REMARKS ON SYSTEMATICS, DEVELOPMENT, AND DISTRIBUTION OF THE HATCHETFISH GENUS *STERNOPTYX* (PISCES, STOMIATOIDEI)

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ABSTRACT

Sternoptyx pseudodiaphana Borodulina is reported from the eastern North Atlantic in sympatry with *S. diaphana*, providing conclusive evidence that the former represents a species distinct from *S. diaphana*. Patterns of geographic variation among various characters are apparent in species of *Sternoptyx* as is allometric growth. These patterns render species identification difficult in certain allopatric populations, particularly those from the Atlantic and Pacific Oceans. Each species has distinct patterns of horizontal and vertical distribution and where species occur in sympatry, their centers of abundance do not coincide. Members of the genus *Sternoptyx* inhabit the "lower mesopelagic depth zone" (sensu Baird) from 500 to 1,500 m. Geographic variation in depth of maximum abundance for various species can be demonstrated. These appear correlated with variations in temperature and light although competitive interactions may also contribute to observed depth ranges. Photophore development is similar in the three species described and postlarval individuals of *S. diaphana* and *S. pseudodiaphana* are readily distinguishable. Characters useful in distinguishing the various species are presented in relation to patterns of geographic variation.

A single ancestral species which gave rise to the four presently recognized species, each exhibiting slight morphological divergence, is advanced as a parsimonious initial hypothesis of evolutionary relationship.

The genus *Sternoptyx* has, until recently, been thought to contain but a single polymorphic species (Schultz 1961, 1964). However, Baird (1971), and more recently Haruta and Kawaguchi (1976), have demonstrated the validity of three morphologically similar species, *S. diaphana* Hermann, *S. obscura* Garman, and *S. pseudobscura* Baird, each with broad but distinct geographic ranges. Baird (1971) also noted a morphologically distinct population of *S. diaphana* from the subtropical convergence region of the South Pacific. In view of the degree of character similarity and lack of sympatry with other populations of *S. diaphana*, he considered his data insufficient to substantiate the Southern Ocean form as a distinct species. Borodulina (1977) subsequently described the Southern Ocean form as *S. pseudodiaphana* and has recently published a synopsis of the hatchetfish genera *Argyropelecus* and *Sternoptyx* based on Russian collections (Borodulina 1978).

Sternoptyx pseudodiaphana from the eastern tropical Atlantic occurs in sympatry with *S. diaphana*. Our new data provide conclusive evidence that *S. pseudodiaphana* represents a species distinct from *S. diaphana*. Patterns of geographic variation are not well known in deep-sea fishes and patterns occur in the genus *Sternoptyx* which tend to obscure species distinctions among certain allopatric populations. Characters found useful in distinguishing among various species and populations are presented which complement and expand the treatments of Baird (1971) and Borodulina (1978). We describe metamorphic and postlarval development for various species and include comparisons among species. Additional data on the geographic and vertical distribution of the genus, including information from discrete-depth trawling studies, are presented which add considerably to our knowledge of the distribution of this widespread group of mesopelagic fishes.

METHODS

All four species of *Sternoptyx* were examined. The material and its sources are listed in Appendix Table 1. The specimens were fixed in Formalin[3] and preserved either in alcohol (70% ethyl or

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40% isopropyl) or in aqueous storage fluid (10% propylene glycol, 1% Formalin, 0.5% phenoxytol, based upon Steedman 1974). Generally, specimens were taken by various open midwater nets; however, a number of samples were taken with opening/closing nets of various designs (Clarke 1969; Baker et al. 1973; Hopkins et al. 1973).

Photophore Nomenclature

The unique pattern of photophore clustering in the family Sternoptychidae (sensu Baird 1971) has resulted in a different system of nomenclature from that used for other stomiatoid families (Figure 1). Weitzman (1974) suggested a revised nomenclature for stomiatoid taxa to include the hatchetfishes and for convenience, both appear in Table 1 (Weitzman's slightly modified). The distinct and unusual specializations in external morphology in the hatchetfishes (sensu Baird 1971) make determinations of homology among photophore groups difficult. We regard the new terms, therefore, as a convenience rather than as suggestions of homologies between similarly named photophore groups throughout the Stomiatoidei. For instance the preorbital photophore (PO) of the genus *Sternoptyx* differs from that of either *Argyropelecus* or *Polyipnus* morphologically, and probably functionally, and is perhaps more aptly termed an oral organ (Herring 1977). Nevertheless, for convenience, the term PO (ORB of Weitzman) is retained.

