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# BIOLOGY AND DISTRIBUTION OF SPECIES OF POLYACANTHONOTUS (PISCES: NOTACANTHIFORMES) IN THE WESTERN NORTH ATLANTIC

## Roy E. Crabtree, Kenneth J. Sulak and John A. Musick

## ABSTRACT

The notacanthid genus *Polyacanthonotus* is represented in the Atlantic by three species of demersal deep-sea fishes at depths from about 500-3,800 m. Recent collections have made available new material from the temperate and tropical western North Atlantic for life history study of P. merretti and P. rissoanus. Species of the genus are browsers on small benthic macrofauna including polychaetes, gammaridean amphipods, and mysids. Reproduction does not appear to be seasonal. Fecundity is positively correlated with size in P. merretti, and ranges between 1,900-5,700 ova. Fecundities are much higher (ca. 20,000-30,000 ova) in P. rissoanus and P. challengeri, which attain a larger size. Sex ratios appear highly skewed. Among western Atlantic material, males were found only in P. merretti, with a female : male sex ratio of 25:1. No "bigger-deeper" relationship was found in P. merretti or P. rissoanus. Despite overlapping geographic and bathymetric ranges, species of *Polyacanthonotus* tend to be allopatric in distribution. The amphi-Atlantic P. merretti is predominantly tropical at bathyal depths (584-2,000 m). The circumglobal species P. challengeri is predominantly antitropical on the continental rise (1,302-3,753 m, mostly below 2,000 m). The Atlantic species P. rissoanus is also predominantly anti-tropical on the continental slope (500-2.875 m, mostly)above 2,000 m).

The notacanthid genus *Polyacanthonotus* comprises three species, *P. challengeri* (Vaillant, 1888), *P. rissoanus* (de Filippi and Vérany, 1859), and *P. merretti* Sulak et al., 1984, all of which occur in the Atlantic. *Polyacanthonotus africanus* (Gilchrist and von Bonde, 1924) is a synonym of *P. challengeri* (Sulak et al., 1984); however, certain records previously attributed to *P. africanus* in McDowell (1973) and elsewhere pertain instead to *P. merretti* (Sulak et al., 1984). Only *P. challengeri* is known in the Pacific and Indian oceans. All three species are demersal. Prior to the present study, very little was known about *Polyacanthonotus* life histories, primarily because few specimens were available for study. Past investigations of notacanths have dealt mainly with morphology and systematics (McDowell, 1973; Greenwood, 1977). Substantial comparative life history information is available only for *Notacanthus bonapartei* (Lozano Cabo, 1952).

As the result of two deep-sea trawling programs conducted in recent years (Musick, 1979; Sulak, 1982) in the western North Atlantic, many specimens of *P. merretti* and *P. rissoanus* have become available for study. This new material has enabled an assessment of the food habits, reproductive biology, and abundance of these two species. A revised understanding of species in the genus (Sulak et al., 1984) and numerous new records subsequent to those available to McDowell (1973) have additionally enabled re-definition of the bathymetric and geographic ranges of the three known species of *Polyacanthonotus*.

## METHODS AND MATERIALS

Specimens examined came from six cruises conducted by the Virginia Institute of Marine Science (VIMS) in the Middle-Atlantic Bight (MAB) (1973–1978) and nine cruises (eight conducted by the University of Miami Rosenstiel School of Marine Science, one by VIMS) in the vicinity of Tongueof-the-Ocean, Exuma Sound, and adjacent regions of the Bahamas (1972–1980). Sampling effort was

Taxon	F	w	N	IRI
Foraminifera	2	1.9	0.1	4
Porifera				
Hexactinellida	2	0.6	1.9	6
Polychaeta	36	67.6	27.8	3,405
Crustacea				
Copepoda	7	0.8	5.6	45
Mysidacea	5	2.5	5.6	39
Amphipoda				
Gammaridea	24	4.4	20.4	590
Unidentified				
Crustacea	29	23.0	24.1	1,366
Total Crustacea	60	30.8	55.6	5,139
Unidentified tubes	19	1.1	14.8	303

Table 1. Gut contents of *Polyacanthonotus merretti* (F = percent frequency of occurrence, N = percent numerical abundance, W = percent weight, IRI = index of relative importance)

distributed over a depth range of 69-4,879 m in the MAB study area and 918-5,267 m in the Bahamas region. Trawl samples were obtained with 9.1-, 12.5- and 13.7-m semi-balloon otter trawls fished on the bottom at approximately two knots for either 30 or 60 min according to standardized trawling routines (Musick, 1979; Sulak, 1982). Based on the sweep of the net employed and the distance traversed, estimates of numerical abundance and standing crop (biomass per unit area) of *P. rissoanus* and *P. merretti* were calculated for the MAB and Bahamas study areas.

