm; however, proportionate mouth width remained constant for fish > 75 mm. Mouth size thus increased rapidly with increasing fish size for early juvenile *P. scitulus*, but by 75 mm the relationship between mouth size and fish length was essentially fixed.

Intestinal length increased rapidly between the 45- and 65-mm size classes. Fish < 50 mm had mean intestinal lengths of 70% SL, while fish > 60 mm had mean intestinal lengths of 102% SL.

Log transformed length-weight values of leopard searobins showed an increase in the slope of the regression line between approximately 55 and 75 mm (Figure 9). The fish were divided into two size groups, < 75 mm and > 75 mm, and sepa-

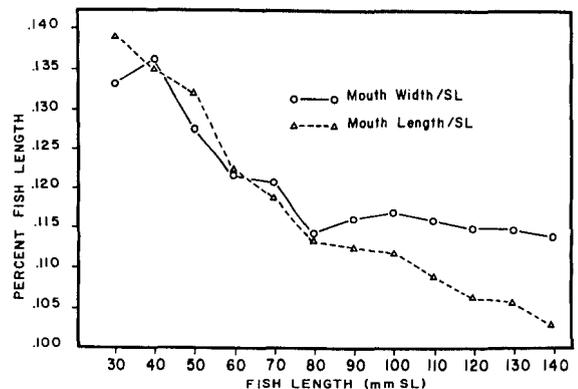


FIGURE 8.—Relative mouth width and relative mouth length versus fish length for *Prionotus scitulus*, Tampa Bay, Fla. Each data point is based on the mean of 20 individuals.

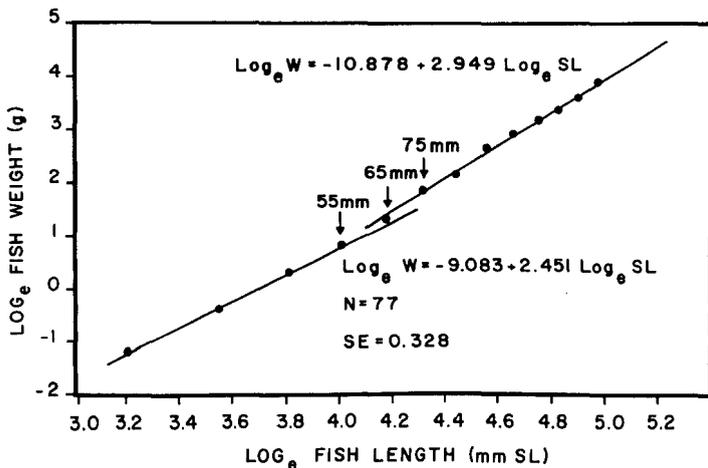


FIGURE 9.—Length-weight relationships for size classes of *Prionotus scitulus*, Tampa Bay, Fla.

rate length-weight regressions were calculated. The 75-mm size was chosen because of its association with changes in relative mouth size. The growth data showed that *P. scitulus* >75 mm were gaining weight much more rapidly than smaller fish, even after allowing for the expected exponential rate of increase by using the log transformation.

Reproduction and Distribution

Mean female GSI's remained below 0.4 for *P. scitulus* between 20 and 90 mm and these fish did not contain mature ova. Leopard searobins 100 mm and larger had mean GSI values between 3 and 6 and were sexually mature. Ross (1974, in press) showed that mean female GSI values during spring to summer spawning were 5 to 10. The GSI values reported here are lower because the fish were combined from all months of the study to avoid possible bias due to differences of spawning times of different size groups. Male searobins showed the same size-related pattern.

Spatial separation between immature and mature *P. scitulus* was quite pronounced (Figure 10). Juvenile searobins consistently had high relative abundances at Station 1 in Old Tampa Bay (5 m deep), while mature fish had high relative abundances near the mouth of Tampa Bay at Station 3 (7 m deep). Overlap between immature and mature searobins was greatest during summer and fall 1972 at Station 2 (5 m). The percent occurrence of juvenile fish in combined collections was highest between March and May (60-75%) and lowest between June and November (25-47%).