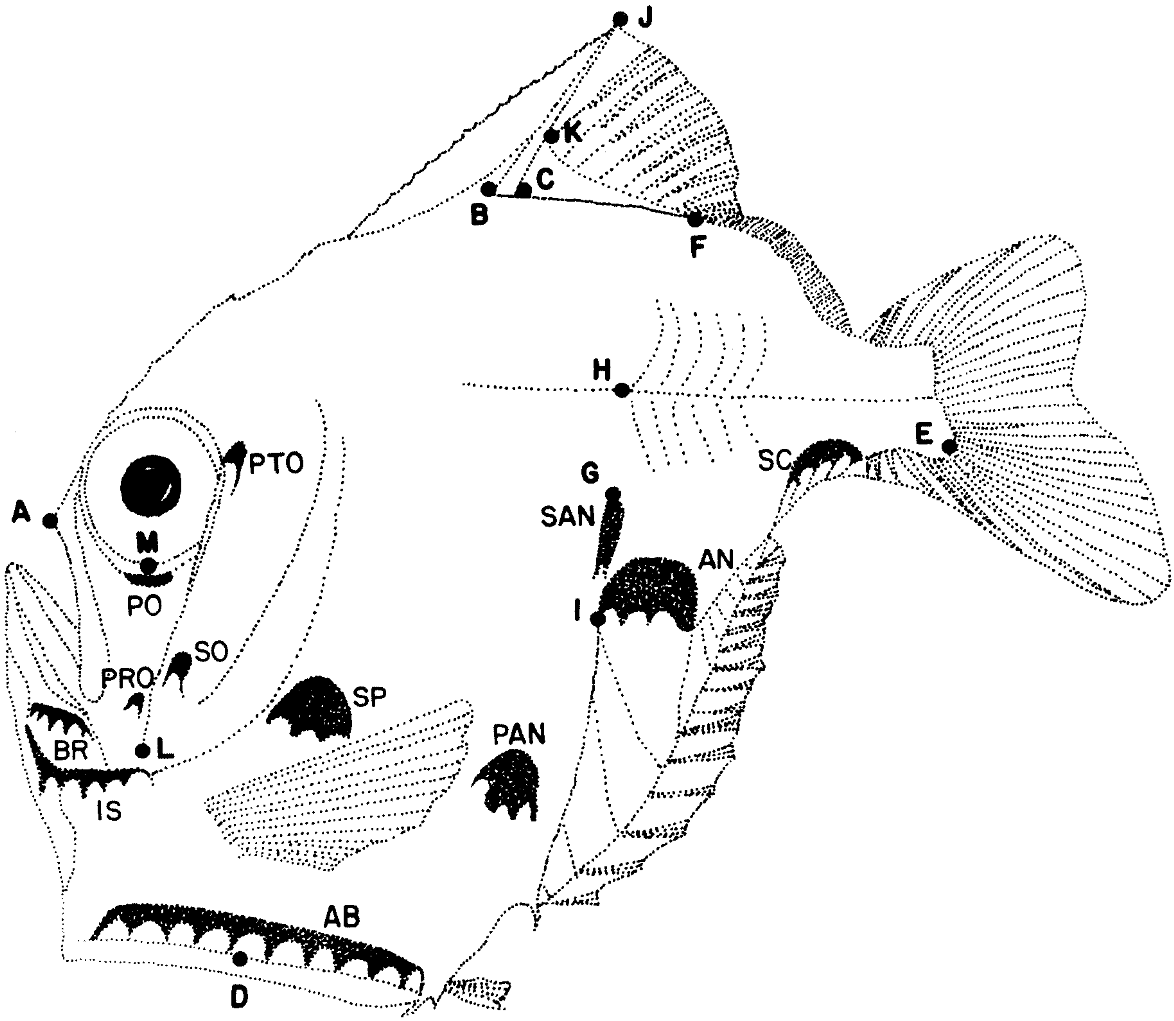

FIGURE 1.—Nomenclature of photophores and basic measurements for *Sternoptyx* spp.