In addition to new western Atlantic material utilized for life history study, many new specimens have become available from other sources since the report of McDowell (1973). Furthermore, McDowell's records of "*P. africanus*" pertained to two species, *P. merretti* and *P. challengeri* (Sulak et al., 1984), precluding meaningful analysis of distribution patterns among species of the genus. Additional new records supplementing those from our western Atlantic study areas come from published and unpublished data (Geistdoerfer and Rannou, 1972; Rass et al., 1975; Rayburn, 1975; Marshall and Merrett, 1977; Haedrich et al., 1980; Haedrich, unpubl.; Merrett and Marshall, 1981; Merrett, unpubl.). All known records of *P. merretti* and *P. challengeri* are listed in Appendix 1 to clarify the identity of previous reports attributed to "*P. africanus*" and to document additional material presently available. We have examined nearly all specimens listed in Appendix 1.

Stomach contents were removed and maintained in 40% isopropyl alcohol following fixation of fish in 10% formalin. The percentage of the total number of stomachs containing prey in which a prey item occurred (percent frequency of occurrence), number of individuals of each food type as a percentage of total number of food items (percent numerical abundance), and wet weight as a percentage of the total weight of all food items (percent weight) were determined. Weights were measured by blotting prey items on filter paper and weighing on an analytical balance. The "index of relative importance" (IRI) of Pinkas et al. (1971) was calculated: IRI = (N + W)F, where N = percent numerical abundance, W = percent weight, and F = frequency of occurrence.

Sex and condition of ovaries were determined for each specimen. Ovaries used in fecundity estimates were preserved in Gilson's solution (Bagenal, 1978). The degree of ovarian maturity was determined according to following criteria: (a) Immature, ovaries very thin; colorless or white; ova discernible only with aid of binocular dissecting microscope; (b) Developing, ovaries slightly dilated; ova visible without magnification, white or yellow in color, 0.5–1.0 mm in diameter; (c) Mature, ovaries substantially dilated, but not noticeably distending body walls; ova cream-colored, ca. 1.0 mm in diameter; Ripe, ovaries filling body cavity, distending body walls, displacing viscera; ova whitish or translucent (clearing), ca. 1.2 mm or more in diameter, some loose in body cavity.

Ova diameters were measured to the nearest 0.1 mm under a dissecting scope utilizing an ocular micrometer. Counts for fecundity determinations were made by counting all ova for *P. merretti*. Gravimetric subsampling techniques were used to estimate fecundity in *P. rissoanus* and *P. challengeri*. Lengths used for all size-related analyses are gnathoproctal lengths (GPL), measured from symphysis of lower jaw to anus. Weights used for length-weight relationships are wet weights of fresh specimens to the nearest gram, with the exception of *P. challengeri* where weights are of preserved specimens.

Taxon	F	w	N	IRI
Polychaeta				
Polynoidae	34	55.7	9.9	2,264
Unidentified Polychaeta	52	19.1	8.4	1,423
Total Polychaeta	86	74.8	18.3	8,031
Crustacea				
Mysidacea	48	5.6	18.3	1,154
Amphipoda				
Gammaridea				
Ampeliscidae	3	0.4	0.5	3
Aoridae (Unciola sp.)	3	0.4	0.5	3
Cressa sp.	3	<0.1	0.5	2
Eusiridae	24	1.5	3.7	124
Oedicerotidae	3	< 0.1	0.5	2
Harpina sp.	3	0.1	0.5	2
Pleustidae	3	0.2	1.6	6
Stegocephalidae	7	0.2	1.6	13
Stegocephalus auratus	3	0.5	1.0	5
Podoceridae	3	0.1	5.8	20
Photidae (Podoceropsis sp.)	3	0.1	0.5	2
Unidentified Gammaridea	59	5.1	28.3	1.057
Total Gammaridea	72	8.3	45.0	3,858
Caprellidae	7	3.4	10.5	96
Total Amphipoda	72	11.6	55.5	4,862
Unidentified Crustacea	31	8.0	7.8	490
Total Crustacea	83	25.2	81.7	8,842