Annual mean salinities varied significantly be-

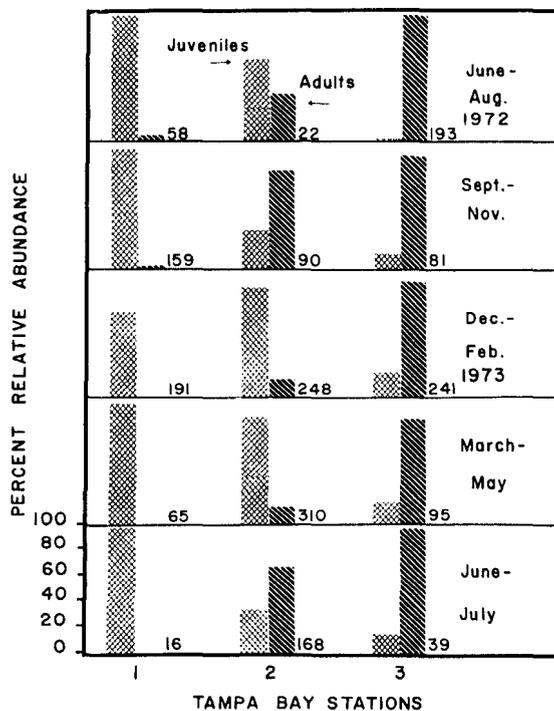


FIGURE 10.—Spatial distribution of juvenile (<100 mm SL), and adult (>100 mm SL) *Prionotus scitulus* at three stations in Tampa Bay, Fla., 1972-73. Percent relative abundance is based on each sample site and date; numbers indicate sample sizes. Adults are indicated by hatching; juveniles by cross-hatching.

tween stations ($P < 0.05$); respective means for Stations 1-3 were 25.7, 28.1, and 33.2%. Consequently, small leopard searobins were occupying somewhat less saline water. Annual mean temperatures did not vary between stations (range = 13°-32°C).

DISCUSSION

Ontogenetic changes in prey utilization by *P. scitulus* showed an early dependence on planktonic or epifaunal prey such as crustacean larvae, copepods, mysids, cumaceans, and gammarid amphipods. Larger *P. scitulus* (>90 mm) ate more infaunal organisms such as lancelets and polychaetes. Separation by prey kind was greatest at 90 mm which corresponded to the transition size between immature and mature fishes.

The greatest percent occurrence of juvenile fish (March-May) coincided with periods of higher utilization of brachyurans, natantians, cumaceans, amphipods, mysids, pelecypods, and polychaetes by adult fish, although lancelets remained the dominant prey. Consequently, size differences in food habits were not biased by seasonal unavailability of certain prey to adults or juveniles. Also, Ross (1974) demonstrated that changes in food habits with increasing fish size were generally consistent between stations.

Other studies on food habits of *P. scitulus* have indicated that small crustaceans and polychaetes were important prey (Reid 1954; Springer and Woodburn 1960; Ross 1977, in press). Ross (1977, in press) found that *P. scitulus* from offshore of Tampa Bay utilized principally brachyurans, polychaetes, cumaceans, gammarid amphipods, natantians, and lancelets.

Total food consumption showed an accelerating rate of increase with fish length, but initially this occurred through a rapid rise in the number of prey consumed, rather than through an increase in prey size. Prey size did not increase with increasing fish size for searobins <90 mm. Although numerous studies have demonstrated positive correlations between prey and predator sizes (e.g., Northcote 1954; Hartman 1958; Wong and Ward 1972; Hespeneide 1973), Schoener (1969, 1971) predicted that prey size would decrease with decreasing predator sizes to a lower horizontal asymptote. Essentially, the energy gained from progressively smaller prey gradually approaches the energy expended in obtaining and digesting prey. Data on prey size-predator size relationships supporting this prediction were reviewed by Schoener (1971), but did not include fishes as examples.

Prey size (both length and volume) was positively correlated with fish size for searobins 90 mm and larger. The increase in mean prey size relative to predator size occurred primarily through a

progressive shift to different, larger prey taxa, and only secondarily by size selection within a single prey taxon.

The transition from numerous small prey to fewer large prey was preceded by rapid growth of jaw size relative to body size and by an increase in intestinal length. Since intestinal absorption may be increased through the development of folds and an increase in length or both (Siankova 1966), the relative increase in intestinal length of *P. scitulus* is perhaps a response to increased energy demands of larger fish or to their utilization of larger prey items.

Growth in fishes may occur as a series of stanzas which are entered by ecological and physiological size thresholds (Parker and Larkin 1959). Growth stanzas may be recognized by changes in weight-length relationships (Ricker 1975). The shift from small to large prey in *P. scitulus* was accompanied by a change in the weight-length relationship indicating the presence of two growth stanzas. Growth efficiency, measured as weight gained per ration weight per unit time, varies extensively with prey kind (Paloheimo and Dickie 1966). For instance, growth efficiency of trout increased as the ration progressed from hatchery mash to gammarid amphipods to minnows. The two growth stanzas in *P. scitulus* may thus reflect an increase in the proportion of food energy available for growth as small crustaceans are replaced by larger lancelets and polychaetes in the diet.

Relative prey size showed a parabolic relationship with fish size. Consequently, small *P. scitulus* were, in effect, predators of large prey. Prey size distributions have been shown to follow a lognormal relationship in various communities (Whittaker 1952; Schoener and Janzen 1968; Griffiths 1975), so juvenile leopard searobins were utilizing an apparently abundant energy source. However, since mean prey size did not increase with increasing fish size for searobins <90 mm, with growth, searobins tended toward being "small" predators due to the continued use of the same-sized prey items. Although prey availability was not monitored, *P. scitulus* between 20 and 90 mm were likely operating as number maximizers (cf. Griffiths 1975). Griffiths presented evidence that juvenile stages of several kinds of vertebrates pass through such a stage during which prey items are utilized in close proportion to their actual occurrence.