TABLE 1.—Photophore development of *Sternoptyx pseudodiaphana* and *S. diaphana*, expressed in stages. Asterisk denotes earliest stage for photophore group completion; parentheses indicate photophore nomenclature in Baird 1971.

Stage	SL range (mm)	Number of photophores per photophore group (each size)												No. of specimens
		OP$_3$ (SO)	ORB (PO)	BR (BR)	PV (AB)	IP (I)	OV (SP)	OP$_2$ (PTO)	AN (AN)	VAV (PAN)	SC (SC)	OP$_1$ (PRO)	SAN (SAN)	
						S. pseudodiaphana: eastern North Atlantic								
1	10.0-10.2	1*	1*	2	6	3-4	2	1*	0	0	0	0	0	2
2	8.3- 9.7	1	1	2	8- 9	4	3*	1	1	0	0	0	0	2
3	7.6- 9.2	1	1	2	8-10*	4	3	1	1	1	0	0	0	5
4	7.9-10.0	1	1	2	10	4-5*	3	1	2	1-2	1-2	0	0	14
5	9.8-10.5	1	1	3*	10	5	3	1	3*	3*	2	0	0	2
6	9.5-11.1	1	1	3	10	5	3	1	3	3	2-3	1*	0	13
7	11.2-14.1	1	1	3	10	5	3	1	3	3	3	1	1*	22
8	[1]13.0/[2]16.2	1	1	3	10	5	3	1	3	3	4*	1	1	
						S. pseudodiaphana: southeastern Pacific								
2	6.5- 8.4	1	1	2	7- 8	4	3	1	1	0	0	0	0	3
4	7.6- 9.6	1	1	2	8-10*	4-5*	3	1	1-2	1-2	1-2	0	0	12
6	9.6- 9.9	1	1	3	10	5	3	1	3*	2-3*	1-2	1	0	2
7	9.7-14.3	1	1	3	10	5	3	1	3	3	2-3	1	1	7
						S. diaphana: western North Atlantic								
2	7.0	1*	1*	2	8	4	3*	1*	1	0	0	0	0	1
3	7.0- 7.6	1	1	2	9-10*	4	3	1	1-2	1-2	0	0	0	7
4	7.6- 8.3	1	1	2	9-10	4-5*	3	1	2	2	1-2	0	0	4
5	7.8- 9.4	1	1	2-3*	10	5	3	1	2-3*	3*	2	0	0	6
6	8.8-10.5	1	1	3	10	5	3	1	2-3*	3*	2	1*	0	11
7	9.8-13.2	1	1	3	10	5	3	1	3	3	2-3	1	1*	22
8	[1]12.8/[2]13.6	1	1	3	10	5	3	1	3	3	4*	1	1	

[1]Smallest observed size.
[2]All specimens equal or larger have all photophores.

In this account, where reference to a particular photophore within a group is made, numbering is in an anteroposterior direction (e.g., AB(PV) 10 is the posteriormost photophore pair).

Measurements and Counts

The peculiar morphology of marine hatchetfishes has necessitated a number of modifications to measurements commonly used to describe teleost fishes. While most of those used here have been described by Baird (1971), it is difficult to precisely determine reference points in the genus *Sternoptyx*. All measurements used here are defined as the shortest distance between two stated points. Standard length (SL) in juveniles and adults was measured to the nearest 1 mm, but in postlarvae, to the nearest 0.1 mm. Other measurements of all specimens were taken to 0.1 mm. Measurements were as follows (letters refer to points on Figure 1):

Standard length (SL): from the tip of the snout (A) to the furthermost extension of the caudal peduncle (E):