Table 2. Gut contents of *Polyacanthonotus rissoanus* (F = percent frequency of occurrence, N = percent numerical abundance, W = percent weight, IRI = index of relative importance)

#### RESULTS

Food Habits.—Of the 109 stomachs of *P. merretti* examined 44 contained prey items (Table 1). In order of importance by the index of relative importance, crustaceans were the dominant prey (IRI = 5,139) with gammaridean amphipods predominating (590). Polychaetes ranked second by the IRI (3,405), but were the dominant prey by percent weight. Identification of most prey items to lower taxonomic categories was generally precluded due to the advanced stage of digestion of food.

Of the 50 stomachs of *P. rissoanus* examined, 30 contained prey items. Crustaceans (IRI = 8,842), primarily gammaridean amphipods (3,858) and mysids (1,154), along with polychaetes (8,031), were dominant prey items (Table 2). As in *P. merretti*, polychaetes were the dominant prey by percent weight.

Reproduction. – Species of Polyacanthonotus display highly skewed sex ratios with females predominating. Among the 89 *P. merretti* available from Bahamas samples, a female : male sex ratio of 29:1 was found. No developed males were found among the 53 MAB specimens of *P. rissoanus*. Only one male *P. challengeri* was found among 34 specimens from around the world. In addition to skewed sex ratios, sexual dimorphism was displayed in at least *P. merretti* and *P. rissoanus*. Mature males of *P. merretti* had black tubular anterior nostrils and enlarged posterior nostrils (Fig. 1a), which contrast with the small, colorless nares of females



Figure 1. The comparative development of the nostrils and snout in breeding condition male (a, UMML 34307; 110 mm, GPL) and female (b, VIMS 05810; 86 mm, GPL) *Polyacanthonotus merretti* and male (c, VIMS 07111; 81 mm, GPL) and female (d, VIMS 07269; 115 mm, GPL) *Polyacanthonotus rissoanus.* 

(Fig. 1b). A similar condition was found in a mature male *P. rissoanus* from the eastern Atlantic (Fig. 1c and 1d).

Mature and ripe female *P. merretti* among Bahamas material ranged between 84–119 mm GPL and had fecundities ranging between 1,932–5,709 ova ( $\bar{x} = 3,695$ , N = 24). The average relative fecundity (ova/g body weight) was 222 (range: 128–333). Fecundity was positively correlated with gnathoproctal length (Fig. 2). The largest ova measured ca. 1.5 mm in diameter. Ripe and mature *P. merretti* occurred in spring, summer, and fall samples from the Bahamas, suggesting the absence of seasonally synchronized spawning in this species (Table 3).

Only two mature female *P. rissoanus* were present among the MAB material. These two specimens, 110 and 150 mm GPL, contained ova of ca. 1.0 mm diameter and were obtained in September and November respectively. Fecundity could be determined only for the larger fish, which contained 23,314 ova. The single specimen of *P. challengeri* captured in VIMS Middle-Atlantic Bight samples was a mature female containing at least 30,000 ova.

Length Relationships.—Specimens of P. merretti captured in the two study areas ranged from 45–125 mm GPL, with length frequencies as shown in Figure 3. MAB specimens attained a slightly greater maximum size ( $\bar{x} = 98$  mm; max. = 125 mm) than fishes from the Bahamas ( $\bar{x} = 90$  mm; max. = 112 mm). Polyacanthonotus rissoanus from MAB (Fig. 4) had a significantly (P < 0.05) greater mean length ( $\bar{x} = 127$  mm, range = 90–165 mm) and attained a greater size than P. merretti from either study area.



Figure 2. Length-fecundity relationship for *Polyacanthonotus merretti* ( $log_{10}$  fecundity = 1.397  $log_{10}$  GPL (mm) + 0.788; N = 24,  $r^2$  = 0.21).

