

B R E V I O R A

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LARVAL DEVELOPMENT, RELATIONSHIPS, AND DISTRIBUTION OF *MANDUCUS MADERENSIS*, WITH COMMENTS ON THE TRANSFORMATION OF *M. GREYAE* (PISCES, STOMIIFORMES)

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ABSTRACT. Larval development of *Manducus maderensis* is described for the first time and additional information is presented on the development of *M. greyae*. Relationships of *Manducus* and its close relative, *Diplophos*, are discussed based on larval pigmentation, transformation size, and the degree of development of annular mucosal intestinal folds. Distribution of *M. maderensis* is updated with extensive new material.

INTRODUCTION

Manducus (Goode and Bean, 1896) occupies a position at or near the base of the teleostean order Stomiiformes; thus it is of considerable interest. Its morphology and relationships have been discussed by Fink and Weitzman (1982) and Ahlstrom *et al.* (1984). Of the two species currently recognized, the larva of only *Manducus greyae* Johnson, 1970 has been described (Ozawa and Oda, 1986). In this paper we describe pretransformation larvae of the second species, *Manducus maderensis* (Johnson, 1890), and provide new information on its distribution. In addition, we describe the transformation of *M. greyae*.

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MATERIALS AND METHODS

The primary material examined by us is from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology (MCZ), Harvard University. Additional material from CAS, IOS, ISH, UMML, URI, and USNM was also examined. All institutional acronyms follow Leviton *et al.* (1985).

Counts and measurements follow Hubbs and Lagler (1964), and photophore terminology follows Weitzman (1986:227). Counts of bilateral structures were made on the left side. Specimen size is given as standard length (SL) in mm. Drawings were made with the aid of a Zeiss SV-8 stereo microscope with a camera lucida attachment.

DESCRIPTION OF *MANDUCUS* LARVAE

Manducus maderensis

The larvae of *M. maderensis* can be distinguished from the larvae of other elongate "gonostomatids" by the combination of: (1) pronounced annular mucosal folds along the intestine, (2) a dorsolateral row of chromatophores, and (3) fewer than 40 anal-fin rays.

The smallest specimen, 10.0 mm (MCZ 82191, Fig. 1A), is completely untransformed although notochord flexation is complete. It is moderately elongate with a body depth approximately 9% of SL. The dorsal and anal fins are fully formed. The dorsal fin is located posterior to the midpoint of the body and slightly anterior to the anal-fin origin. The pectoral fin has a well-developed base and blade but lacks rays. The pelvic fins are just beginning to develop and are located slightly less than one dorsal-fin length anterior to the dorsal-fin origin. The preanal length is 70% of SL. The gut consists of a short esophagus, a short sac-like stomach, and a long intestine. The intestine is externally visible and has pronounced annular mucosal folds. A series of 22 dark chromatophores runs longitudinally along the dorsal part of the body, just ventral to the dorsal midline, from the level of the pectoral fin to the end of the caudal peduncle; this series of chromatophores will be referred to as the dorsal series. There is a

