

**Abstract.**— Atlantic spadefish *Chaetodipterus faber* were collected from South Carolina between July 1985 and May 1987 to examine feeding habits, age and growth, and reproduction. Analysis of stomach contents by habitat showed that fish from estuarine areas and offshore artificial reefs ate mainly hydroids, while Anthozoa were dominant food items for fish from nearshore marine areas. Stomach contents from fish obtained by hook-and-line near offshore artificial reefs, using *Stomolophus meleagris* as bait, indicated that scyphozoan jellyfish were the dominant prey, but fish collected by spear or net had stomach contents dominated by hydroids, anthozoans, and polychaetes. Ages of Atlantic spadefish were determined from whole sagittae. Marginal increment analysis indicated that annuli formed between December and May. The von Bertalanffy growth equation, derived from back-calculated mean total lengths at age was  $l_t = 490(1 - e^{-0.34(t+0.18)})$ , where  $t$  is age in years, and  $l_t$  = total length at age. Mean asymptotic total length was calculated to be 490 mm. The oldest fish examined was age 8 and 504 mm TL. Histological examination indicated that fish matured at age 1 and spawned from May through August.

## Feeding Habits, Age, Growth, and Reproduction of Atlantic Spadefish *Chaetodipterus faber* (Pisces: Ehippidae) in South Carolina\*

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The Atlantic spadefish *Chaetodipterus faber* (Broussonet) is the only member of the family Ehippidae native to the western Atlantic Ocean. This species inhabits coastal waters from Chesapeake Bay to southeastern Brazil, including the Gulf of Mexico (Johnson 1978), and has also been introduced into the waters surrounding Bermuda (Burgess 1978). It is a common fish in South Carolina, particularly from early spring through late fall, and all life stages have been collected in South Carolina.

Since 1978 the Recreational Fisheries Section of the South Carolina Wildlife and Marine Resources Department (SCWMRD) has promoted *C. faber* as a sportfish, primarily due to the attraction of large numbers of adult Atlantic spadefish to offshore artificial reefs that have been created and/or maintained by SCWMRD. Atlantic spadefish have traditionally been a relatively minor recreational species in South Carolina and were only occasionally caught by hook-and-line fishermen using shrimp or squid as bait. Observations of feeding behavior by SCWMRD personnel in the early 1980s suggested that Atlantic spadefish might eat *Stomolophus meleagris*, the cannonball jellyfish. As a result, a technique using can-

nonball jellyfish as bait was developed and has proven extremely effective in attracting and capturing *C. faber* (Moore et al. 1984). This method has since been the subject of some recreational fishing publications (Ogle 1985, 1987). Little, however, is known about the life history, feeding habits, age and growth, or reproductive biology of *C. faber*, even though such information is preliminary to proper assessment and management.

The present study was undertaken with three major objectives. The first was examination of stomach contents from specimens of *C. faber* in order to describe the diet. In addition to a qualitative and quantitative diet analysis, I wished to determine if the mode of collecting fish (hook-and-line vs. net and spearfishing) might bias the results of diet analysis. Since Atlantic spadefish appeared to inhabit different areas depending upon body size and age, I also wished to determine if ontogenetic and habitat differences existed in the diets of the fish collected. The second portion of the study dealt with age and growth of Atlantic spadefish in South Carolina by finding a suitable ageing method and estimating growth rates. The final segment of the research explored the reproductive biology of *C. faber*, specifically determination of spawning period, sex ratios, and the age at sexual maturity of Atlantic spadefish off South Carolina.

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## Materials and methods

### Data collection

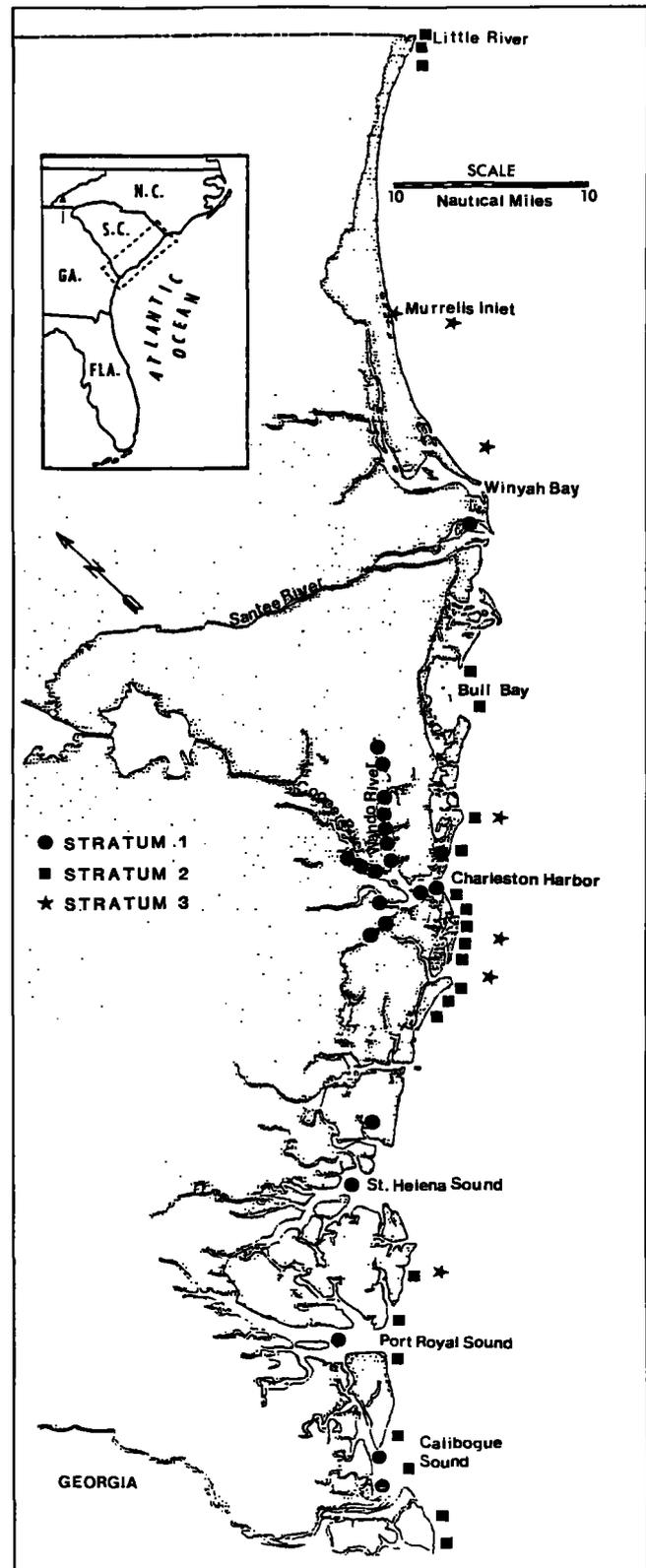
Specimens were collected July 1985 through May 1987, excluding the periods from December 1985–April 1986 and December 1986–April 1987 when Atlantic spadefish were absent from collection sites (Fig. 1). Most of the specimens less than 200 mm total length were provided by other research programs which obtained them as bycatch in trawl tows.

Collections were from three different habitat strata (Fig. 1). Stratum 1 included estuarine habitats. The fish in this stratum were primarily young-of-the-year and were collected by a variety of gear, including dipnets, seines, stopnets, and trawl nets. Stratum 2 consisted of shallow nearshore habitats less than 20 m in depth with bottoms consisting primarily of mud or sand and shell, with rare patches of live bottom (sponges and soft corals, low rock relief). The fish in stratum 2 were all collected by trawling. Stratum 3 contained fish collected primarily by spearfishing while SCUBA diving on artificial reefs located off South Carolina's coast and on the Murrell's Inlet jetties. Some specimens from the artificial reefs were collected by hook-and-line using *Stomolophus meleagris* as bait. The artificial reefs and the jetties were similar habitats in that all were man-made structures providing relatively high relief and all were covered with a variety of fouling organisms such as algae, sponges, corals, hydroids, sea anemones, bryozoans, and ascidians. The fish from stratum 3 were all adults.

Fish ( $n = 832$ ), subsampled from 84 collections, were sexed, weighed to the nearest gram, and total length (TL) and standard length (SL) measured to the nearest millimeter. Subsamples, consisting of 177 stomachs and 233 gonads, were excised from a representative portion of the collections, preserved in buffered 10% seawater formalin, and later transferred to 50% isopropanol. Otoliths (sagittae) were removed from 643 specimens and stored in 95% ethanol.