The length-weight relationships for *P. merretti* and *P. rissoanus* from western North Atlantic samples and *P. challengeri* from specimens assembled from around the world are presented in Table 4. Also given for each species are conversion formulae in order to reference our length-weight equations to previous studies reporting rostroproctal length (RPL) or total length (TL).

Polyacanthonotus merretti showed a weak but statistically significant negative correlation ( $r^2 = 0.055$ , P < 0.05) between size and capture depth, while *P. rissoanus* showed no significant relationship (P > 0.05). The absence of a positive correlation between size and capture depth in *P. merretti* and *P. rissoanus* is in contrast to the "bigger-deeper" generality previously noted among certain species of deep-sea bottom fishes (Markle, 1976; Haedrich and Rowe, 1977; Wenner and Musick, 1977; Wenner, 1978; Musick, 1979; Polloni et al., 1979).

Distribution. — The genus Polyacanthonotus is circumglobal between latitudes  $65^{\circ}$ N and  $50^{\circ}$ S (Fig. 5). The newly described *P. merretti* is amphi-Atlantic and predominantly tropical in range. Most records (Appendix 1) come from the western Atlantic, where the species has been found from New Jersey to the Guianas (including the Gulf and Caribbean). In the eastern Atlantic, the species is known from only a few records (N. Merrett, pers. comm.) off northwestern Africa. As yet, *P. merretti* has not been reported from the South Atlantic. This small species is bathyal on the middle and lower slope, occurring from 598–2,000 m, with most records between 1,200–1,500 m. It inhabits a temperature range of ca.  $3.5-8.0^{\circ}$ C. *Polyacanthonotus challengeri* is the large-bodied counterpart of *P. merretti*. A circumglobal species, *P. challengeri* is known from widely scattered records (Appendix 1) in both hemispheres (Fig. 5). The species appears predominantly antitropical with all but two records (off western Africa) from temperate or boreal

	Month of capture			
Maturity stage	FebMarch N = 41	April N = 4	July-Sept. N = 27	OctNov N = 16
Immature	10	0	4	0
Developing	41	25	26	31
Mature	20	50	44	38
Ripe	29	25	26	31

Table 3. Percent of *Polyacanthonotus merretti* from the Bahamas study area at various maturity stages during the year

latitudes. With a known depth range of 1,302-3,753 m, *P. challengeri* is an abyssal species inhabiting the lower slope and continental rise. Most records are from depths exceeding 2,000 m. The species inhabits a temperature range of ca.  $1.5-4.5^{\circ}$ C. The remaining member of the genus, *P. rissoanus*, is known only from the Atlantic (Fig. 5). The species is amphi-Atlantic and anti-tropical, but as yet is unknown in the western South Atlantic. *Polyacanthonotus rissoanus* occurs from Virginia north to Davis Strait in the northwestern Atlantic, from the Bay of Biscay north to the Wyville Thompson Ridge and in the Mediterranean Sea in the northeastern Atlantic, and off South Africa in the southeastern Atlantic. In the Atlantic proper, *P. rissoanus* spans a depth range of 540–2,875 m, with most records between 1,500–2,000 m. Correspondingly, a temperature range of ca. 3.6–11.0°C applies to open Atlantic records. In the Mediterranean, *P. rissoanus* spans a depth range of ca. 500–2,830 m and a temperature range of approximately 13.0–14.5°C (by correspondence of capture depths with temperature data in Miller et al., 1970).

All three species of *Polyacanthonotus* overlap geographically between Virginia and New Jersey; *P. challengeri* and *P. rissoanus* also overlap in the northeastern Atlantic and off South Africa; *P. challengeri* and *P. merretti* also probably overlap off northwestern Africa (Fig. 5). The bathymetric ranges of any pair of species in the genus overlap extensively as well (Fig. 6). Despite the apparent potential for co-occurrence, however, the species tend not to coincide extensively, each having a distinct center of distribution expressed as a combination of latitude and depth (Fig. 6). Moreover, even within zones of co-occurrence, actual sympatry seems rare. Off Virginia, for example, 23 VIMS trawl samples yielded specimens of