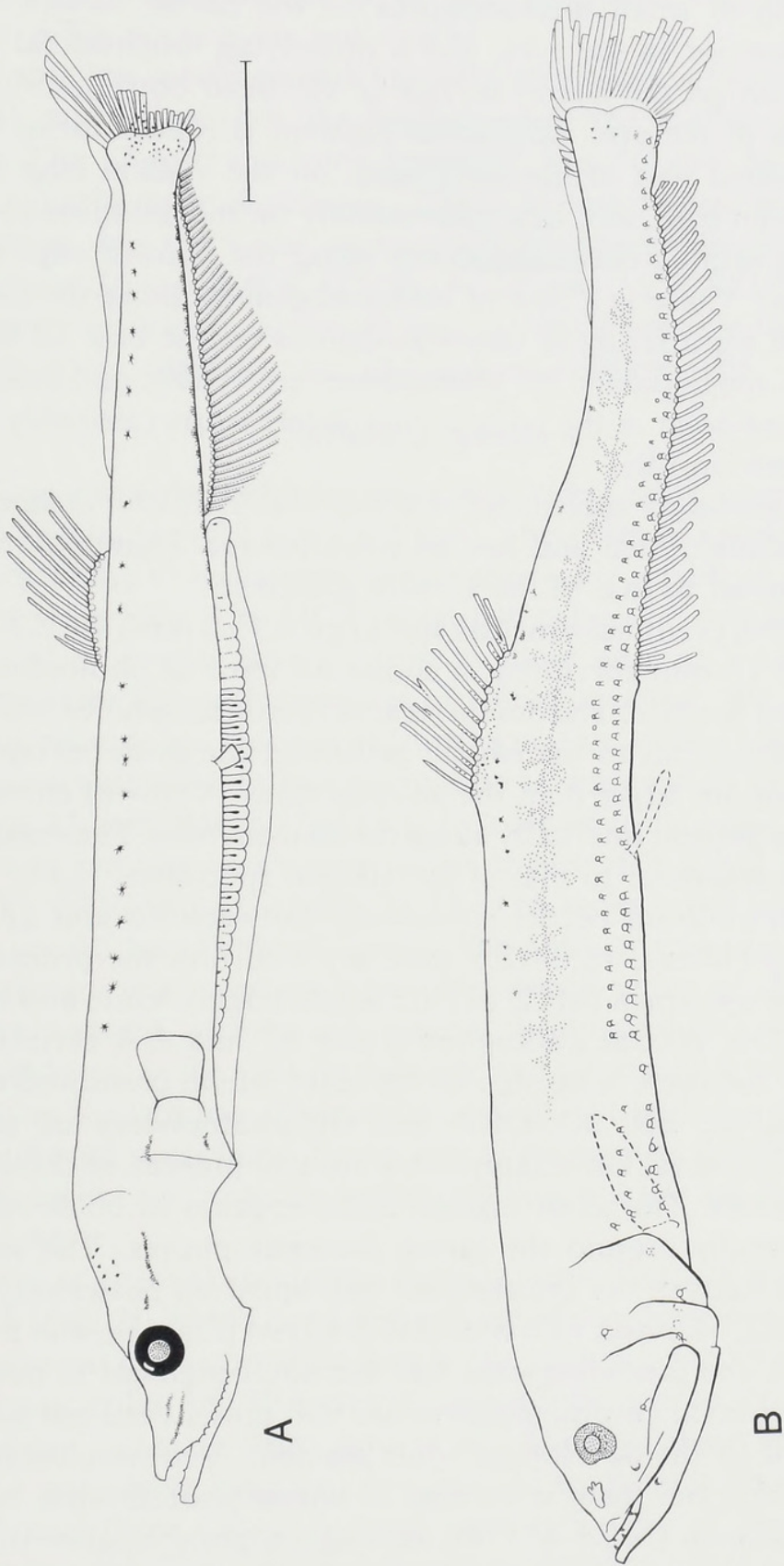


Figure 1. *Manducus maderensis*. A) Larva, 10 mm SL (MCZ 82191). B) Transforming larva, 18 mm SL (MCZ 82194).
Drawn by L. Meszoly.

peppering of small melanophores on the dorsal surface of the head posterior to the eyes, and a deep-lying longitudinal streak of pigment on the lateral surface of the head both anterior and posterior to the eye. Additional pigment is found dorsal to the anteriormost part of the esophagus, on the ventral edge of the pectoral-fin base, as a line midventrally on the isthmus, and as a series of minute chromatophores along the ventral edge of the mandible. There is a row of chromatophores along the anal-fin base and a scattering of chromatophores on the base of the tail opposite the hypurals. No photophores are visible, and in alcohol the ground color of the body is completely white (probably semi-transparent in life).

The next larger specimen (14.5 mm, MCZ 82190) is damaged. It is untransformed and has no photophores. Pigmentation appears similar to that of the 10-mm specimen.

The third pretransformation specimen is 15.0 mm (MCZ 82189). Like the 10-mm specimen, it shows no trace of photophores or scales and is white. The dorsal series of chromatophores is present from the occiput to the caudal peduncle; the posterior spots in this series are larger than the anterior ones. A row of chromatophores is present internally along the anal-fin base. The remaining pigment is similar to that of the 10-mm specimen.

Transformation occurs somewhere between 15 and 18 mm. Three specimens, 18.0–18.5 mm, are well into the process. An 18.5 mm specimen (MCZ 82192) is still largely white and has no scales. The ventral photophores (the IC and OA series) have formed, but there is no sign of the other lateral photophores. On the head, the BR, SO, ORB, and OP photophores are present (Table 1). Larval chromatophores are still present, including the dorsal series. The adult pigmentation appears to be developing dorsolaterally around the larval chromatophores. The annular mucosal folds of the intestine are still apparent posteriorly. Two specimens, 18.0 and 18.5 mm (MCZ 82194 [Fig. 1B], and 82193), resemble the preceding one, but the adult pigment is more extensive. Larval chromatophores are still present but are partially obscured by the developing adult pigment. Ventral photophores are present, but there is no sign of lateral photophores. A 17.5-mm specimen (MCZ 82174), although slightly smaller than the preceding three, is further along in development. It is uniform

light brown in color and the larval chromatophores are no longer visible. Scale pockets are not visible.

