



## Age, growth, and reproductive biology of the blackbelly rosefish from the Carolinas, U.S.A.

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Otoliths and gonads of blackbelly rosefish *Helicolenus dactylopterus dactylopterus* were collected from the commercial fishery off the Carolinas in 1994–1997. Opaque bands on transverse sections of otoliths were determined to be annuli by analysis of marginal increments. Opaque zone formation occurs between July and January. Ages ranged from 7 to 30 years. Blackbelly rosefish have intraovarian gestation. Fertilization is internal, as free spermatozoa were found primarily in resting ovaries from July through early December with peak occurrence in September through November. There was a delay of 1–3 months before fertilization, as oocyte development did not begin until December. Occurrence during January through April of early-celled embryos, the most advanced stage observed, and postovulatory follicles indicated that oocyte development was rapid. Egg development occurs in a clear gelatinous matrix secreted into the ovarian cavity. The reproductive mode is a zygotarous form of oviparity, intermediate between oviparity and viviparity. Population sex ratio departed markedly from 1 : 1 for most length intervals. Males were more abundant at lengths >250 mm  $L_T$  and the overall male : female ratio was 1 : 0.60. © 1998 The Fisheries Society of the British Isles

Key words: life history; otoliths; reproduction; maturity; spawning; zygotarous.

### INTRODUCTION

Blackbelly rosefish *Helicolenus dactylopterus dactylopterus* (Delaroche 1809), is a deep-water (>200 m) species that occurs in the North and South Atlantic Oceans and in the southern Indian Ocean (Eschmeyer, 1969). Off the Carolinas it is captured on the continental slope, predominantly by the bottom longline fishery that targets snowy grouper *Epinephelus niveatus* (Valenciennes) and tilefishes (Malacanthidae), and in the vertical line fishery for wreckfish *Polyprion americanus* (Schneider). Blackbelly rosefish has limited economic importance in the United States at present because the commercial fishery is relatively new and small (Table I). Only five vessels, two in South Carolina, two in North Carolina (F. Rohde, North Carolina Department of Environment, Health, and Natural Resources, pers. comm.), and one in Florida (J. Moran, South Carolina Department of Natural Resources, pers. comm.) are known to land blackbelly rosefish in the south-eastern United States.

Because the fishery is newly developed and the species potentially underutilized, this is an appropriate time to collect baseline life-history information. There are no regulations or management plans for this species in place. To date, no age and growth studies on *H. d. dactylopterus* in the western Atlantic have

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TABLE I. Regional landings of *H. d. dactylopterus* between 1989–1996 from Trip Interview Program (TIP) sampling in North Carolina, South Carolina, Georgia and Florida (J. Moran, pers. comm., South Carolina Department of Natural Resources); no landings of blackbelly rosefish were reported prior to 1989

Year	Tonnes	\$1000(US)
1989*	1.37	2.00
1990*	1.91	2.84
1991	8.96	10.82
1992	42.75	59.37
1993	54.97	75.35
1994	48.48	80.71
1995†	41.66	62.60
1996*	20.95	34.17

\*South Carolina landings only; North Carolina, Georgia and Florida landings not available.

†North Carolina and South Carolina landings only; Georgia and Florida landings not available.

been published, however there have been two studies conducted in the eastern Atlantic (Esteves *et al.*, 1997; Kelly *et al.*, unpublished). *Helicolenus percooides* Richardson (Withell & Wankowski, 1988) and many species in the closely related genus *Sebastes* (Beamish & McFarlane, 1987; Leaman & Nagtegaal, 1987; Wilson & Boehlert, 1990; Pearson *et al.*, 1991) have been studied and found to be long-lived. For example, some scorpaenids attain ages of at least 140 years (Beamish & McFarlane, 1987). The objectives of this study were to examine the age and growth, sex ratio, maturity and reproductive cycle of *H. d. dactylopterus* off the coast of the Carolinas, U.S.A.

## MATERIALS AND METHODS

Otoliths and gonad tissue were taken from blackbelly rosefish specimens that were landed by commercial fishermen in North and South Carolina between December 1994 and June 1996 and between January and March 1997. The specimens were captured between 32°35' N and 33°15' N, at depths of 180–250 m (Fig. 1). Samples collected in 1997 were utilized only in the study of reproductive biology. Lengths (total and standard, mm) and whole weight (g) were measured for all fish sampled. All length measurements in the text refer to total length ( $L_T$ ). The left and right sagittal otoliths were removed from all fish and stored dry prior to processing.