Species:	P. merretti	P. rissoanus	P. challengeri	
Length-weigh	t expressions:			
Log wt =	$3.072(\log GPL) - 4.863$ (N = 17, $r^2 = 0.986$ )	$2.941(\log \text{ GPL}) - 4.330$ (N = 27, $r^2 = 0.869$ )	$3.001(\log \text{GPL}) - 4.716$ (N = 40, $r^2 = 0.945$ )	
BPL to RPL	conversions:			
RPL =	1.032(GPL) + 2.389 (N = 22, $r^2 = 0.999$ )	1.047(GPL) + 0.568 (N = 30, $r^2 = 0.990$ )	1.010(GPL) + 8.394 (N = 32, $r^2 = 0.995$ )	
GPL to TL co	onversions:			
TL =	2.551(GPL) - 1.206 (N = 22, $r^2 = 0.992$ )	2.842(GPL) + 40.076 (N = 28, $r^2 = 0.960$ )	2.201(GPL) + 63.501 (N = 32, $r^2 = 0.932$ )	

Table 4. Length-weight expressions and length measurement conversion formulae for the three species of *Polyacanthonotus* (logarithms are base 10; weights are wet weight in grams; lengths are in millimeters. GPL = gnathoproctal length; RPL = rostroproctal length; TL = total length)



Figure 3. (Left) Length-frequency distributions by 5-mm length increments in GPL of *Polyacan*thonotus merretti from the Middle-Atlantic Bight and Bahamas.

Figure 4. (Right) Length-frequency distributions by 5-mm length increments in GPL of *Polyacan-thonotus rissoanus* from the Middle-Atlantic Bight.

Polyacanthonotus between 1,100-2,000 m (the approximate zone of bathymetric overlap). Yet P. merretti (13 stations, 19 specimens) and P. rissoanus (14 stations, 52 specimens) co-occurred in only three of these samples. Similarly, P. challengeri and P. rissoanus co-occurred in only two of 26 samples yielding Polyacanthonotus between 1,350-2,500 m (the zone of bathymetric overlap) in Institute of Ocean-ographic Sciences trawling conducted off Ireland (N. Merrett, pers. comm.). The two species P. merretti and P. challengeri have never been taken in the same trawl sample.

Abundance and Standing Crop.—Within the Bahamas study region the depth range of *P. merretti* captures was 1,093–1,848 m. The species was never abundant relative to dominant members of the Bahamas bathyal fish fauna; on the average it made up only 0.84% of the catch by number within the species depth range. Between 1,200–1,500 m in Tongue-of-the-Ocean and Exuma Sound, *P. merretti* occurred at 46 of 86 stations. Based on the estimated area swept<sup>1</sup> by the trawl at each of the 86 stations, the numerical abundance of *P. merretti* in these basins, within the specified depth zone, was calculated as 9 fish km<sup>-2</sup> (retransformed 95% confidence interval = 5–14 fish km<sup>-2</sup>). Conversely, a mean foraging area of ca. 115,000 m<sup>2</sup> individual<sup>-1</sup> (retransformed 95% confidence interval = 69,930–196,078 m<sup>2</sup> individual<sup>-1</sup>) is indicated. Similarly, the standing crop of the species was calculated as 45 g km<sup>-2</sup> (retransformed 95% confidence interval = 20–98 g km<sup>-2</sup>).

Within the MAB study area, the depth range of 11 captures of *P. merretti* was 1,190-2,000 m. Within this depth range *P. merretti* averaged less than 0.5% of the catch numerically. Six captures occurred in the 1,300-1,600-m depth zone, where 11 trawl samples were obtained. The estimated numerical abundance of

<sup>&</sup>lt;sup>1</sup> Area swept per 60 min tow at 2.0 kt with 12.5-m trawl =  $2.112 \times 10^4$  m<sup>2</sup>; with 13.7-m trawl =  $2.483 \times 10^4$  m<sup>2</sup>, based on transducer determined net openings under tow = 48.9% of footrope length.



Figure 5. The known distribution of species of the genus *Polyacanthonotus*. Individual capture localities are indicated only for *P. challengeri* (several symbols represent multiple localities).