Our smallest specimen with lateral photophores is 18 mm (MCZ 82158), and it has only the beginnings of the midlateral series (LLP). The 17-mm specimen figured in Grey (1964; fig. 23) appears slightly more developed. The LLP series lengthens as the fish grows, but the small accessory photophores do not appear until about 30 mm (MCZ 82178). At 24 mm (MCZ 82177) scales are clearly visible. By about 48 mm, *M. maderensis* is fully adult in body form, pigment, and photophore development.

Manducus greyae

Ozawa and Oda (1986:80) described larvae of *M. greyae* based on 15 specimens of 7.5 to 21.4 mm. Their largest specimen was just beginning to transform; hence, they were unable to describe that process fully. The MCZ larval-fish collection contains specimens of *M. greyae* from 22 mm to about 46 mm, a range that encompasses the entire process of transformation. We are thus able to provide an account of transformation in this species.

The earliest stage in transformation is represented by a specimen of 22 mm (MCZ 82462). It is somewhat damaged, but the following photophores appear to be present: SO, ORB, OP, BR, IP, PV, VAV, and AC (Table 2). The OA series is not visible and there are no lateral photophores. The annular mucosal folds of the intestine are clearly visible. The dorsal series of chromatophores is absent, and the only ventral chromatophores visible are located dorsal to the anal-fin base and as a longitudinal midventral streak on the isthmus. Pigment is present just posterior to the tip of the flexed notochord. Some lateral pigment is developing on the myosepta and near the midlateral line, but the fish as a whole is still white.

In six additional specimens ranging from 22 to 24 mm (MCZ 82463 [Fig. 2], 82465, and 82466) the photophore complement is somewhat more complete than in the previous specimen (Table 2). In particular, the IP series increases from two to ten, and the OA series increases from zero to 52. Three of these specimens (23–24 mm) have begun to develop the midlateral photophores (LLP) and three (22–23.5 mm) have not. One of the 24-mm specimens (MCZ 82466) has begun to develop adult pigmenta-

Table 1. Selected counts and measurements for larvae of *Manducus maderensis*.

Specimen	MCZ 82191	MCZ 82190	MCZ 82189	MCZ 82194	MCZ 82192	MCZ 82193
Standard length (mm)	10	14.5	15	18	18.5	18.5
Prenatal length (mm)	7	10	10	11	12	11
Dorsal rays	10	—	10	11	10	12
Anal rays	ca. 34	—	ca. 36	36	ca. 35	37
Photophores:						
SO	—	—	—	1	0	1
ORB	—	—	—	2	2	2
OP	—	—	—	3	3	3
BR	—	—	—	9	9	9
IP	—	—	—	12	7	13
PV	—	—	—	17	21	18
VAV	—	—	—	12	13	ca. 11
AC	—	—	—	27	26	29
OA	—	—	—	ca. 44	41	46

Table 2. Selected counts and measurements for transforming larvae of *Manducus greyae*.

Specimen	MCZ 82462	MCZ 82463	MCZ 82463	MCZ 82463	MCZ 82463	MCZ 82465	MCZ 82466
Standard length (mm)	22	22	24	23	23	23.5	24
Prenatal length (mm)	12	13	13	13	13	13.5	ca. 14
Greatest depth (mm)	2.5	2.3	2.2	ca. 2.4	ca. 2.2	2.6	ca. 2.0
Photophores:							
SO	1	1	1	1	1	1	1
ORB	d	3	3	3	3	3	3
OP	3	3	3	3	3	3	3
BR	11	11	13	12	13	11	12
IP	2	7	7	9	10	9	d
PV	18	20	20	20	21	21	d
VAV	10	13	14	13	15	14	12
AC	24	35	36	40	35	36	40
OA	0	ca. 30	ca. 48	51	52	42	d
LLP	—	—	+	—	+	—	+
Acc. LP	—	—	—	—	—	—	—
Intestine	exposed	exposed	exposed	exposed	exposed	exposed	exposed
Adult pigment	—	—	—	—	—	—	+

Key to symbols: d (specimen damaged, character obscured); — (character absent); + (character present).