Each left otolith was embedded in Araldite epoxy resin, and a thin (0.3 mm) transverse section (Fig. 2) was cut through the core with a Buehler Isomet low-speed saw. Sections were mounted on glass slides using a liquid mounting medium (Baxter Scientific Products Accu-Mount 60). Otolith sections ( $n=1154$ ) were examined with transmitted light under a dissecting microscope that was equipped with an Hitachi KP-C550 video camera and monitor, a personal computer with a Matrox frame grabber and Optimas image analysis software. Otolith increments were counted independently by two readers. If counts differed, both readers examined the otolith by viewing the image on the video monitor. If

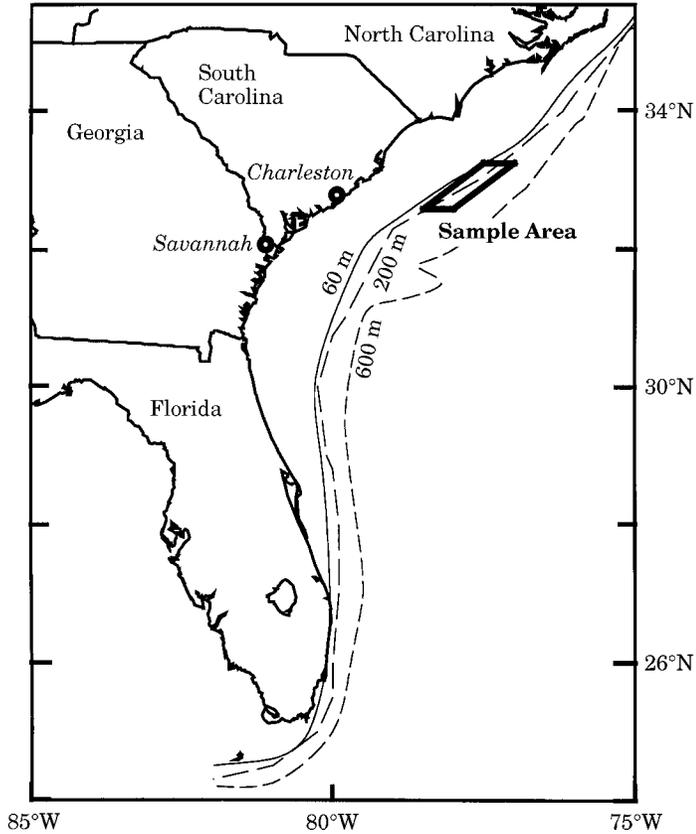


FIG. 1. Approximate area of fishing effort for *H. d. dactylopterus* off the Carolinas between December 1994 and March 1997.

no agreement could be reached, the otolith was rejected. Otoliths that were rejected were those that could not be interpreted easily because of random preparation problems. There were no obvious growth effects that caused difficulty in interpretation. Von Bertalanffy's growth equation was used to relate length and age. With the exception of sex ratio data, analysis was performed using SAS software (SAS Institute Inc., 1991).

The width of the marginal increment was measured on the digitized image with Optimas software. Each measurement was standardized by dividing marginal increment width by the largest marginal increment for that age class. Due to the change in growth axis, only a subsample ( $n=294$ ) of otoliths was utilized for marginal increment analysis.

Samples of gonad tissue were obtained from 1343 specimens. The posterior portion of the gonad was fixed in 10% seawater-formalin for 7–14 days and transferred to 50% isopropanol for 7–14 days. Gonad samples were processed and vacuum infiltrated in a Modular Vacuum Tissue Processor, and blocked in paraffin. Three transverse sections (6–8  $\mu\text{m}$ ) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y. Sex and reproductive stage were then determined microscopically by two readers independently using histological criteria (Table II). If their assessments differed, both readers examined the section by viewing the image on a video monitor. If no agreement could be reached, the section was rejected. Sex and reproductive stage could not be determined for 2.8% ( $n=38$ ) of the specimens.

Specimens in developing, spawning, spent, or resting stages were considered to be sexually mature. For females, this definition of sexual maturity included specimens with



FIG. 2. Sectioned otolith from a 284 mm *L<sub>T</sub> H. d. dactylopterus*, age 17 years, captured June 1996, viewed with transmitted light. Alternate annuli are shown by arrows. Note: the otolith core is not visible in order to show all annuli.

TABLE II. Histological criteria used to determine reproductive stage in *H. d. dactylopterus* (Wallace & Selman 1981; Hunter & Macewicz 1985; Wenner *et al.*, 1986)

Reproductive stage	Male	Female
Uncertain maturity Immature (virgin)	Inactive testes; resting or immature Small transverse section compared to resting male; spermatogonia and little or no spermatocyte development; lobules and spermatid duct not as evident as in resting stage	Inactive ovaries; previtellogenic oocytes only; immature or resting Previtellogenic oocytes only, no evidence of atresia. In comparison to resting female, most previtellogenic oocytes <70 µm in diameter, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles and are not as elongate, germinal epithelium along margin of lamellae is thicker, and ovarian wall is thinner See below
Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and ducts	
Spawning	Predominance of spermatozoa in lobules; spermatozoa abundant in spermatid duct; little or no occurrence of spermatogenesis	Completion of yolk coalescence and hydration in most advanced oocytes; zona radiata becomes thinner; early-celled embryos present
Spent	No spermatogenesis; some residual spermatozoa in lobules and spermatid duct	More than 50% of vitellogenic oocytes with alpha- or beta-stage atresia
Resting	Large transverse section compared to immature male; little or no spermatocyte development; residual spermatozoa in ducts, though less than in spent stage	Previtellogenic oocytes only with traces of atresia possible. In comparison to immature female, most previtellogenic oocytes >70 µm, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, germinal epithelium along margin of lamellae is thinner, ovarian wall is thicker Most advanced oocytes in cortical-alveoli stage
Early developing, cortical alveoli		
Developing, vitellogenesis		Most advanced oocytes in yolk-granule or yolk-globule stage
Final oocyte maturation		Most advanced oocytes in migratory-nucleus stage; partial coalescence of yolk globules possible
Developing, recent spawn		Presence of postovulatory follicles and vitellogenic oocytes