Body depth: from the dorsal blade origin (B) to the midpoint of the ventral body margin (D):

SAN photophore depth: from the dorsalmost point (G) of the photophore SAN to the dorsal body margin (F) at the base of the posteriormost dorsal ray;

Midline height: from the anteroventral edge (I) of the photophore group AN to the trunk midline of horizontal septum (H) on a line passing through the photophore SAN;

SAN photophore height: from the anteroventral edge (I) of the photophore group AN to the dorsalmost point (G) of the photophore group SAN;

Trunk depth (TD): from the posterior end of the dorsal fin base (F) to the anteroventral edge (I) of the photophore group AN;

Trunk length: from the point of the trunk midline defined by the midline height measurement (H) to the posteriormost extent of the caudal peduncle (E);

Photophore lengths (AN and SC): the distance between the farthest extensions of the darkly pigmented photophore margins;

Dorsal fin base: from the origin of the first (K) to that of the last (F) dorsal ray;

Dorsal blade height: from the dorsal body margin (C) to the blade tip (J), along blade axis;

Orbital diameter: the length of the longest orbital axis (fleshy orbit);

Suborbital length: from the midventral point of the orbit (M) to the tip (L) of the preopercular spine.

It was not possible for one person to measure or take counts on all the specimens examined. The results obtained, however, were in good agreement, although it is inevitable that some variation expressed may have been due to the individual measurer. All postlarval measurements and comparisons were made by one person (i.e., SL <18 mm). The postlarval phase was considered concluded at the attainment of a full complement of pigmented photophores (ca. 14-18 mm), at which stage individuals were classified as subadults. Meristic counts were made in accordance with Baird (1971) and vertebral counts included all separated vertebrae with the exception of the urostylar complex.

SYSTEMATIC REMARKS

Species Distinction

Morphological distinctions among species of *Sternoptyx* are relatively slight and distinctive characters tend to be obscured in allopatric populations, making identification difficult in the absence of other species. As an aid to the identification of specimens with a full complement of photophores (ca. 18 mm SL), the distinctive species characteristics reported by Baird (1971), Haruta and Kawaguchi (1976), and Borodulina (1978) are combined and expanded in relation to observed patterns of geographic variation. Characters used in distinguishing the four species are discussed below and each species is illustrated (Figures 2-5). Selected meristic and morphometric data are presented in Tables 2 and 3. Table 4 provides a synopsis of characters useful in differentiating adults and subadults.

The genus can be divided into two morphological groups or species pairs. In one, containing *S. pseudodiaphana* (Figure 2) and *S. diaphana* (Figure 3), the AN photophores completely fill the anal fin base, the horizontal part of the ventral body margin extends very little posterior to AN, and the posterior anal fin pterygiophores are relatively short. The second group, with *S. obscura* (Figure 4) and *S. pseudobscura* (Figure 5) is characterized by species having an appreciable extension of the horizontal part of the ventral body margin posterior to AN, long posterior anal fin pterygiophores, and smaller AN and SC (Table 3).

Within these two groups, species may be readily separated from one another, albeit more through a combination of characters than by virtue of a single one. *Sternoptyx pseudodiaphana* and *S.*