### Stomach contents

Stomachs of *Chaetodipterus faber* are well-defined structures, and contents of the digestive tracts between the pharynx and the pyloric sphincter were examined using compound and stereoscopic microscopes. Stomachs were scored for fullness and food items were sorted, identified to the lowest practical taxa, and counted. Colonial organisms, such as hydroids and bryozoans, and multiple fragments of individual species were counted as single individuals unless numbers could be estimated from the fragments by counting structures such as eyes or legs. After removing excess water by blotting on absorbent paper, the volume of



**Figure 1**

Positions of collection sites in South Carolina for *Chaetodipterus faber*. Symbols indicate general collection areas, and some indicate more than one collection in a particular area. Circles (●) represent estuarine sites (stratum 1), squares (■) represent shallow nearshore sites with sandy bottoms (stratum 2), and stars (★) represent artificial reef habitats (stratum 3).

each taxon was determined by displacement, except in the case of small items. Volumes of small items were estimated using a 1 × 1 mm grid. Percent frequency of occurrence (%*F*), percent of total number (%*N*), and percent of total volume (%*V*) of stomach contents were calculated by higher taxonomic categories for the entire data set and for the data separated by length intervals and collection strata, and these values were used to calculate an index of relative importance (*IRI*) (Pinkas et al. 1971):

$$IRI = (\%N + \%V) \times \%F.$$

Shortly after laboratory analysis of stomach contents commenced, it became apparent that most of the prey items observed were either colonial or fragments of soft-bodied organisms that could only be counted as one individual per stomach each time they were encountered. The primary countable organisms were amphipods and copepods, which were present in large numbers, but accounted for only a small portion of the volume. In the opinion of some researchers (Lagler 1956, Crow 1982), percent number can lead to a somewhat distorted view if small organisms are present in large numbers even though they are of minor importance to the diet of a fish. Consequently, a modified index (*MI*) of relative importance which did not incorporate %*N* into the formula was also calculated for each taxonomic category:

$$MI = \%F \times \%V.$$

Stomach contents from 27 fish taken by hook-and-line were analyzed separately in the above manner and compared with the data from fish collected by nets and spearfishing.

### Age and growth

Sagittae were chosen as structures for age determination since they were easily accessible, easily stored, and exhibited well-defined growth zones. Other structures were deemed unsuitable as ageing structures for various reasons. Scales were small, frequently regenerated, and the marks on them were considerably more difficult to interpret than those on the sagittae. Vertebrae were difficult to obtain and time-consuming to prepare for analysis.

No differences were observed between the left and right sagittae of individual fish and, unless damaged or unavailable, the left sagitta was used in age analysis. Cleaned whole sagittae were examined using both reflected and transmitted light, as necessary, in order to establish the location of presumed annuli. Whole otoliths were used since 100% agreement was obtained

between counts of opaque zones from a subsample ( $n = 18$ ) of otolith sections and counts from the corresponding whole otoliths. Sagittae were placed, concave-side-up, in a dish containing cedar oil and viewed with reflected light against a dark background at 25× using a stereoscope equipped with an ocular micrometer (1 ocular unit = 0.04 mm). The distance (in ocular units) from the kernel to each opaque mark and from the outermost mark to the edge of the sagitta (marginal increment) was determined from measurements made along the ventral radius of each sagitta (Fig. 2). These measurements were performed on two occasions separated in time by at least 2 weeks, and the two sets of measurements were compared to see if otolith measurements were repeatable.

Both least-squares linear regressions (Sokal and Rohlf 1981) and geometric mean (GM) functional regressions (Ricker 1973, Sokal and Rohlf 1981) were used to describe the relationship of TL to ventral otolith radius (OR), SL to TL, and lengths to weight. Mean back-calculated TL at age was derived by the Fraser-Lee method using the intercept of the OR-TL relationship (Poole 1961, Carlander 1982). Mean back-calculated TLs were weighted by the reciprocal of the standard error of the mean squared, and the von Bertalanffy growth equation (Bertalanffy 1938) was then fitted to mean back-calculated TL at age by using the SAS NLIN procedure while employing Marquardt's algorithm and the SAS NLIN weight statement (Helwig and Council 1979).

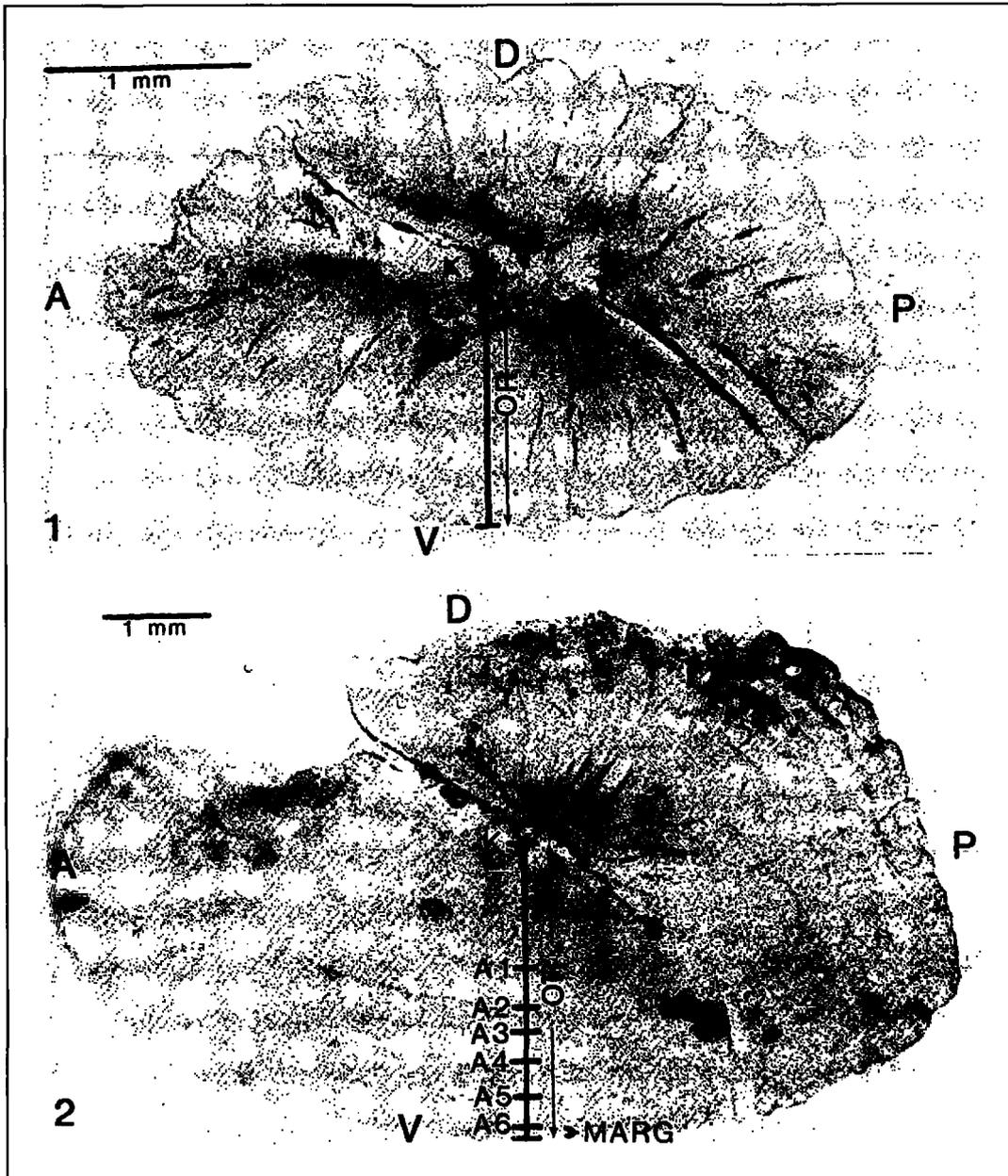
### Reproduction

Reproductive tissues were processed in an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, blocked in paraffin, and sectioned (6–10 μm thick) on a rotary microtome. Sections were stained with Harris hematoxylin and counter-stained with eosin-Y. Mounted sections were then examined with a compound microscope, and sex and maturity stages were assigned according to the criteria of Waltz et al. (1979). The ratio of males to females and maturity stages by month were examined to determine sex ratios and spawning period of *C. faber* off South Carolina.