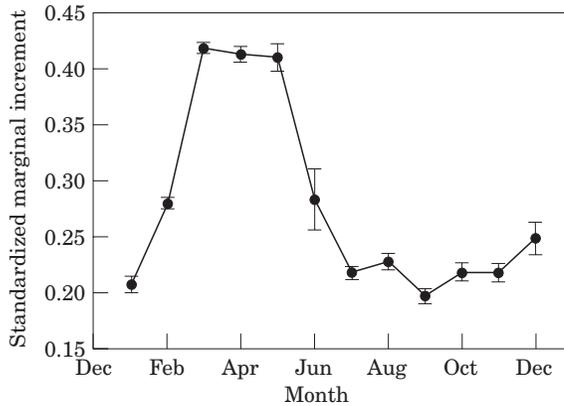


FIG. 3. Marginal increment ( $\pm 1$  S.E.) by month for *H. d. dactylopterus* captured off the Carolinas.  $n=294$ .

oocyte development at or beyond the cortical granule (alveoli) stage and specimens with beta, gamma, or delta stages (Hunter & Macewicz, 1985) of atresia. To ensure that females were assigned correctly to the immature and resting categories, the length–frequency histograms of females with evidence of certain maturity (developing, ripe, or spent) and resting females were compared.

To estimate the sex ratio in the population, the data were restricted to collections that represented random sampling; collections in which females were sampled selectively for the study of reproductive biology were eliminated. The  $\chi^2$  goodness-of-fit test (Zar, 1984), with Yates' correction for continuity, was used to compare the sex ratio in each 25-mm length interval with a hypothetical 1 : 1 ratio. The result was considered significant if  $P < 0.01$ .

## RESULTS

Ages could be determined for 98.3% ( $n=1134$ ) of the sectioned otoliths examined. Initial agreement between readers was 11.3% ( $n=128$ ); however, counts differed by only one or two annuli for 48.8% ( $n=554$ ) of the specimens. The mean width of the marginal increments by month for all age groups combined indicated that opaque zone formation occurs once a year between July and January (Fig. 3). Specimens ranged in length from 165–412 mm (Fig. 4) and in age from 7 to 30 years, with a mean age of 15.97 (Fig. 5).

Mean lengths increased with increasing age for the first 25 years. At ages >25 years, the mean length at age appeared to decrease (Fig. 6); however, the sample size of fish >25 years was small ( $n=19$ ). The mean length of all females was significantly less (12 mm) than the mean length of all males [ $t=5.037$ ,  $P < 0.00001$ , d.f.=1125 (Fig. 7)]; however the mean length of females was significantly less than the mean length of males only for age classes 9, 13, 14, 16, 18, and 26 (Table III). We were unable to fit the von Bertalanffy growth equation, or any other growth function, to our mean length at age data.

No conclusively immature specimens were collected. Two of the 748 males examined, 14 years/256 mm and 15 years/275 mm, were either immature or resting [Fig. 8(a)]. There was no evidence of spermatogenesis and residual spermatozoa were not present in lobular lumina and ducts [Fig. 9(a)], indicating

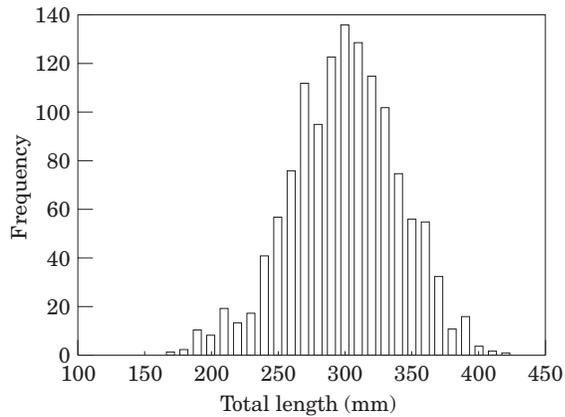


FIG. 4. Length–frequency distribution of *H. d. dactylopterus* captured off the Carolinas.  $n=1309$ ; mean=295.59.