*P. merretti* was calculated as 12 fish km<sup>-2</sup> (retransformed 95% confidence interval = 1-71 fish km<sup>-2</sup>); the standing crop was calculated as 52 g km<sup>-2</sup> (retransformed 95% confidence interval = 3-725 g km<sup>-2</sup>).

Fourteen captures of *P. rissoanus* in the MAB study area were recorded between 1,190–1,823 m. The average numerical contribution of this species to the total catch was 0.97% over its depth range. Ten samples yielding *P. rissoanus* came from the 1,400–1,800-m zone, where in all 20 trawl samples were available for quantification. The resulting estimate of numerical abundance within this depth zone is 12 fish km<sup>-2</sup> (retransformed 95% confidence interval = 3–48 fish km<sup>-2</sup>); the estimate of standing crop is 120 g km<sup>-2</sup> (retransformed 95% confidence interval = 11–1,235 g km<sup>-2</sup>).

#### DISCUSSION

Food Habits. – Polyacanthonotus rissoanus and P. merretti may be categorized as predators of the benthic macrofauna, consuming small benthic crustaceans and polychaetes. The diets of the two species are similar except that relatively fewer mysids are consumed by P. merretti than by P. rissoanus. This difference may reflect feeding selectivity or differences in prey abundances between the Bahamas and MAB. Our findings correspond with those of McDowell (1973) with respect to dominant prey items.

Sessile invertebrates seem less important in the diets of the small-mouthed species of *Polyacanthonotus* than in those of other notacanthiform fishes. The Atlantic species of *Notacanthus*, *N. chemnitzi* and *N. bonapartei*, have specialized premaxillary teeth which form a continuous serrate cutting edge probably used to crop sessile invertebrates (McDowell, 1973). In keeping with this adaptation sea anemones and corals were reported by McDowell in stomachs of *N. chemnitzi*, and Lozano Cabo (1952) found bryozoans and colonial hydrozoans, as well as copepods and amphipods, in a large series of *N. bonapartei*. In contrast to *Notacanthus*, species of *Polyacanthonotus* do not possess specialized cutting teeth



Figure 6. Capture depth as a function of latitude in species of the genus *Polyacanthonotus* to indicate extent of potential bathymetric and geographic overlap. Broken lines circumscribe the known latitudinal and depth limits of the three species of *Polyacanthonotus*. Hatching distinguishes the limits of Mediterranean records of *P. rissoanus*, in contrast to limits of open Atlantic records (dashed outline). Some symbols represent multiple records.

(McDowell, 1973); we found only one sessile invertebrate (hexactinellid sponge in *P. merretti*) in stomachs of either species of *Polyacanthonotus*.

The larger mouths of halosaurs probably enable them to ingest a broader size spectrum of prey items than taken by *Polyacanthonotus*. Marshall and Merrett (1977) found mixed crustaceans and fish in Halosaurus ovenii, polychaetes and mixed crustaceans in Halosauropsis macrochir and Aldrovandia phalacra, and copepods in Halosaurus johnsonianus. Rayburn (1975) reported polychaetes, gammaridean amphipods, cumaceans, bivalves, and isopods in Halosaurus guentheri. Sedberry and Musick (1978) found natant decapods to be prominent components of the diet of Halosauropsis macrochir. In the same study infaunal bivalves were recorded as common stomach contents of halosaurs. In contrast, we found no fish, decapod crustaceans, or infaunal bivalves in *Polyacanthonotus*. Additionally, halosaurs tend to root in the sediment in contrast to Polyacanthonotus as indicated by Sedberry and Musick's finding of sediment in 48.2% of H. macrochir stomachs and 20.5% of Aldrovandia stomachs examined. We recorded sediment in less than 3% of Polyacanthonotus stomachs. However, other data on Aldrovandia species from the Bahamas (Crabtree, unpubl. data) indicate much less ingestion of sediment than found by Sedberry and Musick. Thus, feeding habits of species appear to vary regionally.

Species of the genus have an elongate capacious gasbladder in combination



Figure 7. A specimen of *Polyacanthonotus rissoanus* at 800 m in the Middle-Atlantic Bight to illustrate typical hovering attitude above the substrate.

with the attenuate body form typical of many demersal deep-sea fishes. Submersible observations indicate that species of *Polyacanthonotus* hover over or move along the substrate, often in an inclined attitude appropriate to a habit of browsing on small epibenthic prey at the sediment-water interface (Fig. 7).