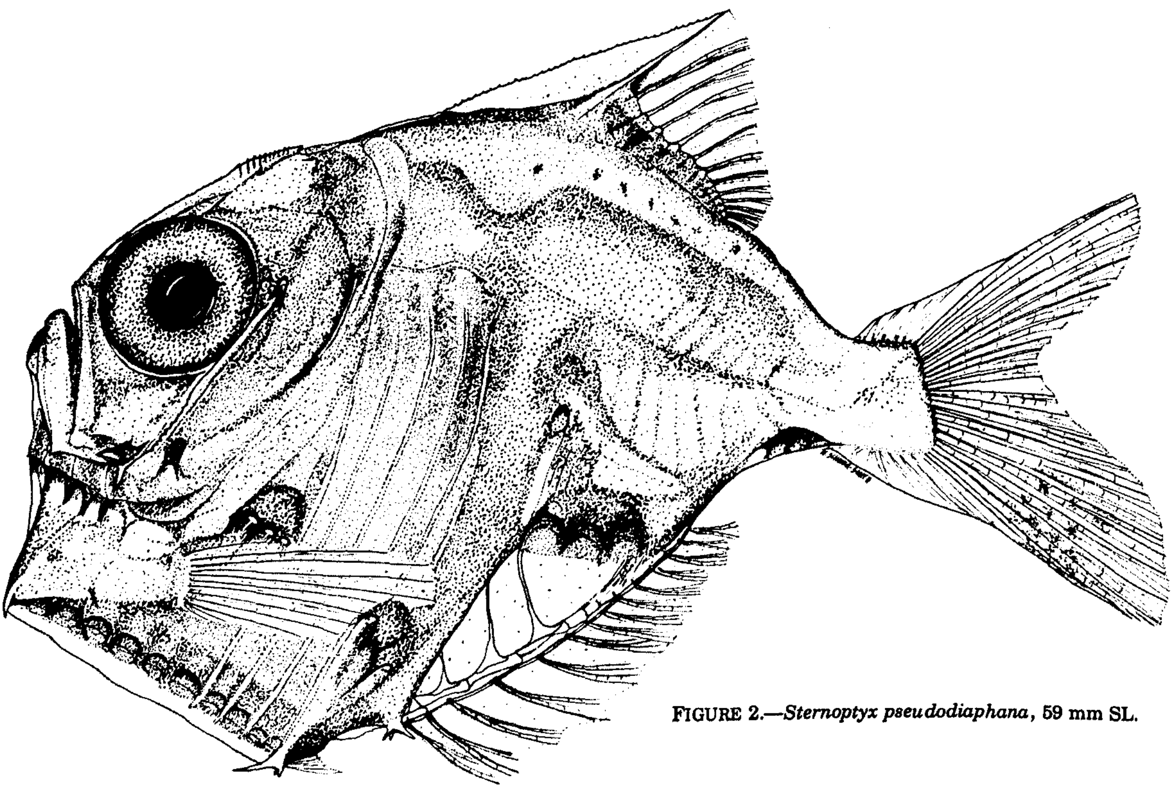

FIGURE 2.—*Sternoptyx pseudodiaphana*, 59 mm SL.