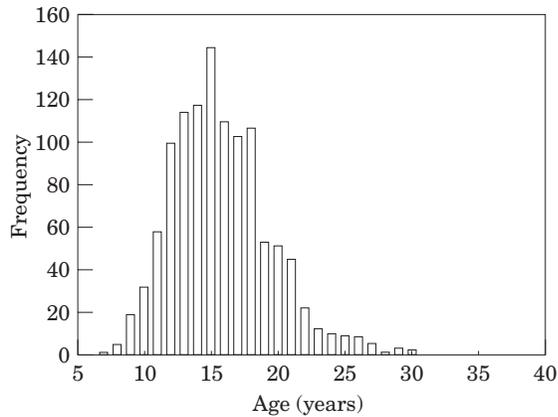


FIG. 5. Age–frequency distribution of *H. d. dactylopterus* captured off the Carolinas.  $n=1135$ ; mean=15.97.

that these specimens had not spawned previously. In mature males including most resting-stage males, spermatozoa were present throughout the year in lobular lumina and the stalk-like system of ducts [Fig. 9(b)]. Nine of the 445 females examined were either immature or resting [Fig. 8(b)]. Their ages and sizes ranged from 10 to 15 years and 215–289 mm. For both sexes, the general overlap in the length–frequency histograms for resting specimens and specimens with evidence of certain maturity indicated that males and females were assigned accurately to immature and resting stages.

The reproductive mode appeared to be intermediate between oviparity and viviparity. Histological sections contained evidence of internal fertilization, as free spermatozoa [Fig. 10(a)] were observed in resting or developing ovaries between July and early December, with peak occurrence between September and November (Table IV). This peak corresponded to the spawning peak noted for

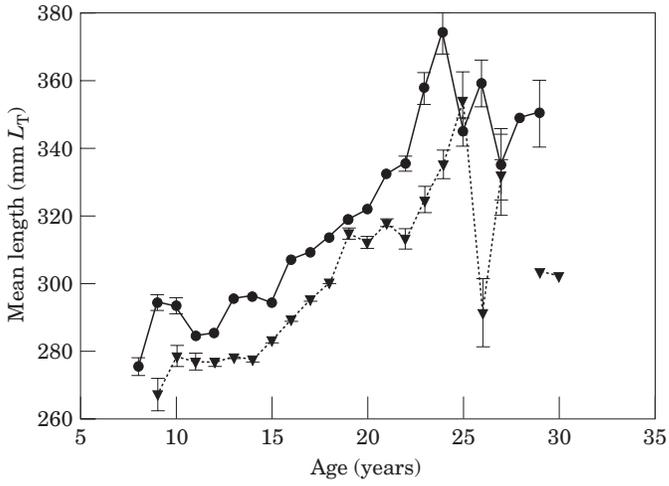


FIG. 6. Mean observed growth curves ( $\pm$  1 S.E.) of male ( $\bullet$ ,  $n=639$ ) and female ( $\blacktriangledown$ ,  $n=405$ ) *H. d. dactylopterus* captured off the Carolinas.

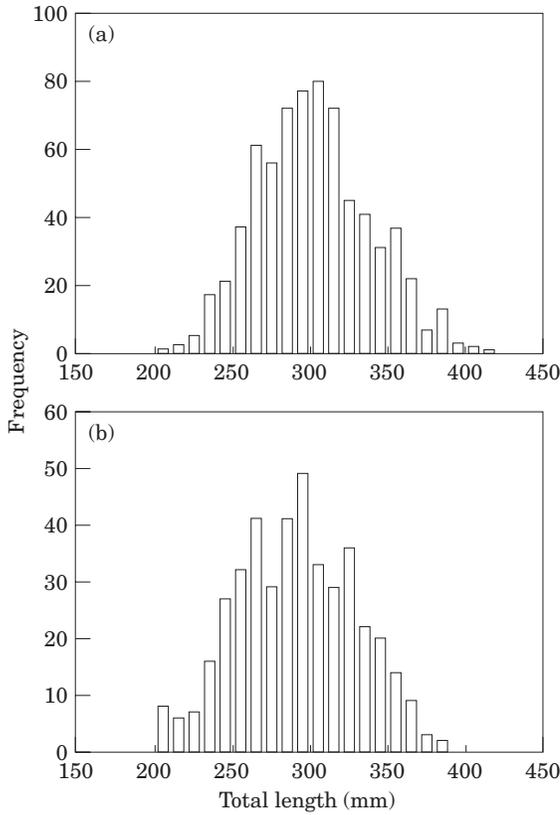


FIG. 7. Length-frequency histograms for male (a) and female (b) *H. d. dactylopterus* sampled randomly.

TABLE III. Comparisons of observed mean  $L_T$  of male and female *H. d. dactylopterus* by age class using analysis of variance (ANOVA)

Age	<i>P</i>	<i>F</i>	d.f.
7	—	—	—
8	—	—	—
9	0.0472*	4.99	12
10	0.4020	0.73	25
11	0.4649	0.54	49
12	0.3064	1.06	88
13	0.0217*	5.43	102
14	0.0016*	10.52	111
15	0.0654	3.45	133
16	0.0136*	6.31	102
17	0.0588	3.66	99
18	0.0406*	4.30	101
19	0.6426	0.22	51
20	0.2380	1.43	49
21	0.0776	3.27	44
22	0.0650	3.86	19
23	0.0787	3.83	11
24	0.0507	5.28	9
25	0.6117	0.29	7
26	0.0351*	7.35	7
27	0.9068	0.02	3
28	—	—	—
29	0.3022	3.76	2
30	—	—	—

\* $P < 0.05$ .

Dashed lines indicate that samples were not available for one sex.

males [Fig. 11(a)]. Spermatogenesis occurred in males during all months and resting individuals were common only between January and March.