## Results

### Analysis of stomach contents

Eighty percent of the stomachs obtained by hook-and-line contained food, and at least seven prey species



**Figure 2**

Measurements taken from each sagitta of *Chaetodipterus faber* used in age analysis. (1) Photograph of the left sagitta from a young-of-the-year (115 mm TL) specimen. (2) Photograph of a whole left sagitta from an age-6 (396 mm TL) specimen. Orientation of the sagittae within the neurocranium is indicated: A anterior; P posterior; D dorsal; V ventral. A1-A6 represent successive measurements to each annulus; OR is the ventral sagitta radial measurement; MARG is the marginal increment; K is the kernel of the sagitta.

were present (Table 1). *Stomolophus meleagris* was, by far, the dominant organism according to all numeric indicators (%F, %N, %V, IRI, and MI). Hydroids, epifaunal amphipods, and anthozoans (sea anemones) were observed in considerably lower volumes, numbers, and frequencies than *S. meleagris*.

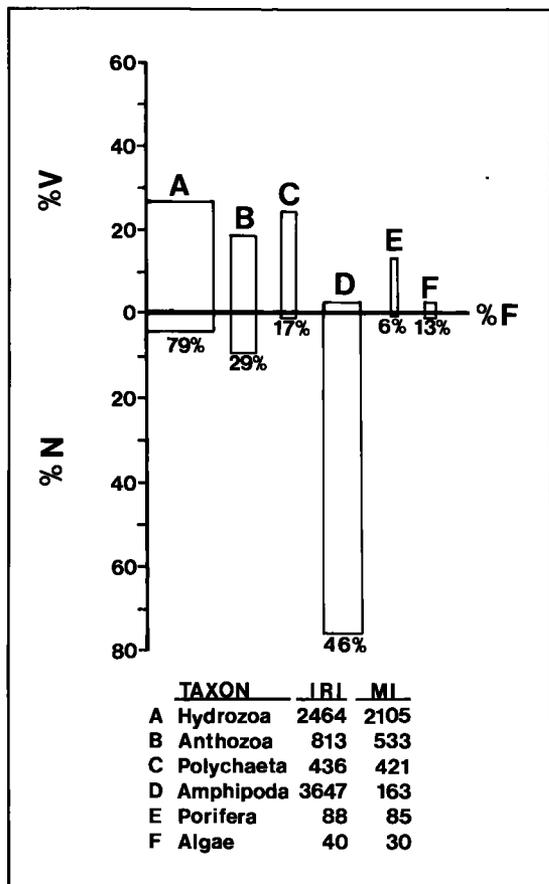
Ninety percent of the stomachs from Atlantic spadefish obtained by other collection methods (nets and

spearfishing) contained food, and at least 75 prey species were represented (see Appendix). In sharp contrast to the hook-and-line samples, jellyfish occurred in only one stomach collected by nets or spearfishing even though *S. meleagris* and other jellyfish were common in the artificial reef areas during many of the spearfishing expeditions and were abundant in trawl catches. Furthermore, the species of jellyfish eaten was identified, by

**Table 1**

Percent frequency of occurrence (%F), percent of total number (%N), percent of total volume (%V), index of relative importance (IRI), and modified index of importance (MI) for food items of *Chaetodipterus faber* obtained by hook-and-line in South Carolina using *Stomolophus meleagris* as bait.

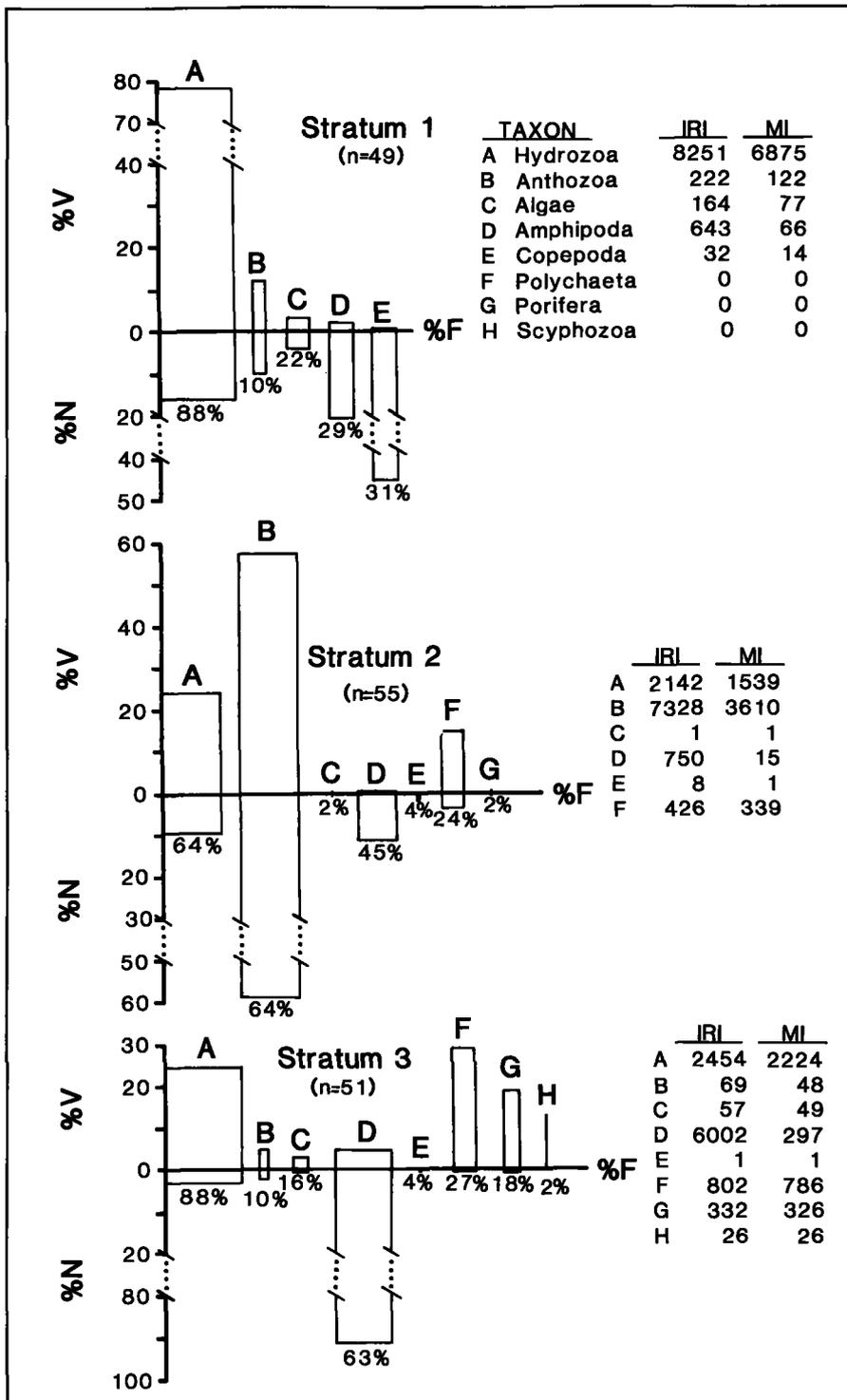
Prey item	%F	%N	%V	IRI	MI
<b>Cnidaria</b>					
Hydrozoa					
<i>Eudendrium</i> sp.	18.18	9.52	0.69	185.62	12.54
<i>Obelia</i> sp.	4.55	2.38	0.01	10.88	0.05
Hydrozoa undetermined	4.55	2.38	0.04	11.03	0.18
Total Hydrozoa	27.27	14.29	0.74	409.67	20.17
Anthozoa					
Actiniaria	4.55	2.38	0.55	13.33	2.50
Scyphozoa					
<i>Stomolophus meleagris</i>	95.45	50.00	98.66	14,189.60	9417.10
<b>Crustacea</b>					
Amphipoda					
<i>Caprella penantis</i>	13.64	19.05	0.03	260.25	0.41
<i>Erichthonius brasiliensis</i>	9.09	9.52	0.01	86.63	0.09
<i>Jassa falcata</i>	4.55	4.76	<0.01	21.67	0.01
Total Amphipoda	27.27	33.33	0.04	910.12	1.09
Number of stomachs examined: 27					
Examined stomachs with food: 22					



examining tentacle arrangement and nematocyst morphology, as *Chiropsalmus quadrumanus*, a cubomedusa known as the sea wasp. In stomachs obtained by nets and spearing, hydroids were dominant by volume (27%) and were the most frequently observed organisms (seen in about 80% of the stomachs examined) (Fig. 3). Amphipods were in 45% of the stomachs and accounted for about 76% of the individual organisms, but had a low volume (4%). Nearly all of the amphipods were epifaunal, species primarily caprellids and tubicolous gammarids, that are frequently associated with hydroids. Anthozoans, consisting nearly equally of anemones (Actiniaria) and sea pansies *Renilla reniformis* were present in 29% of the stomachs, accounted for 10% of the individuals, and were the third-ranking taxon in terms of percent volume. Polychaetes were seen in 17% of the stomachs and accounted for 24% of total volume, but comprised less than 1% of the number of individuals. This category consisted primarily of terebellid feeding tentacles, which were probably cropped by *C. faber*

**Figure 3**

Percent frequency (%F), percent number (%N), percent volume (%V), index of relative importance (IRI), and modified index of importance (MI) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters by nets and spearing.