Reproduction. – Available data indicate that females predominate in populations in *P. merretti*, *P. rissoanus*, and *P. challengeri* to a greater extent than in populations of other notacanthiform fishes. Sex ratios in halosaurs have shown females to predominate in four species of *Aldrovandia*: 2:1 to 4:1 (Sulak, 1977); and in *Halosauropsis macrochir*: 2:1 (Wenner, 1978). These fail to approach the ratio of 29 females to each male in *P. merretti* (and potentially similar sex ratios in the remaining two congeners).

The modifications of the olfactory regions in mature male *Polyacanthonotus* (Fig. 1a, c) suggest that olfaction is important in spawning. Efficient location of mates by male notacanths may in part explain the highly skewed sex ratios. A modified condition of the nostrils of some male *P. merretti* and *P. rissoanus* has previously been noted (McDowell, 1973). This type of sexual dimorphism has also been reported in the halosaur genus *Aldrovandia* (Sulak, 1977), and may be typical of breeding males of notacanthiform fishes. However, the swollen condition of the snout observed in *P. rissoanus* (Fig. 1c) has not been reported for other notacanths.

The apparent absence of seasonal spawning in *P. merretti* from the Bahamas may be associated with its tropical range. However, relationships between low latitudes and the absence of spawning periodicity are ambiguous among other species of notacanthiform fishes. Lozano Cabo (1952) found that *Notacanthus bonapartei*, a slope-dwelling species from temperate latitudes, spawned during the summer. But in the Bahamas at tropical latitudes, ripe females of the bathyal halosaur *Aldrovandia gracilis* were found only in September (Sulak, 1977). Wenner (1978) found no evidence of seasonal spawning in *Halosauropsis macrochir* from the lower slope and continental rise of the MAB.

Based on an observed size disparity between eastern and western Atlantic specimens of P. rissoanus, McDowell (1973) suggested the possibility that spawning occurred only in the eastern Atlantic, the western Atlantic subsequently receiving only large emigrants. However, the presence of ripe female P. rissoanus in the MAB indicates that spawning also occurs in the western Atlantic. Moreover, there appear to be geographic size differences in notacanths unrelated to ontogenetic migration. For example, while ripe female P. merretti were found in both the MAB and Bahamas study regions, mature individuals in the more northern region displayed a slightly larger maximum size than their southern counterparts. Thus, it seems unlikely that maximum or mean size in regional populations of notacanths is indicative of local spawning or ontogenetic migration patterns.