There was a delay between insemination and fertilization, as oocyte development did not begin until December, which was after the peak occurrence of free spermatozoa in ovaries [Fig. 11(b)]. Seventy-seven per cent of the 116 females with free spermatozoa were in the resting stage. After insemination, spermatozoa were stored until fertilization in crypts that formed near the bases of lamellae. These crypts were often adjacent to blood vessels [Fig. 10(b)]. The abrupt appearance of yolk globule-stage oocytes in early December and the subsequent short (<2 months) period before the occurrence of spawning individuals indicated that oocytes develop rapidly. Developing oocytes were suspended on stalks radiating from lamellae which in turn projected radially from the central stroma. The stroma extended longitudinally through the ovary and was connected to the ovarian wall only at the anterior end of each lobe. Stalk length increased over time with the result that there was a progressive increase in oocyte size from the centre of the ovary to the ovary wall [Fig. 12(a)].

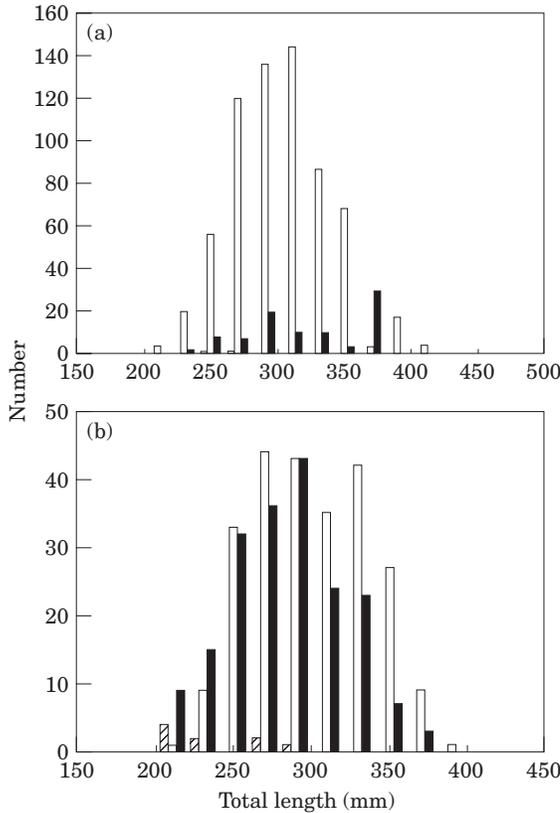


FIG. 8. A comparison of length-frequencies for 748 male (a) and 445 female (b) specimens of *H. d. dactylopterus* categorized as uncertain maturity (immature or resting) (▨), definitely mature (□), and resting (■). Specimens categorized as definitely mature were developing, spawning, or spent.

Capillaries in the stalk [Fig. 12(b)] provide blood flow to an individual oocyte and the stalk functions to place the oocyte into the ovarian cavity and near the ovary wall, where a clear gelatinous matrix envelops the eggs after ovulation and fertilization.

Eggs developed within the gelatinous matrix into early-celled embryos composed of an undifferentiated mass of cells approaching the blastula stage and a large yolk mass [Fig. 12(c)]. At parturition, the embryos are extruded presumably in the gelatinous matrix. Based on the percentage frequencies of spawning-stage individuals and postovulatory follicles, female rosefish spawned between December and April, with a peak in February and March [Fig. 11(b)].

The population sex ratio departed markedly from 1:1 for most length intervals (Table V). The overall ratio was  $1\text{♂} : 0.60\text{♀}$ . At lengths  $\leq 250$  mm, the ratio was not significantly different from 1:1, whereas males were more abundant at lengths  $>250$  mm. Females were most abundant during September ( $1\text{♂} : 1.03\text{♀}$ ), October ( $1\text{♂} : 0.83\text{♀}$ ), and November ( $1\text{♂} : 1.03\text{♀}$ ), which corresponded to the spawning peak for males.



FIG. 9. Transverse sections of testes in (a) immature (275 mm  $L_T$ , bar=100  $\mu\text{m}$ ) and (b) late developing (280 mm  $L_T$ , bar=400  $\mu\text{m}$ ) *H. d. dactylopterus*. d, Efferent ducts.

## DISCUSSION

Growth of blackbelly rosefish described here is that of mature males and females. Our samples contained no specimens ages 0–6 years, and therefore offer little insight into the life history of the juvenile stage. The relatively slow growth of mature fish cannot be extrapolated to young (ages 0–6) fish.

Withell & Wankowski (1988) reported an age range of 2–42 years for *H. percoides*, which is similar to *H. d. dactylopterus* ages (7–30 years) found in this study. Esteves *et al.* (1997), reading whole otoliths from specimens of a similar size, found *H. d. dactylopterus* from the Azores to be age 3–14 years but the ages are possibly underestimated because reading whole otoliths is inaccurate for long-lived species (Beamish & McFarlane, 1987; Maceina & Betsill, 1987).