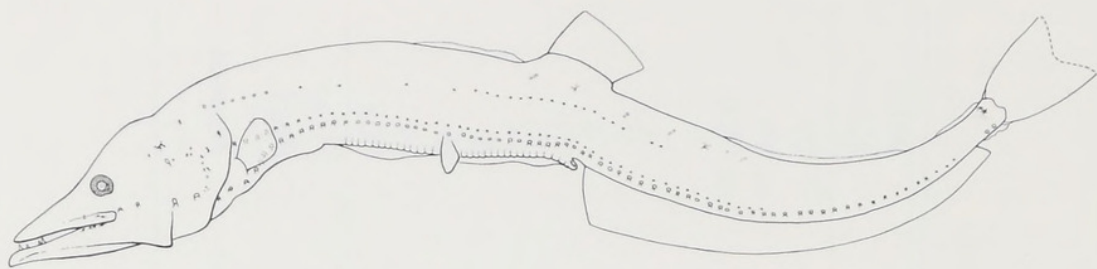


Figure 2. Transforming larva of *Manducus greyae*, 24 mm SL (MCZ 82463). Drawn by L. Meszoly.

tion, the esophagus and stomach are black, and it is the only one of these specimens in which the intestine has withdrawn inside the contours of the body. The second 24-mm specimen (MCZ 82463) is still white. The smallest specimen that shows the accessory lateral photophores is 30 mm (MCZ 82464). By 46 mm the species is largely adult in body form, pigmentation, and photophore development.

Ozawa and Oda (1986:82) claimed that in *M. greyae* the mid-lateral photophores develop before the ventral photophores. This is not the case in the specimens examined by us. The ventral photophores, especially the IC series, are well developed and conspicuous before the LLP series begins to appear. In this, *M. greyae* resembles all the other species in *Manducus* and *Diplophos* that we have examined.

Manducus–*Diplophos* Relationships

Opinions and evidence about the status of *Diplophos* Günther, 1873 and *Manducus* Goode and Bean, 1896 have differed among authors and over the years. Goode and Bean (1896:514) established *Manducus* to contain *Gonostoma maderense* Johnson, 1890. While they recognized that this species was not a true *Gonostoma*, they did not comment on any resemblance to *Diplophos taenia* Günther. Grey (1960:76) reduced *Manducus* to a subgenus of *Diplophos* because the distinction between the two nominal genera (i.e., differences in certain proportional measurements and numbers of fin rays, photophores, and vertebrae) seemed trivial compared to differences among other gonostomatid genera. Johnson (1970:442) went further and concluded that even subgeneric rank was unwarranted. His new species, *Diplophos greyae*, seemed to

him to be intermediate between the type species of the two nominal genera. Mukhacheva (1978) reviewed *Diplophos* on a worldwide basis, recognizing four species (*taenia*, *rebainsi* Krefft and Parin, 1972, *greyae*, and *maderensis*) and agreed with Johnson (1970) that subgenera are unnecessary. Fink and Weitzman (1982) described the osteology of *taenia* and *maderensis* and treated them both as *Diplophos*. Ahlstrom *et al.* (1984), however, resurrected *Manducus* based on the condition of the pectoral-fin radials. *Manducus* has the cartilages of the third and fourth proximal radials separate, and the ninth distal radial is in line with the others; *Diplophos* has the cartilages (though not the bones) of the third and fourth proximal radials fused, and the ninth distal radial is out of line with the others (see figs. 18 and 19 in Fink and Weitzman, 1982). These authors recognized two species in each genus: *Diplophos taenia*, *D. rebainsi*, *Manducus maderensis*, and *M. greyae*. Ozawa and Oda (1986) recognized seven species, all in *Diplophos*. Ozawa *et al.* (1990) revised the *D. taenia* complex, which includes four species: *D. taenia*, *D. proximus* Parr, *D. orientalis* Matsubara, and *D. australis* Ozawa *et al.*

The species of *Diplophos* and *Manducus* represent the most primitive of the stomiiform fishes (Fink and Weitzman, 1982; Ahlstrom *et al.*, 1984; Fink, 1984). *Diplophos* shares one derived feature, the partially fused third and fourth proximal radials, with the Photichthyidae (an ill-defined group) and Stomiidae, but *Manducus* retains the primitive state of this character. Ahlstrom *et al.* (1984:198) were unable to find any derived characters that would unite *Diplophos* and *Manducus* as a stomiiform subgroup. Early-life-history characters could not be used because the larvae of *M. maderensis* and *M. greyae* were unknown at the time.