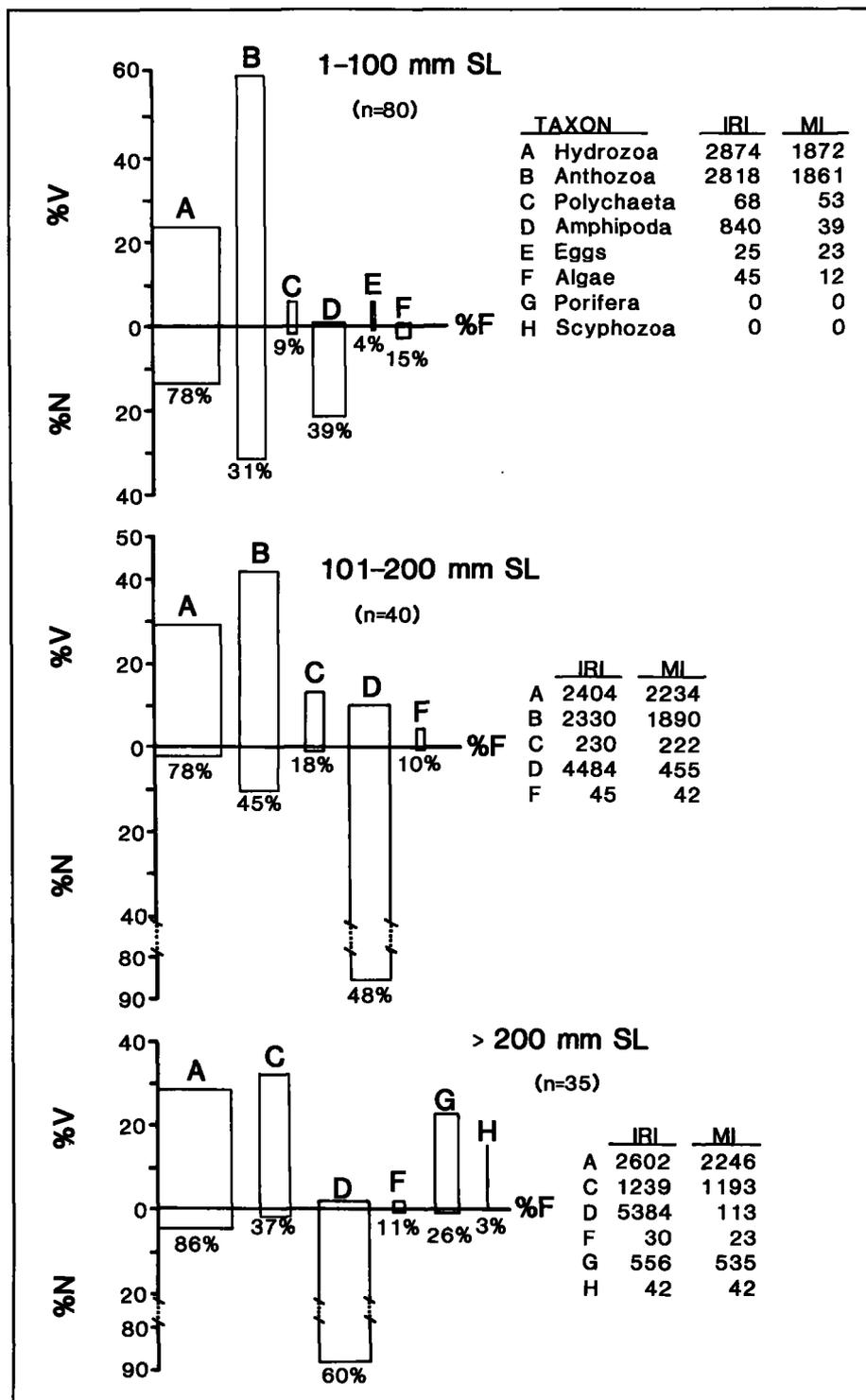
**Figure 4**

Percent frequency (%F), percent number (%N), percent volume (%V), index of relative importance (IRI), and modified index of importance (MI) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters, by strata. Stratum 1 is composed of inshore estuarine habitats; stratum 2 encompasses shallow (<20 m), nearshore habitats with sandy bottoms; stratum 3 includes offshore artificial reef areas and the Murrells Inlet jetties.

while these polychaetes were feeding. Since heads or mouthparts of the polychaetes were usually absent, there were often no countable body parts, making it impossible to determine the number of individuals eaten. I had similar problems in enumerating hydroids, sponges, algae, bryozoans, and occasionally sea anemones and sea pansies. The IRI ranked amphipods as

the dominant prey, followed by hydroids, anthozoans, polychaetes, and sponges. The MI ranked hydroids as the most important taxon, followed by anthozoans, polychaetes, amphipods, and sponges.

Hydroids were the dominant food item for fish from stratum 1, as shown by both the IRI and the MI (Fig. 4). Less important were anthozoans, algae, amphipods

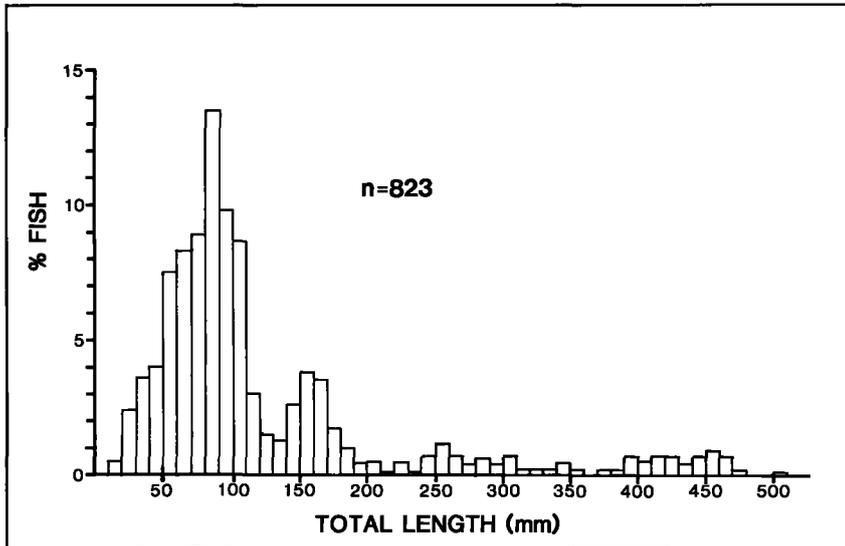


**Figure 5**

Percent frequency (%F), percent number (%N), percent volume (%V), index of relative importance (IRI), and modified index of importance (MI) for higher taxonomic groups of food in the diet of *Chaetodipterus faber* collected in South Carolina waters, by standard length (SL) intervals.

and copepods. In stratum 2, the relative-importance indices indicated anthozoans were the major component of the diet, followed by hydroids. Anthozoans in stomachs of fish from stratum 2 consisted mainly of *Renilla reniformis*. Jellyfish (Scyphozoa) were never seen in stomachs of fish from stratum 1 or stratum 2. The IRI indicated that amphipods were the most impor-

tant prey in stratum 3, while the MI ranked hydroids as the dominant food item. Amphipods composed 91% of the individuals and were found in 63% of the stomachs containing food, but accounted for only 5% of total volume of food in stomachs from stratum 3. Hydroids, on the other hand, were observed in 88% of the stomachs from stratum 3 which contained food and



**Figure 6**  
Percent frequency of *Chaetodipterus faber* within 10-mm TL size classes.

composed 25% of total volume in stratum 3. Percent number was low for hydroids in stratum 3, but they could only be counted as one individual per stomach each time they were encountered, whereas there were usually many amphipods per stomach. The *IRI* ranked hydroids as the second-most important food source, followed by polychaetes (feeding tentacles) and sponges. The *MI* ranked polychaetes second, followed by sponges and amphipods. Although Scyphozoa ranked as one of the top seven food items in stratum 3, it occurred in only one stomach, which was distended with 16 mL (after blotting) of jellyfish. Most stomachs from stratum 3 that were considered full contained 3–6 mL of food.