The absence of younger age classes (0–6) in this study suggests that *H. d. dactylopterus* is not recruited into the commercial deep-water longline fishery until *c.* age 7. Juvenile *H. d. dactylopterus* are present in the deep-water fish community as they have been observed, via submersible, to occupy tilefish burrows (C. Grimes, National Oceanic Atmospheric Administration/National

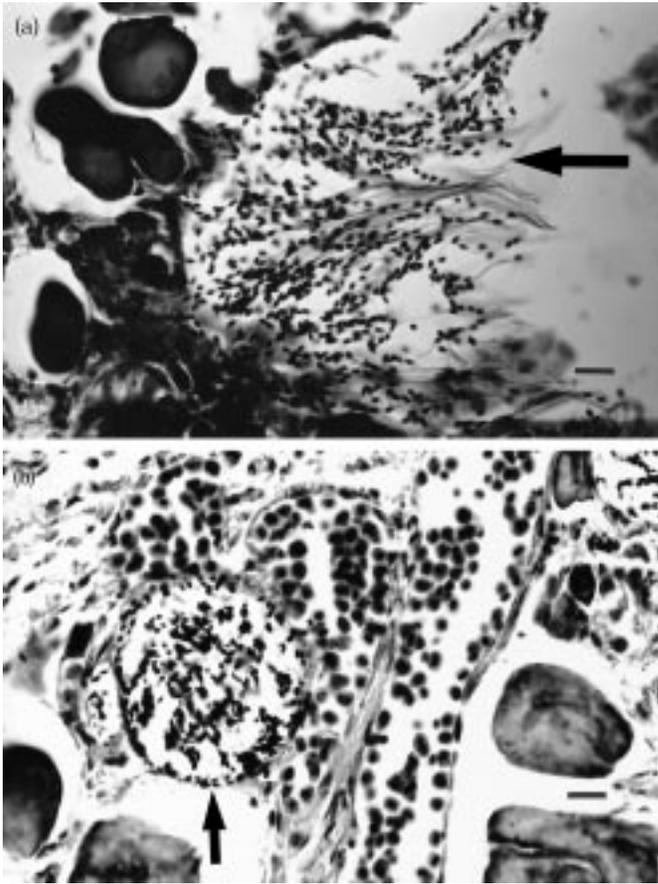


FIG. 10. Transverse sections of (a) free spermatozoa in a resting female *H. d. dactylopterus* captured in October and (b) crypt of spermatozoa in a developing female *H. d. dactylopterus* captured in early December (bar = 10  $\mu$ m).

Marine Fisheries Service, pers. comm.). The decrease in size-at-age after age 25 is possibly a result of small sample sizes for these older age classes, although Pearson *et al.* (1991) reported a similar decrease in size-at-age for female *Sebastes jordani* (Gilbert). Marginal increment formation suggests that somatic growth of blackbelly rosefish is primarily between March and May, which substantiates their slow growth and small size.

The findings of Kelly *et al.* (unpublished) that male blackbelly rosefish mature at 11–15 years (260 mm), and females at 14–19 years (230 mm) off the coast of Ireland, supports our preliminary findings that males and females mature potentially at 14–15 years (256–275 mm) and 10–15 years (215–289 mm) respectively. Additional juvenile and small adult specimens are needed to define size and age at maturity conclusively.

Blackbelly rosefish exhibit an atypical reproductive mode for teleosts, as they have internal fertilization and intraovarian gestation (Krefft, 1961; Sánchez & Acha, 1988). This mode of reproduction is found in only two teleost families, the Scorpaenidae and Zoarcidae (Wourms *et al.*, 1988). Internal fertilization is the

TABLE IV. Occurrence of free spermatozoa in the ovaries of 534 *H. d. dactylopterus*

Month	Number examined	% with spermatozoa
January	39	0.0
February	50	2.0
March	82	0.0
April	55	0.0
May	41	0.0
June	15	0.0
July	26	11.5
August	24	12.5
September	37	64.9
October	65	63.1
November	52	71.2
December	48	14.6

rule in the subfamily Sebastinae (Boehlert & Yamada, 1991), which is composed of the genera *Hozukius*, *Helicolenus*, *Sebastes*, and *Sebastes*. In the present study, the period of gestation was probably 20–30 days, as yolk globule-stage oocytes were present in early December and embryos were noted in late January. This estimate seems reasonable because species of *Sebastes* that release larvae at parturition (viviparity) have gestation periods of 30–60 days (Moser, 1967; Bowers, 1992; Nichol & Pikitch, 1994). Reproductive mode in *Helicolenus* ranges from a zygoparous form of oviparity, characteristic of *H. d. dactylopterus*, to viviparity (release of full-term embryos) in *H. percooides* (Wourms, 1991).