Larvae of *D. taenia* are distinguished by their elongate body and the conspicuous series of dorsal and ventral chromatophores (Ahlstrom *et al.*, 1984: fig. 98; Ozawa and Oda, 1986: fig. 2). The intestine has pronounced annular mucosal folds. The dorsal fin is located slightly anterior to the anal fin. Larvae of *D. orientalis* closely resemble those of *D. taenia* but are somewhat less elongate and transform at a smaller size (ca. 30 mm vs. 50 mm; Ozawa and Oda, 1986:77, fig. 3). Larvae of *M. greyae* resemble those of *D. taenia* and *D. orientalis* but are shorter-bodied and have less conspicuous dorsal and ventral chromatophores (Ozawa and Oda,

1986:81, fig. 5); in larger larvae, the dorsal series disappears. The intestine has pronounced annular mucosal folds as in *D. taenia*, *D. orientalis*, and *M. maderensis*. *Manducus greyae* transforms at about 21–24 mm. Larvae of *M. maderensis* resemble those of *M. greyae* in their short body and inconspicuous dorsal and ventral chromatophores (Figs. 1A–B). The dorsal chromatophores are better developed than those of *greyae* and remain throughout the larval stage, but the ventral chromatophores are present only over the anal-fin base. *Manducus maderensis* transforms at a smaller size (15–18 mm) than any of the other species.

The larvae of the species of *Diplophos* and *Manducus*, then, differ primarily in their relative body depth, the extent of dorsal and ventral pigmentation, and the size at metamorphosis. Even these characters show a certain amount of gradation among the species. *Diplophos orientalis* is intermediate between *D. taenia* and *M. greyae* in both body depth and size at metamorphosis. *Manducus maderensis* has a relatively deep body, like *M. greyae*, but its dorsal pigmentation is stronger and more persistent through growth. The most striking similarity between the larvae of all these species is the pronounced annular mucosal folds of the intestine.

In assessing the significance of these larval characters, we face the same problem as in assessing the significance of adult characters: to find shared specializations that link *Manducus* and *Diplophos* to each other or to other stomiiform genera. Ahlstrom *et al.* (1984) were able to find only one adult synapomorphy that links *Diplophos* to photichthyids and stomiids (the condition of the pectoral-fin radials) and no synapomorphies that link *Manducus* to any other stomiiform genus. The larval characters described in the present paper do not alter this situation. The resemblances between larvae of the species of *Diplophos* and *Manducus* are considerable, but none of these characters is clearly specialized below the ordinal level. Similarities in body shape and pigmentation could simply represent the primitive stomiiform condition. Even the most conspicuous character shared by larvae of *Diplophos* and *Manducus*, the annular mucosal folds of the intestine, is a matter of degree of expression rather than presence or absence. Other stomiiformes have mucosal folds although they are not as pronounced. Indeed, a similar intestine is found in a