The *MI* indicated that hydroids were the dominant food for all size classes of *C. faber*, being found in over 75% of the stomachs from each size class and accounting for approximately 25% of the volume in each of the groups (Fig. 5). The *MI* also showed that anthozoans were nearly as important as hydroids for fish up to 200 mm SL, but were not important to fish >200 mm SL. The second-ranking prey for fish >200 mm SL was polychaete-feeding tentacles according to the *MI*. The *IRI* denoted amphipods as a major source of food for fish of all sizes (dominant, by far, for fish >100 mm SL), but this was certainly due to the numerical bias of the *IRI*. The *MI* indicated amphipods were a minor dietary component except for fish 100–200 mm SL, where they were the third-most important prey. Unidentified egg masses, probably gastropod eggs, were found in 4% of the stomachs from fish up to 100 mm, but were a relatively minor component of the diet from fish this size. Sponges were observed in 26% of the stomachs from fish >200 mm SL and accounted for 21% of total volume of prey for these fish, making it

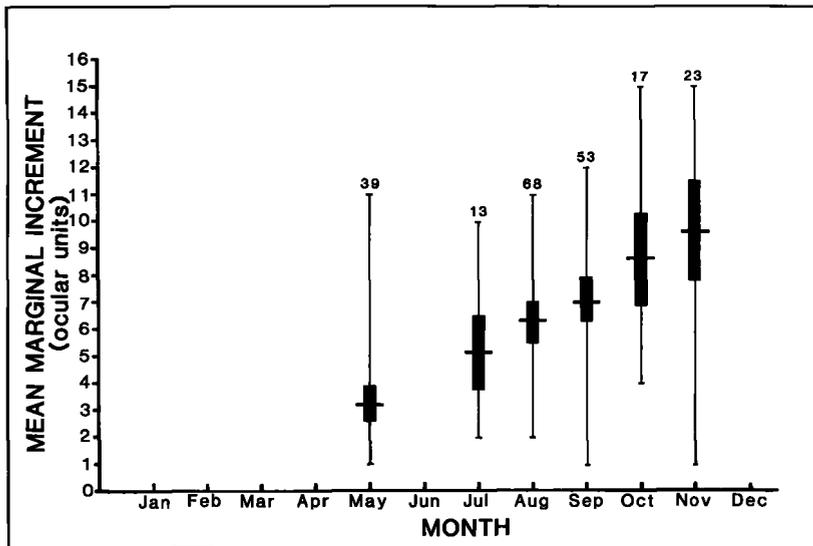
the third-ranked food item for fish in this group according to the *MI*.

### Age and growth

All but 6 of the 643 pairs of otoliths obtained were used in age analysis, since 6 pairs were deemed unreadable due to deformities in otolith structure. Discernment of check marks on whole otoliths of *C. faber* was relatively easy in either reflected or transmitted light, and there was 93% agreement between the two series of counts and measurements. The differences between the remaining 7% (attributable to measurement and recording errors) were satisfactorily resolved, allowing all 637 otolith pairs to be utilized in ageing analysis. The pattern of alternating opaque and translucent bands which were observed on the sagittae were believed to be permanent records of the physiological growth of the Atlantic spadefish from which they had been obtained.

Length-frequency distributions are often used to separate fish of different lengths into age groups and are also utilized to validate ageing techniques, particularly for younger age groups (Lagler 1956, MacDonald 1987). Good agreement was seen between the TLs of fish determined to be age 0 and age 1 by counting opaque zones on otoliths and the range of TLs for the first and second groups in a length-frequency distribution (Fig. 6). Consequently, the innermost opaque zone on each sagitta was believed to be the first annulus.

Since marginal increments on the otoliths should approach zero during the time of annulus formation, the monthly means were calculated to determine if one opaque band was laid down on the sagittae during each year. Generally, the mean marginal increment was lowest in May and increased steadily, by month, through



**Figure 7**  
Mean marginal increments, in ocular units, on the otoliths of *Chaetodipterus faber* by month of capture in South Carolina. Heavy horizontal bars represent mean values, heavy vertical bars represent 95% confidence intervals, and vertical lines represent ranges of measurements. Numbers over each series of values are sample sizes.

**Table 2**  
Sample sizes (*n*), means ( $\bar{x}$ ), and standard deviations (SD) for observed lengths (mm), and weight (g) by age for *Chaetodipterus faber*.

Age	Total length			Standard length			Weight		
	<i>n</i>	( $\bar{x}$ )	SD	<i>n</i>	( $\bar{x}$ )	SD	<i>n</i>	( $\bar{x}$ )	SD
0	421	84	24	424	67	20	424	30	21
1	121	163	21	121	133	17	121	185	74
2	36	265	29	36	216	25	36	670	202
3	21	309	43	21	250	36	21	1063	469
4	10	396	61	10	332	53	10	2107	810
5	17	440	27	17	367	24	17	3025	586
6	7	439	34	7	369	30	7	3087	867
7	0	—	—	0	—	—	0	—	—
8	1	472	—	1	405	—	1	—	—

November (Fig. 7). Although a marginal increment of zero was never observed, there was a strong indication that the opaque zones on the sagittae formed once a year between December and April, and, therefore, justified their use as annular marks. However, these were months when Atlantic spadefish were absent from collection sites and, consequently, no specimens were obtained.

The oldest fish was age 8, although no age-7 fish were collected. Observed mean lengths (TL and SL) and weight increased with age (Table 2), and all least-squares regression relationships were very highly significant ( $P < 0.001$ ) (Table 3). Analysis of the age composition of Atlantic spadefish by stratum showed that all fish taken in stratum 1 were young-of-the-year (age 0) and the fish from stratum 2 were predominantly age 1, although age-0 fish were seen in stratum 2 in

increasing numbers from late summer to late fall. All fish taken on the artificial reefs (stratum 3) were age 2 or older.

Mean back-calculated TLs at age were lower than mean observed TLs for all age groups. Mean back-calculated lengths at preceding annuli, weighted mean back-calculated lengths, and growth increments for all fish age 1 and older are in Table 4. Growth rates differed little between sexes. The von Bertalanffy growth equation, derived from back-calculated mean total lengths at age was:

$$l_t = 490(1 - e^{-0.34(t+0.18)}),$$

where *t* is age in years and *l<sub>t</sub>* is total length at age (Table 5). There was good agreement between the mean observed, mean back-calculated, and theoretical

**Table 3**

Least-squares linear and geometric mean (GM) regression equations of weight (WT) on total length (TL) and standard length (SL), length-length, and TL-ventral otolith radius (OR) for *Chaetodipterus faber* from South Carolina waters. Weight unit in grams, SL and TL units in millimeters, and OR expressed as ocular units (1 ocular unit = 0.04 mm). All least-squares linear regressions were significant at  $P < 0.001$ .

Least-squares equation	n	r <sup>2</sup>	GM functional equation
$\log_{10} \text{ WT} = -10.10 + 2.98 \log_{10} \text{ TL}$	815	0.99	$\log_{10} \text{ WT} = -10.17 + 3.00 \log_{10} \text{ TL}$
$\log_{10} \text{ WT} = -9.08 + 2.90 \log_{10} \text{ SL}$	823	0.99	$\log_{10} \text{ WT} = -9.16 + 2.92 \log_{10} \text{ SL}$
$\text{TL} = 3.9 + 1.2 \text{ SL}$	823	0.99	$\text{TL} = 3.8 + 1.2 \text{ SL}$
$\text{SL} = -3.1 + 0.8 \text{ TL}$	823	0.99	$\text{SL} = -3.2 + 0.8 \text{ TL}$
$\text{TL} = 14.1 + 0.1 \text{ OR}$	634	0.93	$\text{TL} = 13.5 + 0.1 \text{ OR}$

**Table 4**

Mean observed and back-calculated total lengths (mm) at preceding annuli for *Chaetodipterus faber*.