A notable feature, previously undescribed, of the reproductive mode in *H. d. dactylopterus* is the delay of *c.* 1–3 months between insemination and fertilization. Delays of 1–5 months have been reported in species of *Sebastes* off Japan (Takahashi *et al.*, 1991). Details of the mechanism by which spermatozoa remain viable in ovaries until oocytes have developed are still not known, particularly for species of *Sebastes* that lack structures for sperm storage (Takahashi *et al.*, 1991). Sorokin (1961) proposed that spermatozoa in the ovary of *S. marinus* (L.) are stored in a state of physiological rest during the months prior to fertilization and at the appropriate time are activated by changes in the pH of ovarian fluid. The crypts of spermatozoa [Fig. 10(b)] that we observed in female blackbelly rosefish appear to be a structure for sperm storage. The same structure was noted at the base of ovarian lamellae in *H. lengerichi* (Norman) from the Pacific coast of South America (Lisovenko, 1979). Spermatozoa were observed within the ovarian stroma of *S. crameri* (Jordan) by Nichol & Pikitch (1994), although no storage structure was described.

The reproductive mode and spawning season of *H. d. dactylopterus* off the south-east coast of the United States is similar to that found in other locations. Male spermatozoa production peaked in the fall (September–November), and female rosefish spawn during the winter and early spring (December–April). Off the Azores, the spawning peak in male *H. d. dactylopterus* occurs in September,

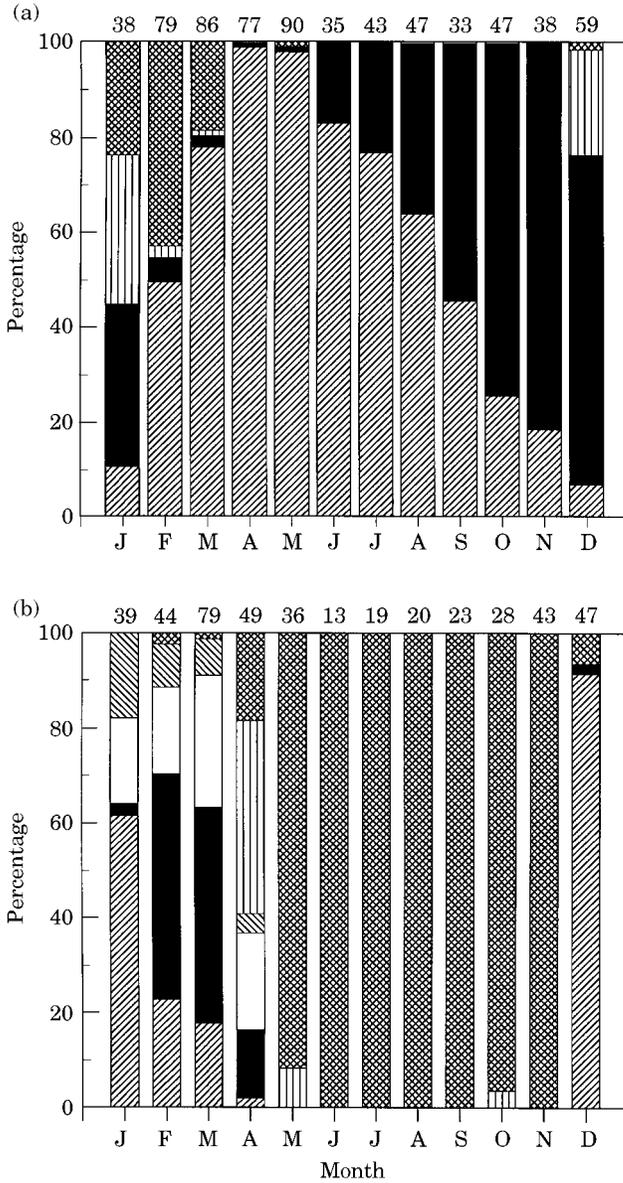


FIG. 11. Reproductive seasonality of male (a) and female (b) *H. d. dactylopterus* based on histological criteria. Number of specimens examined by month is above each bar. ▨, Developing; ▩, migrating nucleus; ■, spawning; □, postovulatory follicles; ▧, spent; ▦, resting.

and female *H. d. dactylopterus* are reported to spawn in January–April (Isidro, 1987, in Esteves *et al.*, 1997). The subspecies of *H. dactylopterus* found off Argentina, Uruguay, and southern Brazil (*H. d. lahillei*) also spawns during the winter and early spring, as Sánchez & Acha (1988) reported the capture of eggs at the stage of tail bud formation in September plankton samples and females with early-celled embryos (pre-cleavage) in a clear gelatinous matrix in trawl collections 2 months later.