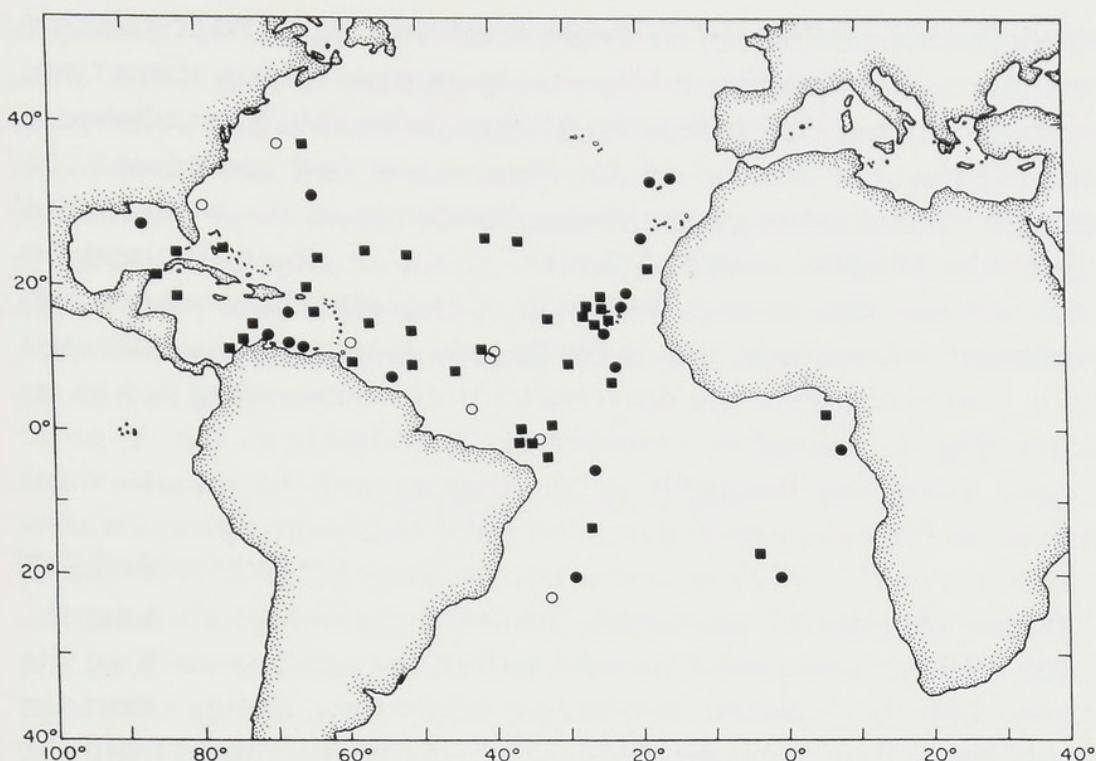


Figure 3. Distribution of *Manducus maderensis* based on all known material; ○ = specimens <18.5 mm, ■ = >19 mm, and ● = >95 mm. Symbols may represent more than one specimen or collection.

variety of lower teleosts, including clupeids, engraulidids, and certain myctophids. Whether these mucosal folds are identical structurally and developmentally in all the taxa that possess them is unknown. A phylogenetic analysis of larval characters in stomiiform fishes is clearly beyond the scope of the present paper, and without such analysis the significance of these characters cannot be determined. Clearly much work remains to be done before a useful phylogeny of stomiiformes can be constructed. In the meantime, we offer the present study as one more piece of a puzzle that may one day be assembled into a coherent picture.

DISTRIBUTION

At the time of Grey's (1960 and 1964) revisions of the "Gonostomatidae" *M. maderensis* was known from fewer than 50 specimens. Of these, 31 were adults, all from near land—at Madeira in the eastern Atlantic, and off Suriname and Mississippi in the western Atlantic. The 16 juveniles (<90 mm) were from the central North Atlantic (11 specimens), near the Bahamas (4), and the

South Atlantic off Brazil (a single specimen from 0°22'S). Based on these records and five additional specimens (two of them from between 1° and 2°S off Brazil), Mukhacheva (1978) published a map of the distribution of *M. maderensis* and considered the species to be distant neritic, being "endemic to the western and eastern parts of the central Atlantic . . . but . . . absent in the open waters." She was correct in that it is probably land-associated, especially when adult, but, according to more recently collected data, it also occurs in the open ocean both when young and as an adult (Fig. 3). *Manducus maderensis* is endemic to the Atlantic Ocean, occurring primarily in the tropics and the equatorward halves of the subtropical gyres (tropical-semisubtropical pattern of Backus *et al.*, 1977); it is now known from 37°39'N to 23°02'S.

There are only 13 specimens known from the South Atlantic, none of them from the poleward half of the subtropical gyre. Its rarity there is probably a reflection of the low fishing effort. In the North Atlantic, however, there are many specimens from the poleward half of the subtropics; most of these are adults from near Madeira (Maul, 1948; Grey, 1964; ISH, IOS). In the northern Sargasso Sea, there are but five specimens—three Gulf Stream waifs (MCZ 82193, 82194, and 88254) and two specimens reported by Bond (1974) from Ocean Acre off Bermuda (USNM 248766 and MCZ 91350, ex URI).

Since few specimens of *M. maderensis* have been collected with opening/closing nets, we can say little with precision about its vertical distribution, especially at the deeper limit of its depth range. We can say, however, that it occurs in the upper mesopelagic zone (about 450–600 m) at the edge of continental (and island) slopes and in the open ocean. The species makes a diel vertical migration into the upper 100 m at night at sizes between 20 and 100 mm. The shallowest records of large adults are the 177 mm individual at 200 m (ISH 748/66) and the 209 mm gravid female (MCZ 91350) from off Bermuda at 150 m. Of the 193 known specimens, 55, between 18 and 64 mm, were collected with neuston nets at the very sea surface.

LIST OF MATERIAL

The following *M. maderensis* (141 specimens, 10 to 220 mm) have been collected since the papers of Grey (1964) and Mu-

khacheva (1978), or were not reported by them. Each entry contains the museum catalog number, the number and size(s) of specimens, and collection data (station number, position, maximum depth reached by net, and the time of the beginning of the collection). Specimens not examined by us are marked with an asterisk. The collections at ANSP, GCRL, GMBL, MZUSP, ZMUC, TCWC, USF, SAM, and VIMS have no *M. maderensis*. Also included is the material of *M. greyae* used for the transformation description.