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Institution*	Research vessel	Cruise	Station (& museum No.†)
P. merretti:			
VIMS	<b>R/V EASTWARD</b>	7506	7 (03482)
	R/V Iselin	7310	95 (03103), 97 (03102)
	R/V Iselin	8007	41 (05811), 63 (06988), 70 (05810)
	R/V GILLISS	7404	71 (03349), 105 (03331), 106 (03348)
	R/V GILLISS	7508	88 (05306), 93 (05279)
	R/V GILLISS	7601	29 (04844), 30 (03692), 52 (03725),
			54 (03705)
	R/V Delaware II	7402	3 (04082)
UMML	R/V Iselin	7203	12, 19
	R/V Iselin	7305	40, 41, 42 (31534), 43, 46, 47, 50, 53 (31539), 57 (31540), 58, 59, 72, 76, 79, 80, 81, 85, 87
	R/V Iselin	7315	104, 107, 111, 117, 122, 123
	R/V Iselin	7402	150, 154 (34302), 159, 163
	R/V ISELIN	7406	247, 250 (34303), 251 (34304), 253, 254, 255, 256, 261 (34305), 272
	R/V ISELIN	7504	304, 314, 321, 336 (34306)
	R/V Iselin	7511	356, 359, 360, 361, 362, 363, 364, 365, 366, 370 (34307), 385
	R/V ISELIN	7603	408, 410, 413, 414, 416, 434, 435 (34308)
	R/V PILLSBURY	-	454 (23228), 675 (24646), 718, 954 (32766), 1235 (28509)
WHOI	R/V CHAIN	_	223* [lost]
MCZ	M/V OREGON	_	2577 (51631)
NMFS	M/V OREGON	_	2824* [lost]
USNM	M/V OREGON	_	3601 (204216), 3663 (204217)
	R/V ISELIN	7305	57 (261461)
IOS	RRS DISCOVERY	-	7853-1, 8519-7, 9017 (BMNH 1983-9,14.1), 9018
TAMU	<b>R/V</b> Alaminos	67-A-5	2H*
AMNH	R/V GILLISS	7601	30 (55498)
LACM	R/V GILLISS	7508	93 (43615-1)
MNHN	R/V ISELIN	7305	57 (0000-000)
FMNH	R/V GILLISS	7404	71 (94950)
ISH	R/V GILLISS	7404	106 (000/00)
P. challengeri:			
VIMS	R/V Guliss	7508	34 (05305)
TIMMI	P/V Put coupy		314 (20890)
MCZ		111	253 (55226)
MOL	R/V CHAIN	124	500 & 505 (58610)
เรษ	FFS WALTHER HERWIC	17/1078	300 (217/75)
1311	PPS DISCOVERY	-	8071 8072 9640-1 9774-1 10884-1
103	PPS CHALLENCEPT	-	50511 + 50512 + 50712 - 50823 - 50006
	KKS CHALLENGER		51011,* 51016,* 51201-1, 51308,* 51412, 51413, 51610-1,* 51611-1, 51804, 51805
MNHN	Talisman	-	40 (1887-130)* [radiograph]
	NO Jean Charcot	Incal	21/34 (1982-899), 21/35 (1982-900)
	NO Jean Charcot	BIACORES	202 (1982-891)
	NO Jean Charcot	MD03	16/49 (1977-207)
BMNH	HMS CHALLENGER		237 (1887.12.7.247)
BC	G. B. REED	-	11 IX 1964§ (64-444)*
OSUO	R/V YAQUINA	_	19 III 1970§ (2181)
	R/V YAQUINA	6910-A	CP-1-A (1891)

Appendix 1. All known records of *Polyacanthonotus merretti* and *P. challengeri*. Identifications verified by examination of preserved specimens except for lots denoted with asterisks

## Appendix 1. Continued

Institution*	Research vessel	Cruise	Station (& museum No.†)
SAM	SS PICKLE	_	524 (21918)
	-	_	- (22896)
ZMB	HEMS MAHABISS	_	53* [radiograph]
USNM	USS Albatross	-	3308 (48691), 3604 (48774), 3607 (48775), 4975 (135625)
	<b>R/V ELTANIN</b>	_	371 (263242)

<sup>\*</sup> Institutional abbreviations: AMNH = American Museum of Natural History, New York; BC = University of British Columbia, Vancouver, Canada; BMNH = British Museum (Natural History), London; FMNH = Field Museum of Natural History, Chicago; IOS = Institute of Oceanographic Sciences, Wormley, England; ISH = Institut für Seefischerei, Hamburg, West Germany; LACM = Los Angeles County Museum; MCZ = Museum of Comparative Zoology, Harvard University; NMHN = Museum Natural History, Chicago; IOS = Institute of Oceanographic Sciences, Wormley, England; ISH = Institut für Seefischerei, Hamburg, West Germany; LACM = Los Angeles County Museum; MCZ = Museum of Comparative Zoology, Harvard University, NMHN = Museum National d'Histoire Naturelle, Paris; NMFS = U.S. National Marine Fisheries Service; OSUO = Oregan State University, School of Oceanography, Corvallis, Oregon; SAM = South African Museum, Cape Town; TAMU = Texas A&M University Collection, College Station, Texas; UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida; USNM = National Museum of Natural History, Washington, D.C.; VIMS = Virginia Institute of Marine Science, Gloucester Point, Virginia; WHOI = Woods Hole Oceanographic Institution, Woods Hole, Massachusetts; ZMB = Zoologis Museum, Bergen, Norway.
† Most UMML and IOS lots are in uncatalogued research collections.
† IOS "Discovery Collection" numbers refer to specimens from both RRS DiscoverRY and RRS CHALLENGER.
§ Station numbers apparently not assigned; collection dates substituted here.
|| Michael Sars Deep-Sea Expedition.