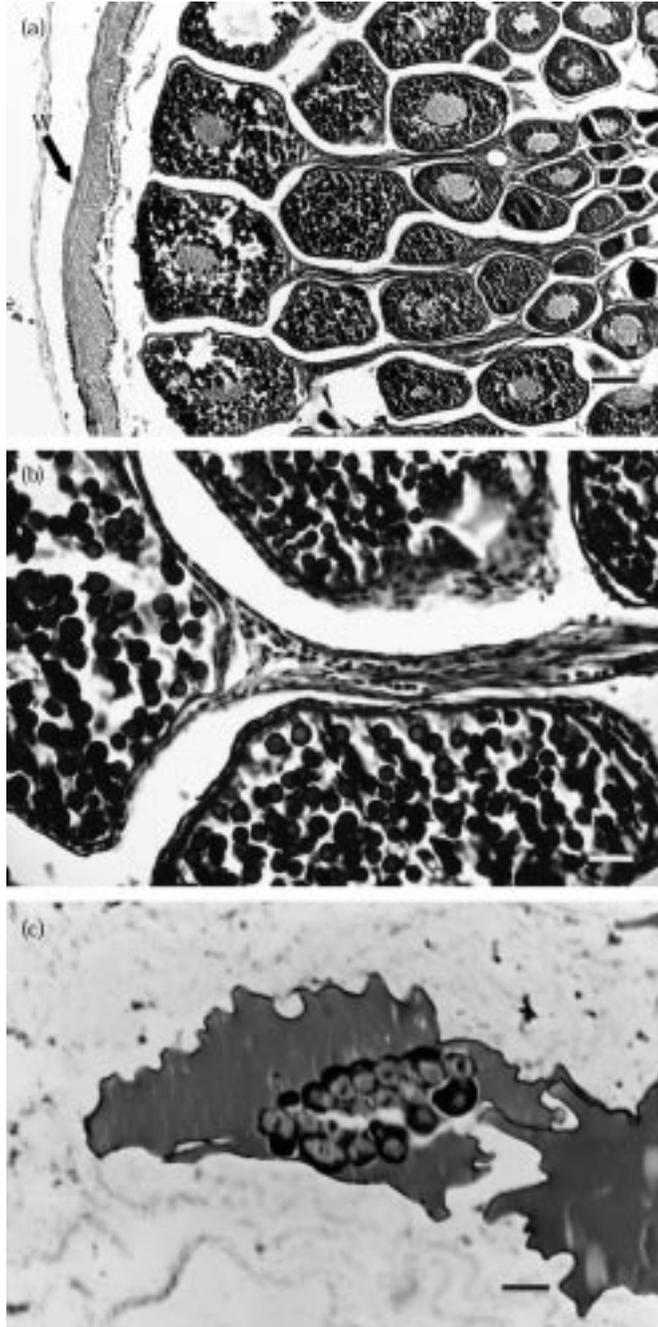


FIG. 12. Transverse sections of oocytes and embryos in *H. d. dactylopterus*. (a) Yolk globule-stage oocytes are suspended on stalks that radiate from lamellae (bar=100  $\mu$ m). (b) Blood flows to an oocyte through capillaries in the stalk (bar=25  $\mu$ m). (c) Early-celled embryo imbedded in the clear gelatinous matrix found in the ovarian cavity (bar=50  $\mu$ m). w, Ovary wall.

TABLE V. Sex ratio of *H. d. dactylopterus* by 25-mm  $L_T$  intervals and  $\chi^2$  values of tests for a 1 : 1 ratio

$L_T$	Male	Female	♂ : ♀	$\chi^2$
201–225	6	16	1 : 2.67	3.68
226–250	40	48	1 : 1.20	0.56
251–275	127	87	1 : 0.68	7.11*
276–300	176	105	1 : 0.60	17.44†
301–325	170	87	1 : 0.51	26.16†
326–350	99	53	1 : 0.54	13.32†
351–375	61	26	1 : 0.43	13.29†
376–400	21	2	1 : 0.10	10.24*
401–425	3	0		
Total	703	424	1 : 0.60	68.57†

\* $P < 0.01$ , 1 d.f.; † $P < 0.001$ , 1 d.f.

The presence of early-celled embryos in a gelatinous matrix was also observed by Krefft (1961) in *H. d. dactylopterus* from the northeast Atlantic. This gelatinous matrix is characteristic of *Helicolenus* (Wourms, 1991) and also occurs in some species of *Scorpaena* (Orton, 1955) and *Sebastes* (Wourms, 1991). Wourms (1991) proposes that the matrix enhances embryo survival by repelling potential predators. Although *H. dactylopterus* has been considered viviparous by some investigators (Krefft, 1961), full-term embryos have not been observed in the gelatinous matrix. This inconsistency is probably the result of differing definitions of viviparity. In the present study, we have accepted the definition presented by Wourms (1991).

The present study found that male *H. d. dactylopterus* grew significantly faster and were more abundant than females. Golovan' *et al.* (1991) reported that male *H. lengerichi* were more abundant than females. Although our results could be related to commercial gear bias, the data of Golovan' *et al.* (1991) were collected independent of a commercial fishery, via trawl.

Our findings are consistent with those of other investigations of scorpaenid life history (Echeverria, 1987; Withell & Wankowski, 1988; Golovan' *et al.*, 1991; Pearson *et al.*, 1991). *Helicolenus d. dactylopterus* is slow growing and long-lived. This implies that the natural mortality rate is almost certainly low. The relatively slow growth of this species may limit further expansion in the United States fishery given that slow growing fish are easily overexploited. This slow growth makes the usefulness of an age-length key extremely limited. Although *H. d. dactylopterus* was not commercially landed until 1989, it has been captured off the Carolinas as bycatch since the bottom longline fishery began *c.* 1981–1982 (Low & Ulrich, 1983). Although current fishing pressure is low, even low levels of fishing may result in significant harvest of the sustainable yield of *H. d. dactylopterus*. The fishery for *H. d. dactylopterus* may need to be reassessed if fishing pressure increases.

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