Manducus maderensis

IOS Discovery

7089#03* (2:31–42) 17°41'N, 25°23'W, surface, 0145 hrs.;
7089#12* (3:19–24) 17°34'N, 25°26'W, surface, 0245 hrs.;
7089#13* (2:18–21) 17°48'N, 25°29'W, 515–600 m, 0950 hrs.;
7089#21* (9:21–26) 17°52'N, 25°27'W, surface, 2145 hrs.;
7089#26* (5:22–41) 17°52'N, 25°25'W, surface, 2100 hrs.;
7089#27* (2:@ 22) 17°52'N, 25°25'W, 25–60 m, 0138 hrs.;
7089#32* (6:20–25) 17°45'N, 25°22'W, surface, 0100 hrs.;
7089#37* (1:28) 17°50'N, 25°29'W, surface, 0145 hrs.; uncat.*
(1:220) off Madeira.

ISH

64/66* (1:163) WH 177/66, 33°45'N, 16°00'W, 600 m, 2110 hrs.;
296/66* (3:145–167) WH 181/66, 19°11'N, 21°58'W, 460 m, 2100 hrs.;
399/66* (8:52–82) WH 183/66, 6°30'N, 24°33'W, 50 m, 2100 hrs.;
620/66* (1:163) WH 187/66, 5°34'S, 26°58'W, 320 m, 2000 hrs.;
748/66* (1:173) WH 191/66, 21°00'S, 30°00'W, 200 m, 2000 hrs.;
313/68* (1:177) WH 8-III/68, 26°10'N, 19°26'W, 580 m, 2233 hrs.;
1125/68* (1:56) WH 20-III/68, 13°56'S, 27°38'W, 580 m, 2255 hrs.;
1665/71* (1:157) WH 443/71, 21°35'S, 2°00'W, 2,100 m, 2025 hrs.;
2742/71* (1:98) WH 498-I/71, 17°22'N, 22°58'W, 105 m, 1955 hrs.;
2819/71* (1:125) WH 498-III/71, 17°27'N, 22°55'W, 610 m, 2203 hrs.

MCZ

52541 (5:48–52) SUN1207, 9°16'N, 27°55'W, surface, 0015 hrs.;
52566 (1:44) RHB1290, 21°17'N, 85°22'W, 124 m, 0020

hrs.; 54303 (1:110) Oregon 2007, 7°34'N, 54°49'W, 445 m; 56952 (1:145) RHB3052, 11°22'N, 65°01'W, 350 m, 1700 hrs.; 61476 (1:96) RHB2290, 2°57'S, 8°05'E, 75 m, 2005 hrs.; 82170 (1:70) RHB2269, 18°33'S, 4°00'W, 100 m, 2005 hrs.; 82171 (1:49) RHB1207, 9°16'N, 27°55'W, 51 m, 0010 hrs.; 82172 (1:61) RHB 1266, 12°44'N, 74°10'W, 575 m, 1255 hrs.; 82173 (1:130) Oregon 4419, 11°43'N, 69°13'W, 455 m; 82174 (1:17.5) RHB966, 1°13'S, 34°35'W, 102 m, 0335 hrs.; 82175 (1:48) RHB1253, 16°38'N, 64°27'W, 133 m, 0038 hrs.; 82176 (1:29) RHB1286, 19°46'N, 83°07'W, 86 m, 0010 hrs.; 82177 (1:24) RHB2035, 22°25'N, 19°00'W, 500 m, 0845 hrs.; 82178 (1:30) RHB2069, 15°23'N, 24°28'W, 320 m, 0420 hrs.; 82179 (1:22) RHB2077, 15°30'N, 26°12'W, 95 m, 2135 hrs.; 82180 (2:33 & 41) RHB2084, 17°12'N, 27°59'W, 80 m, 0215 hrs.; 82181 (1:20) RHB2095, 25°52'N, 36°48'W, 140 m, 2110 hrs.; 82182 (1:19) RHB2930, 11°00'N, 41°31'W, 475 m, 0055 hrs.; 82183 (1:61) RHB2946, 9°03'N, 51°05'W, 510 m, 0220 hrs.; 82184 (1:73) RHB2979, 13°34'N, 50°50'W, 490 m, 0210 hrs.; 82185 (1:20) SUN2078, 15°43'N, 26°28'W, surface, 0120 hrs.; 82186 (2:22 & 52) SUN2083, 17°08'N, 27°55'W, surface, 0001 hrs.; 82187 (2:25 & 27) SUN2101, 26°37'N, 41°18'W, surface, 0005 hrs.; 82188 (1:49) SUN1313, 23°55'N, 83°12'W, surface, 0034 hrs.; 82189 (1:15) RHB2924, 10°59'N, 40°22'W, 490 m, 2330 hrs.; 82190 (1:14.5) RHB2923, 11°00'N, 40°10'W, 500 m, 2045 hrs.; 82191 (1:10) RHB2966, 12°21'N, 59°34'W, 495 m, 0035 hrs.; 82192 (1:18.5) MOC10-137, 4, 30°08'N, 79°30'W, 140–160 m, 0254 hrs.; 82193 (1:18.5) SUN9452, 37°36'N, 69°03'W, surface, 0115 hrs.; 82194 (1:18) same data as 82193; 82197 (2:79 & 84) RHB982, 6°51'S, 33°34'W, 85 m, 2105 hrs.; 82198 (1:40) SUN2958, 9°13'N, 59°06'W, surface, 0115 hrs.; 82199 (1:57) RHB1222, 13°55'N, 57°00'W, 300 m, 2300 hrs.; 82200 (1:64) same data as 82198; 88250 (1:18) SUN1431, 23°02'S, 32°15'W, surface, 0120 hrs.; 88251 (1:29) SUN3102, 22°57'N, 64°12'W, surface, 2020 hrs.; 88252 (1:19) SUN2966, 12°21'N, 59°34'W, surface, 0035 hrs.; 88253 (1:62) JEC7741, 8°33'N, 44°37'W, 100 m, 0155 hrs.; 88254 (1:48) KEH7716, 37°00'N, 65°38'W, surface, 0325 hrs.; 88255 (1:29) SUN1253, 16°38'N, 64°27'W, surface, 0030 hrs.; 88256 (1:27) JEC7745, 9°15'N, 46°50'W, 100 m, 0300 hrs.; 88257 (1:24) JEC7712, 0°01'N, 37°40'W, 80 m, 2235 hrs.; 88258 (1:18)