Age (years)	Number of specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli								
			I	II	III	IV	V	VI	VII	VIII	
1	121	163	112								
2	36	265	125	195							
3	21	309	128	199	274						
4	10	396	162	236	305	361					
5	17	440	168	251	317	374	414				
6	7	439	132	210	278	338	383	417			
7	0	—	—	—	—	—	—	—	—	—	—
8	1	472	186	230	302	356	382	409	436	454	
		Weighted mean	123	213	294	363	404	416	436	454	
		Growth increment	123	89	81	69	41	12	20	18	

**Table 5**

Estimated parameters, their standard errors (SE), and 95% confidence limits (CL) of the von Bertalanffy growth equation for *Chaetodipterus faber*. Weighted residual sums of squares = 424.80;  $L_{\infty}$  is the mean asymptotic total length;  $K$  is the growth coefficient; and  $t_0$  is the time (years) at which total length would theoretically be zero.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% CL	
			Lower	Upper
$L_{\infty}$	490.41	15.21	451.31	529.50
$K$	0.34	0.03	0.25	0.42
$t_0$	0.18	0.11	-0.11	0.48

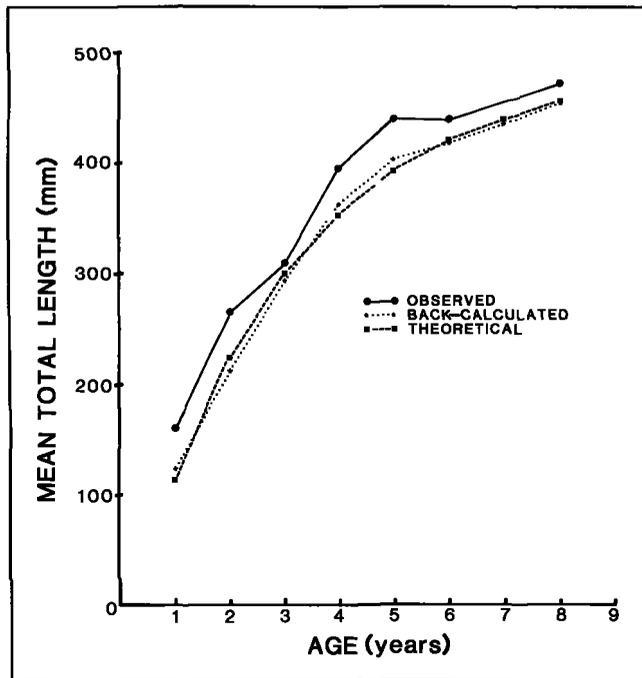
TLs at age (Fig. 8). A mean asymptotic TL ( $L_{\infty}$ ) of 490 mm may be reasonable for fish off South Carolina. The largest recorded *C. faber* landed in South Carolina to date, which was captured and examined during the course of this study, measured 504 mm TL.

## Reproduction

Chi-square tests of the ratios of males to females indicated that there were no significant ( $P > 0.05$ ) deviations from 1♂:1♀ ratios for *C. faber* of all ages combined or for fish grouped by ages 0-6.

Histological examination of reproductive organs revealed that 64% of age-0 males were mature and all males age 1 and older were mature. The smallest spent male was age 0 and 94 mm TL. Ovaries of all age-0 females were immature, while all females age 1 and older were mature. The smallest spent female was 120 mm TL.

Analysis of maturity stages by month indicated spawning activity for *C. faber* lasted from May through September, and the greatest percentage (97%) of developing and ripe gonads was observed in May (Fig. 9). From June to October the percentage of developing and ripe gonads decreased steadily to 0%. All reproductive organs from fish captured in October and November were resting, and no developing gonads were collected after August. Collapsed follicles in various



**Figure 8**

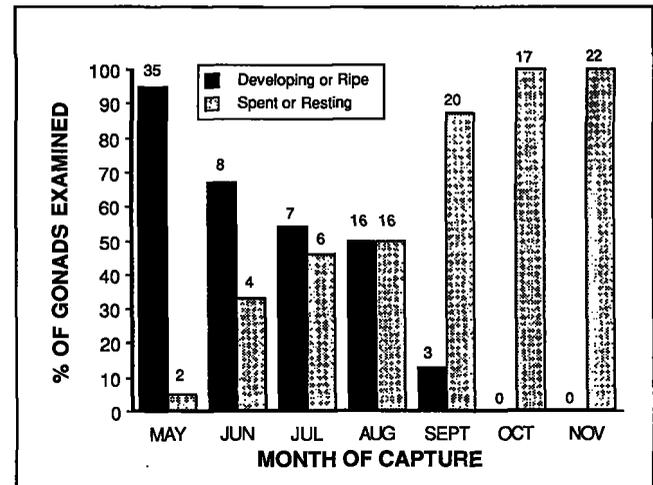
Mean observed, mean back-calculated, and theoretical (von Bertalanffy) total lengths (mm) at age for both sexes of *Chaetodipterus faber* from South Carolina waters.

states of atresia were observed in some histological sections of ovaries which also contained developing oocytes, indicating that some serial spawning took place during the period May–August.

## Discussion

### Analysis of stomach contents

Dietary analysis indicated that *Chaetodipterus faber* in South Carolina eat mostly hydroids, anthozoans such as sea anemones and sea pansies, and polychaete tentacles. Pearce and Stillway (1976) reported the presence of an unusual fatty acid in the liver of *C. faber*. Since coelenterates appear to be the source of this fatty acid in certain fishes and marine turtles, the authors suggested that the elevated levels in Atlantic spadefish could be a reflection of a high dietary intake of coelenterates. Gallaway et al. (1981) believed that the hydroids and other fouling organisms they observed in the stomachs of Atlantic spadefish were being taken from the water column after being sloughed off the understructure of oil platforms. My underwater observations while SCUBA diving provided no evidence that Atlantic spadefish are primarily planktivores as suggested by Gallaway et al. (1981) and I never observed anything to suggest that the ingested hydroids were



**Figure 9**

Maturity stages of age-1 and older *Chaetodipterus faber*, by month of capture in South Carolina waters, to illustrate spawning period. Fishes were grouped according to those with gonads that were developing or ripe and those with gonads that were spent or resting. Numbers over bars are sample sizes.

being culled from the water column. The results of this study agreed with the assessments of Gallaway et al. (1981) and Randall and Hartman (1968) that sponges comprise a portion of the diet. Randall and Hartman (1968) also found that zoantharians, polychaetes, and tunicates were a portion of the stomach contents of Atlantic spadefish.

Although the *IRI* indicated that amphipods were highly important in stomachs obtained by nets and spearing, the numerical bias against the colonial and soft-bodied organisms made it difficult to determine the relative importance of prey of Atlantic spadefish with this index. For this reason, the *MI* was a more reliable measure of relative importance of food in stomachs of *C. faber*. If only soft-bodied and colonial prey were involved, the *IRI* would serve quite adequately; however, when noncountable and countable organisms occur in the same stomachs, numerical bias will make such an index less indicative of the relative importance of different prey. Although it is possible that Atlantic spadefish eat hydroids as a means of simplifying capture of epifaunal invertebrates (such as amphipods) that are usually associated with hydroids, the frequent occurrence of other cnidarians, such as sea anemones and sea pansies (which appeared to support fewer epifaunal invertebrates) in the diet, suggests otherwise.

The diet of *C. faber* collected by hook-and-line was quite different from that of fish obtained by nets and spearfishing. Hook-and-line sampling apparently created a biased overestimate of the importance of jellyfish in the diet of *C. faber*. Moore et al. (1984) used

the same hook-and-line method to capture Atlantic spadefish for stomach content analysis, and similarly found a preponderance of cannonball jellyfish in the diet. Spearfishing may have introduced some bias as well, since this method of collection concentrated on nearbottom fish that were closely associated with the artificial reefs. I observed that Atlantic spadefish spend some time higher in the water column, and schools were occasionally seen at the surface. Atlantic spadefish have also been observed eating *Stomolophus meleagris* and ctenophores at the surface in artificial reef areas (D.L. Hammond, SCWMRD, Charleston, SC 29412, pers. commun., May 1987). Although few ctenophores were identified in this study, their importance to the diet may have been underestimated since the mutilation of ctenophores by ingestive and digestive processes could have made them difficult to detect during analysis of stomach contents. Although jellyfish occurred in the stomach of only one Atlantic spadefish obtained by spearfishing and nets, it was possible that these organisms were more important in the diet than indicated. However, they appear to be considerably less important than indicated by hook-and-line collections.