Searobins >90 mm showed an increase in relative prey size, thus tending again towards being

predators of large prey. The data suggest a switch in feeding strategy to an energy maximizer (cf. Griffiths 1975) in which predators feed in such a manner as to maximize their energy intake. In *P. scitulus* this is perhaps accomplished by a switch in feeding behavior after achieving a critical size threshold requisite for capturing partially buried infaunal prey.

The shift to utilization of large prey occurs slightly before the onset of reproduction. Increased energy demands, or a decrease in foraging time, brought about by gonadal development and breeding activity or both, might be critical factors in selecting for the change in the feeding strategy of *P. scitulus*.

Mature and immature *P. scitulus* were effectively segregated along both spatial and trophic dimensions in Tampa Bay. Spatial segregation might occur through the ability of juvenile searobins to occupy shallower water or to withstand lower salinity, a characteristic of many juvenile marine fishes (Gunter 1961). Trophic overlap in prey kind between immature and mature size groups was closely comparable with trophic overlap between adult individuals of different species of searobins on the West Florida Shelf (Ross 1977). Consequently, *P. scitulus* in Tampa Bay were effectively reducing the potential for intraspecific competition.

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LITERATURE CITED

- BRAY, J. R., AND J. T. CURTIS.
1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325-349.
- CARR, W. E. S., AND C. A. ADAMS.
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102:511-540.
- DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publ. Inst. Mar. Sci. Univ. Tex.* 5:353-416.
- GRIFFITHS, D.
1975. Prey availability and the food of predators. *Ecology* 56:1209-1214.
- GUNTER, G.
1961. Salinity and size in marine fishes. *Copeia* 1961:234-235.
- HARTMAN, G. F.
1958. Mouth size and food size in young rainbow trout, *Salmo gairdneri*. *Copeia* 1958:233-234.
- HELLAWELL, J. M., AND R. ABEL.
1971. A rapid volumetric method for the analysis of the food of fishes. *J. Fish Biol.* 3:29-37.
- HESPENHEIDE, H. A.
1973. Ecological inferences from morphological data. *Annu. Rev. Ecol. Syst.* 4:213-229.
- HUBBS, C. L., AND K. F. LAGLER.
1958. Fishes of the Great Lakes region. Revised ed. Cranbrook Inst. Sci. Bull. 26, 213 p.
- HURTUBIA, J.
1973. Trophic diversity measurement in sympatric predatory species. *Ecology* 54:885-890.
- IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. (Translated from Russ.) Yale Univ. Press, New Haven, Conn., 302 p.
- KEAST, A., AND D. WEBB.
1967. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Board Can.* 23:1845-1874.
- NORTHCOTE, T. G.
1954. Observations on the comparative ecology of two species of fish, *Cottus asper* and *Cottus rhotheus*, in British Columbia. *Copeia* 1954:25-28.
- PALOHEIMO, J. E., AND L. M. DICKIE.
1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. *J. Fish. Res. Board Can.* 23:1209-1248.
- PARKER, R. R., AND P. A. LARKIN.
1959. A concept of growth in fishes. *J. Fish. Res. Board Can.* 16:721-745.
- PIELOU, E. C.
1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13:131-144.
- REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. *Bull. Mar. Sci. Gulf Caribb.* 4:1-94.
- RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can., Bull.* 191, 382 p.
- ROSS, S. T.
1974. Resource partitioning in searobins (Pisces: Triglidae) on the west Florida shelf. Ph.D. Thesis, Univ. South Florida, Tampa, 205 p.
1977. Patterns of resource partitioning in searobins (Pisces: Triglidae). *Copeia* 1977:561-571.
In press. Searobins (Pisces: Triglidae). *Mem. Hourglass Cruises.*

- SCHOENER, T. W.
 1969. Models of optimal size for solitary predators. *Am. Nat.* 103:277-313.
 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404.
- SCHOENER, T. W., AND D. H. JANZEN.
 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *Am. Nat.* 102:207-224.
- SIANKOWA, L.
 1966. The surface area of the intestinal mucosa in bream - *Abramis brama* (L). *Stud. Soc. Sci. Torun., Sect. E (Zool.)* 8:1-54.
- SNEATH, P. H. A., AND R. R. SOKAL.
 1973. Numerical taxonomy, the principles and practice of numerical classification. W. H. Freeman and Co., San Franc., 573 p.
- SOKAL, R. R., AND F. J. ROHLF.
 1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.
- SPRINGER, V. G., AND K. D. WOODBURN.
 1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv. Mar. Lab., Prof. Pap. Ser. 1, 104 p.
- WHITTAKER, R. H.
 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monogr.* 22:1-44.
- WONG, B., AND F. J. WARD.
 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. *J. Fish. Res. Board Can.* 29:1761-1764.