JEC7705, 3°08'N, 42°52'W, 25 m, 0130 hrs.; 91350 (1:220) Ocean Acre 12-55N, 32°11'N, 64°10'W, 150 m, 2240 hrs.

UMML

14824 (1:32) Gerda 205, 23°20'N, 82°55'W, 1,000 m, 1843 hrs.; 22740 (1:156) Pillsbury 455, 13°01'N, 71°55'W, 1,445 m; 23074 (1:29) P-383, 10°19'N, 75°59'W, 70 m, 0101 hrs.; 27541 (2:53 & 58) P-384, 10°24'N, 75°58'W, 40 m, 0302 hrs.; 27747 (6:17-45) P-302, 2°26'N, 4°51'E, surface, 0230 hrs.; 29036 (1:22) P-821, 19°07'N, 65°28'W, 3,000 m, 1145 hrs.

CAS

61060 (1:124) Oregon II 46092, 18°27'N, 67°15'W, 1,499 m, 0852 hrs.

USNM

186282 (5:85-128) Oregon 2007, 7°34'N, 54°49'W, 445 m; 186364 (14:90-140) Oregon 2008, 7°38'N, 54°43'W, 490 m; 248711 (1:27) Ocean Acre 1-18C, 32°10'N, 63°48'W, 100 m, 0145 hrs.

Manducus greyae

MCZ

75518 (1:43) GRH1046, 12°38'S, 148°55'E, 3,240 mwo, 1740 hrs.; 82462 (1:22) GRH1011, 6°25'S, 152°09'E, 2,380 mwo, 0000 hrs.; 82463 (4:22-24) GRH1014, 4°55'S, 152°30'E, 2,380 mwo, 0015 hrs.; 82464 (2:29 & 30) GRH1017, 6°54'S, 152°06'E, 2,380 mwo, 2245 hrs.; 82465 (2:24 & 47) GRH1016, 6°43'S, 152°14'E, 2,380 mwo, 1840 hrs.; 82466 (1:24) GRH1069, 7°44'S, 151°05'E, ca. 1,950 m, 0001 hrs.

Comparative material

Larvae and transforming specimens of the following taxa in the MCZ larval fish collection were examined (number of specimens examined is given in parentheses): *Bonapartia pedaliota* (215), *Cyclothone* spp. (1,092), *Diplophos taenia* (36), *Gonostoma atlanticum* (1,157), *G. denudatum* (282), *G. elongatum* (547), *Ichthyococcus* (97), *Margrethia obtusirostra* (54), Maurolicine cf. "al-

pha" (4), *Maurolicus muelleri* (269), *Photichthys argenteus* (1), *Pollichthys maui* (79), *Valenciennellus tripunctulatus* (553), *Vinciguerria attenuata* (1,059), *V. nimbaria* (1,807), *V. poweriae* (825), *Yarella blackfordi* (1).

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