The shift from a diet dominated by hydroids in strata 1 and 3 to a diet composed primarily of anthozoans in stratum 2 was probably a reflection of differences in food resources available in the different habitats. Juvenile Atlantic spadefish in estuaries (stratum 1) frequent wharves, pilings, and piers (Hildebrand and Schroeder 1928) where hydroids are a major part of the fouling community (Sutherland 1977). Hydroids are also a dominant component of fouling communities on offshore structures (stratum 3) (Wendt et al. 1989). Hydroids were probably less abundant in stratum 2 since unstable substrates, such as sand, generally support fewer hydroids (Calder 1976). However, sea pansies are typically located in sandy bottoms (Barnes 1980) and have been reported as a benthic component in South Carolina's sandy nearshore areas (Shealy et al. 1975, Van Dolah et al. 1983). A similarity in the diets of fish collected from strata 2 and 3 was the presence of an appreciable amount of terebellid polychaete tentacles. Perhaps polychaete tentacles and sea pansies presented a somewhat similar target to *C. faber* since both prey commonly feed with a mass of feeding structures extended from the sand; this suggested that a grazing-type feeding behavior was taking place along sandy bottoms.

Examination of the differences in diets among size classes of Atlantic spadefish showed all size classes relied heavily on hydroids. Although young-of-the-year fish in stratum 1 ate mainly hydroids and relied little on anthozoans for food, the high value for Anthozoa in the diets of small fish (<101 mm SL) was a reflection of numerous young-of-the-year fish which were

collected from stratum 2 in increasing numbers beginning in the early fall. The high values for amphipods in fish 101–200 mm SL was primarily due to unusually large numbers (>1200 individuals in one stomach) found in three stomachs from a single collection at the Murrell's Inlet jetties; a large volume of hydroids was also present in these stomachs. Overall, major changes in food habits within the size range examined were not apparent; even the smallest fish examined (19 mm SL) had eaten primarily hydroids. Differences that existed probably reflected changes in habitat with increasing size. No information is currently available about food habits of larval *C. faber*.

### Age and growth

Some information is available about early development of *C. faber* (Ryder 1887, Hildebrand and Cable 1938, Johnson 1978); however this study presents the only known information of this species' later growth with age. Although the location of the first annular mark on the otoliths has not been thoroughly validated, the size of fish with only one opaque zone on the sagittae corresponded well with the lengths of fish in the second group of a size-frequency distribution (Fig. 6). This also agreed with Hildebrand and Cable (1938), who believed Atlantic spadefish in North Carolina attained a length of 55–100 mm by the end of the first summer and a length of 135 mm (type of measurement unspecified; probably TL) during their second summer. Consequently, I am confident that the first opaque zone is the first annulus. Since young-of-the-year Atlantic spadefish are easily obtained from South Carolina estuaries during the summer and they can survive relatively well in captivity, more thorough validation of the first annulus, as well as additional yearly marks, may be obtained through daily growth studies and marking of otoliths with a chemical such as tetracycline (Beamish and McFarlane 1987).

Marginal increment analysis supported the hypothesis that the opaque zones on sagittae are annuli since they appeared to be formed once a year (over the winter months), although fish were available at collection sites only between May and December. In addition, the data showed (1) a strong relationship between otolith radius and length of the fish; (2) a decrease in growth rate in length with age (except where obscured by small sample sizes); and (3) close agreement between back-calculated lengths and observed lengths at age. The mean asymptotic TL ( $L_{\infty} = 490$  mm TL) was reasonable for South Carolina's Atlantic spadefish population, but small for tropical regions where Atlantic spadefish with lengths up to 900 mm (presumably TL) have been reported (Breder 1948, Johnson 1978).

## Reproduction

Few studies have dealt with the reproductive biology of *C. faber*. Hildebrand and Cable (1938) observed fully mature ripening females at around 135 mm, a size thought to have been attained during the second year (age 1); similarly, I found that all females age 1 and older were mature. Spawning of *C. faber* off South Carolina occurred May to October, and some females spawned more than once (serially) during this period. Serial spawning may allow fishes to produce a greater number of eggs than would be possible if they spawned only once during the year (DeMartini and Fountain 1981). The largest percentage of the fish were prepared to spawn in May, and histological evidence indicated that spawning continued periodically until August. Herrema et al. (1985) found Atlantic spadefish in spawning condition March through June along the east coast of Florida; however, few Atlantic spadefish were collected or examined. Chapman (1978) observed spawning aggregations of *C. faber* during late July off the coast of Georgia. No fecundity estimates for *C. faber* exist, but researchers investigating this would probably wish to use batch fecundity methods which utilize ova diameters to establish groups of eggs that will develop and be spawned at different times (DeMartini and Fountain 1981, Hunter et al. 1985).

The complete life history of the Atlantic spadefish is not well known and warrants further investigation. This study indicated that Atlantic spadefish in South Carolina waters spawn offshore late spring through early fall, with the juveniles subsequently moving into and inhabiting estuarine areas. In the fall, young-of-the-year Atlantic spadefish move into shallow offshore areas, which are also inhabited by age 1 individuals. Historical trawl data from SCWMRD indicated that *C. faber* juveniles were rarely taken in trawls off the coast of South Carolina during winter months, although they were taken in increasing numbers when proceeding southward toward Cape Canaveral, Florida (C.A. Werner, Mar. Resour. Res. Inst., SCWMRD, Charleston, SC 29412, pers. commun., March 1987). In addition, analysis of trawl data from 1973 to 1980, by depth, showed that during the summer young (TLs corresponded to age 0 and age 1) Atlantic spadefish off the coasts of Georgia and Florida were located in depths of 20 m or less, while during the winter the majority of the catches were from depths of 28–56 m (G.R. Sedberry, Mar. Resour. Res. Inst., SCWMRD, Charleston, SC 29412, pers. commun., March 1987). This suggests that the age 0–age 1 group may move southward and into deeper water as the nearshore water cools. Age-2 and older Atlantic spadefish, which are common on South Carolina's artificial reefs and in high-relief

live-bottom areas during the summer, are apparently rare in these areas during the winter.

Practically nothing is known of the whereabouts of South Carolina's Atlantic spadefish during the winter, although a commercial trawler reported capturing several thousand *C. faber* in a single trawl during the winter 50 km off South Carolina's coast (Ogle 1987). Perhaps the fish from artificial reef areas move into deeper water during the winter, returning to these structures the following spring as water temperatures increase along the coast.

Presently, there is an effort by SCWMRD personnel to promote tagging of Atlantic spadefish by recreational fishermen (D.L. Hammond, SCWMRD, Charleston, SC 29412, pers. commun., May 1987). Many more fish will probably have to be tagged before adequate returns are seen, but tagging could lead to an increased understanding of *C. faber* movements, allow population estimates to be made, and, if used in conjunction with tetracycline marking of otoliths, could lead to thorough validation of the ageing technique presented here.

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## Appendix

Percent frequency of occurrence (%F), percent of total number (%N), percent of total volume (%V), index of relative importance (IRI), and the modified index of importance (MI) for food items of *Chaetodipterus faber* collected in South Carolina waters using nets or pole spears.

Prey item	%F	%N	%V	IRI	MI
<b>Algae</b>					
<i>Cladophora laetiverens</i>	0.65	0.03	0.01	0.03	0.01
<i>Gracilaria folifera</i>	3.23	0.14	1.25	4.49	4.04
<i>Hypnea musciformis</i>	3.87	0.17	0.82	3.83	3.17
<i>Ulva</i> sp.	0.65	0.03	0.03	0.04	0.02
Algae undetermined	8.39	0.37	0.12	4.08	1.01
Total Algae	12.90	0.73	2.33	39.56	30.06
<b>Porifera</b>					
<i>Leucoselenia</i> sp.	0.65	0.03	0.02	0.03	0.01
<i>Scypha barbadiensis</i>	0.65	0.03	0.50	0.34	0.33
<i>Scypha</i> sp.	0.65	0.03	0.42	0.29	0.27
Porifera undetermined	5.16	0.23	11.74	61.76	60.58
Total Porifera	6.45	0.31	13.25	87.50	85.46
<b>Cnidaria</b>					
<b>Hydrozoa</b>					
<i>Aglaophenia rigida</i>	0.65	0.03	0.07	0.06	0.05
<i>Aglaophenia</i> sp.	1.29	0.06	0.05	0.14	0.06
<i>Campanularia</i> sp.	0.65	0.03	0.01	0.03	0.01
<i>Clytia</i> sp.	1.29	0.06	0.04	0.12	0.05
<i>Dynamena cornicina</i>	0.65	0.03	0.22	0.16	0.14
<i>Dynamena</i> sp.	0.65	0.03	<0.01	0.02	<0.01
<i>Eudendrium rameum</i>	1.29	0.06	0.67	0.94	0.86
<i>Eudendrium ramosum</i>	3.87	0.17	1.98	8.31	7.66
<i>Eudendrium</i> sp.	21.94	0.96	12.55	296.39	275.35
<i>Halocordyle disticha</i>	3.23	0.14	0.38	1.67	1.23
<i>Lafaea fruticosa</i>	1.29	0.06	0.53	0.76	0.68
<i>Lytocarpus</i> sp.	1.29	0.06	0.02	0.10	0.03
<i>Monostaechas quadridens</i>	0.65	0.03	0.08	0.07	0.05
<i>Obelia dichotoma</i>	1.94	0.08	0.18	0.51	0.35
<i>Obelia geniculata</i>	1.94	0.08	0.41	0.95	0.80
<i>Obelia</i> sp.	3.87	0.17	0.72	3.46	2.79
<i>Plumularia</i> sp.	0.65	0.03	0.56	0.38	0.36
<i>Sertularia distans</i>	5.81	0.25	0.04	1.70	0.23
<i>Sertularia</i> sp.	3.23	0.14	0.07	0.68	0.23
Sertulariidae	2.58	0.11	1.69	4.66	4.36
Tubulariidae	0.65	0.03	0.22	0.16	0.14
Hydrozoa undetermined	43.87	1.92	4.91	299.29	215.40
Total Hydrozoa	79.35	4.51	26.53	2463.62	2105.16
<b>Anthozoa</b>					
<b>Actiniaria</b>					
Actiniaria	14.84	3.41	7.73	165.34	114.71
<b>Octocorallia</b>					
Octocorallia	0.65	0.03	0.50	0.34	0.33
<i>Renilla reniformis</i>	16.77	6.20	9.33	260.56	156.46
Total Anthozoa	29.03	9.64	18.35	812.54	532.70
<b>Scyphozoa</b>					
<i>Chiropsalmus quadrumanus</i>	0.65	0.03	9.37	6.06	6.09
<b>Ctenophora</b>					
Ctenophora	4.52	0.20	0.36	2.52	1.63
<b>Annelida</b>					
<b>Polychaeta</b>					
<i>Sabellaria</i> sp.	1.29	0.11	<0.01	0.15	<0.01
Sabellariidae	0.65	0.08	0.01	0.06	0.01
Terebellidae	12.90	0.56	22.72	300.39	293.09
Polychaeta undetermined	3.23	0.14	0.39	1.70	1.26
Total Polychaeta	17.42	0.90	24.14	436.17	420.52

Appendix (continued)					
Prey item	%F	%N	%V	IRI	MI
<b>Mollusca</b>					
<b>Gastropoda</b>					
<i>Anachis</i> sp.	0.65	0.06	0.01	0.04	0.01
<i>Mitrella lunata</i>	0.65	0.03	0.01	0.02	0.01
<i>Nudibranchia</i>	0.65	0.11	0.01	0.08	0.01
<i>Turbonilla</i> sp.	0.65	0.03	<0.01	0.02	<0.01
Gastropoda undetermined	2.58	0.11	0.03	0.37	0.08
Total Gastropoda	5.16	0.34	0.06	2.03	0.31
<b>Pelecypoda</b>					
<i>Anadara transversa</i>	0.65	0.03	<0.01	0.02	<0.01
<i>Musculus lateralis</i>	4.52	0.31	0.02	1.47	0.09
Pelecypoda undetermined	5.16	0.42	0.14	2.89	0.72
Total Pelecypoda	9.68	0.76	0.16	8.91	1.55
<b>Arthropoda</b>					
<b>Pycnogonida</b>					
<i>Anoplodactylus insignis</i>	0.65	0.03	0.02	0.03	0.01
<b>Crustacea</b>					
<b>Ostracoda</b>					
Ostracoda	1.94	0.11	<0.01	0.22	<0.01
<b>Copepoda</b>					
Calanoida	1.29	0.08	<0.01	0.11	<0.01
Cyclopoida	1.29	0.37	<0.01	0.48	<0.01
Harpacticoida	9.68	3.35	0.03	32.76	0.29
Copepoda undetermined	0.65	0.17	<0.01	0.11	<0.01
Total Copepoda	12.26	3.98	0.04	49.17	0.49
<b>Cirripedia</b>					
<i>Balanus</i> sp.	5.16	0.37	0.07	2.24	0.36
Cirripedia undetermined	1.94	0.14	<0.01	0.28	<0.01
Total Cirripedia	7.10	0.51	0.07	4.13	0.50
<b>Mysidacea</b>					
Mysidacea	0.65	0.06	<0.01	0.04	<0.01
<b>Tanaidacea</b>					
Tanaidacea	0.65	0.03	<0.01	0.02	<0.01
<b>Isopoda</b>					
<i>Paracerceis caudata</i>	0.65	0.17	0.02	0.12	0.01
<b>Amphipoda</b>					
<i>Ampithoe</i> sp.	5.16	1.30	0.06	7.00	0.31
<i>Batea catherinensis</i>	7.10	1.01	0.03	7.41	0.21
<i>Caprella equilibra</i>	11.61	3.07	0.15	37.44	1.74
<i>Caprella penantis</i>	17.42	42.46	2.25	778.74	39.20
Caprellidae undetermined	3.23	0.54	0.01	1.76	0.03
<i>Cerapus tubularis</i>	1.94	8.09	0.18	16.01	0.35
<i>Dulichthella appendiculata</i>	1.94	0.28	0.04	0.62	0.08
<i>Erichthonius brasiliensis</i>	18.71	6.06	0.22	117.50	4.12
Gammaridea undetermined	11.61	0.90	0.03	10.83	0.35
<i>Gammaropsis</i> sp.	2.58	0.23	0.01	0.60	0.03
Hyperiididae undetermined	0.65	0.03	<0.01	0.02	<0.01
<i>Jassa falcata</i>	7.74	8.91	0.31	71.39	2.40
<i>Lembos</i> sp.	1.29	0.14	<0.01	0.19	<0.01
<i>Luconacia incerta</i>	2.58	0.54	0.02	1.44	0.05
<i>Phtisica marina</i>	4.52	1.16	0.05	5.43	0.23
<i>Stenothoe georgiana</i>	5.16	1.10	0.03	5.83	0.15
<i>Stenothoe minuta</i>	3.23	0.23	0.01	0.74	0.03
<i>Stenothoe</i> sp.	0.65	0.03	<0.01	0.02	<0.01
Total Amphipoda	45.81	76.06	3.55	3646.63	162.63
<b>Decapoda</b>					
Natantia undetermined	1.29	0.11	0.05	0.21	0.06
Xanthidae undetermined	0.65	0.03	0.01	0.02	0.01
Brachyura undetermined	2.58	0.17	0.02	0.48	0.05
Decapoda undetermined	1.29	0.06	0.01	0.09	0.01
Total Decapoda	4.52	0.37	0.09	2.05	0.41

Appendix (continued)					
Prey item	%F	%N	%V	IRI	MI
<b>Bryozoa</b>					
<i>Anguinella palmata</i>	1.94	0.08	0.02	0.19	0.04
<i>Bugula neritina</i>	7.74	0.34	0.15	3.75	1.16
<i>Bugula</i> sp.	1.29	0.06	0.01	0.09	0.01
<i>Schizoporella errata</i>	0.65	0.03	<0.01	0.02	0.01
<i>Sundanella sibogae</i>	1.29	0.06	0.07	0.16	0.09
Bryozoa undetermined	7.10	0.31	0.07	2.68	0.50
Total Bryozoa	17.42	0.87	0.33	20.92	5.75
<b>Echinodermata</b>					
Ophiuroidea undetermined	1.94	0.08	0.04	0.24	0.08
<b>Chordata</b>					
Urochordata					
Ascidiacea					
<i>Didemnum candidum</i>	0.65	0.03	<0.01	0.02	<0.01
<i>Distaplia bermudiensis</i>	1.29	0.06	0.07	0.16	0.09
<i>Eudistoma carolinense</i>	1.94	0.08	0.30	0.75	0.58
Ascidiacea undetermined	0.65	0.03	0.04	0.04	0.03
Total Ascidiacea	3.23	0.20	0.43	2.03	1.39
Pisces (scales)	0.65	0.03	<0.01	0.02	<0.01
Eggs undetermined	1.94	0.08	0.84	1.72	1.63
Number of stomachs examined:	177				
Examined stomachs with food:	155				