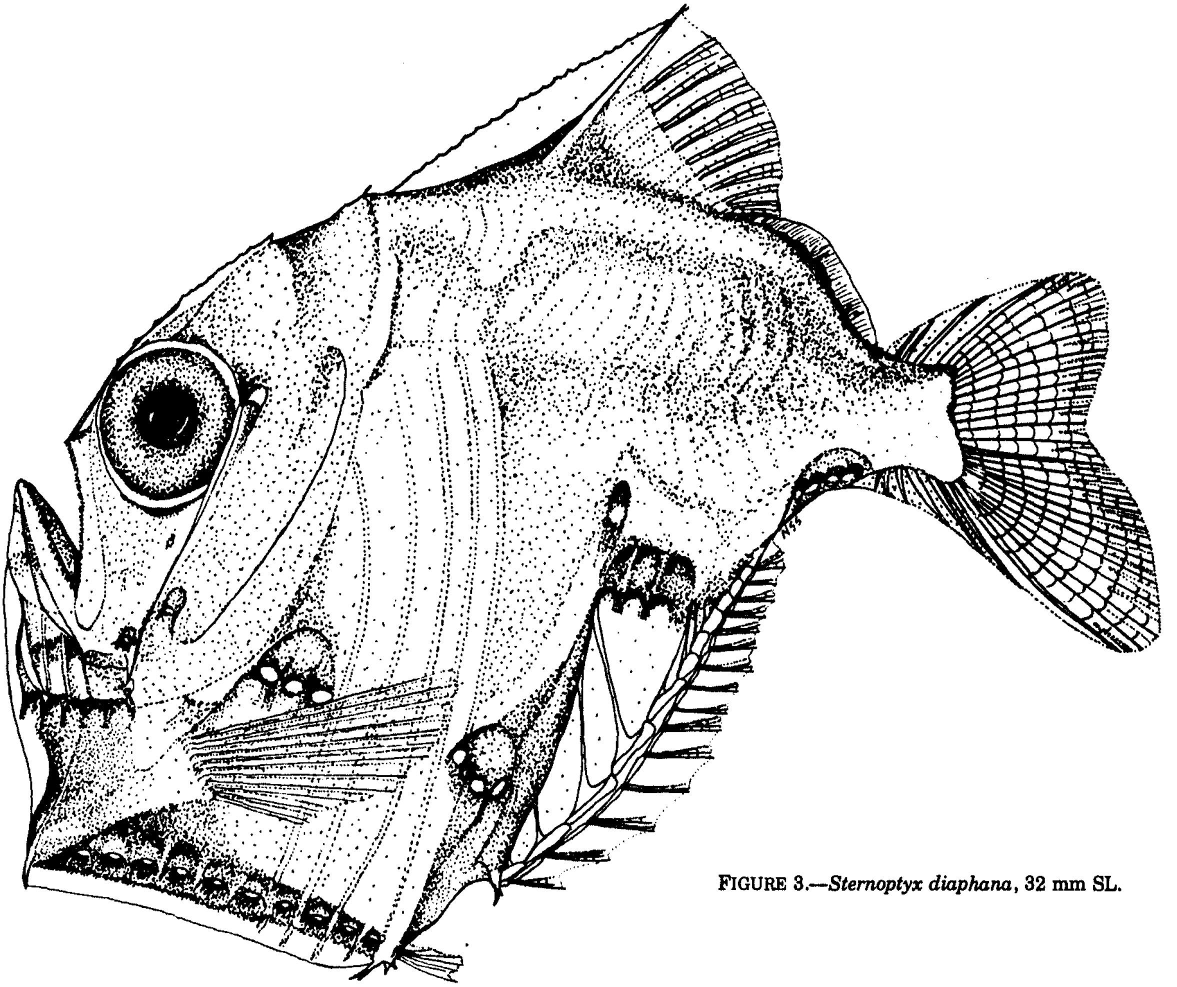

FIGURE 3.—*Sternoptyx diaphana*, 32 mm SL.

TABLE 2.—Meristic counts of *Sternoptyx* species.

	Vertebral no.						Dorsal rays					Anal rays					Gill rakers (1st arch)			
Species	27	28	29	30	31	32	9	10	11	12	13	12	13	14	15	16	6	7	8	9
S. diaphana[1]	2	30	12	—	—	—	7	7	3	—	—	—	2	9	4	—	2	39	3	—
S. pseudobscura[2]	1	8	19	1	—	—	3	4	3	—	—	—	3	5	2	—	—	18	34	3
S. obscura[3]	—	—	2	8	—	—	3	5	1	—	—	3	7	—	—	—	—	9	4	3
S. pseudodiaphana[4]	—	—	4	40	53	8	4	11	54	53	4	—	1	21	5	1	2	68	11	—
S. pseudodiaphana[5]	—	—	3	20	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. pseudodiaphana[6]	—	—	—	1	21	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[1]Atlantic and Pacific populations represented.
[2]Atlantic and central Pacific populations represented.
[3]East Pacific populations only.
[4]Northeastern and southern Atlantic and southeastern Pacific populations represented.
[5]Tropical Atlantic subset (included in 4).
[6]Southeastern Pacific subset (included in 4).

diaphana (>18 mm SL) can be distinguished on the basis of vertebral number 29-32 versus 27-29, respectively, Table 2; see also Borodulina 1978), and the placement of the photophore SAN (described by SAN depth/SL and trunk depth/SAN height, Figures 6, 7) which is appreciably raised in *S. pseudodiaphana*. Overlap of more than one of these three characters in any given specimen was rarely observed. Other differences, most noticeable in sympatric populations, occur in body shape and pigmentation. *Sternoptyx diaphana* is generally deeper in body and especially trunk, appreciably less pigmented, and lacks streaks on the outer ventral caudal fin margin in larger individuals (Tables 3, 4).

Sternoptyx obscura is distinguished from *S.*

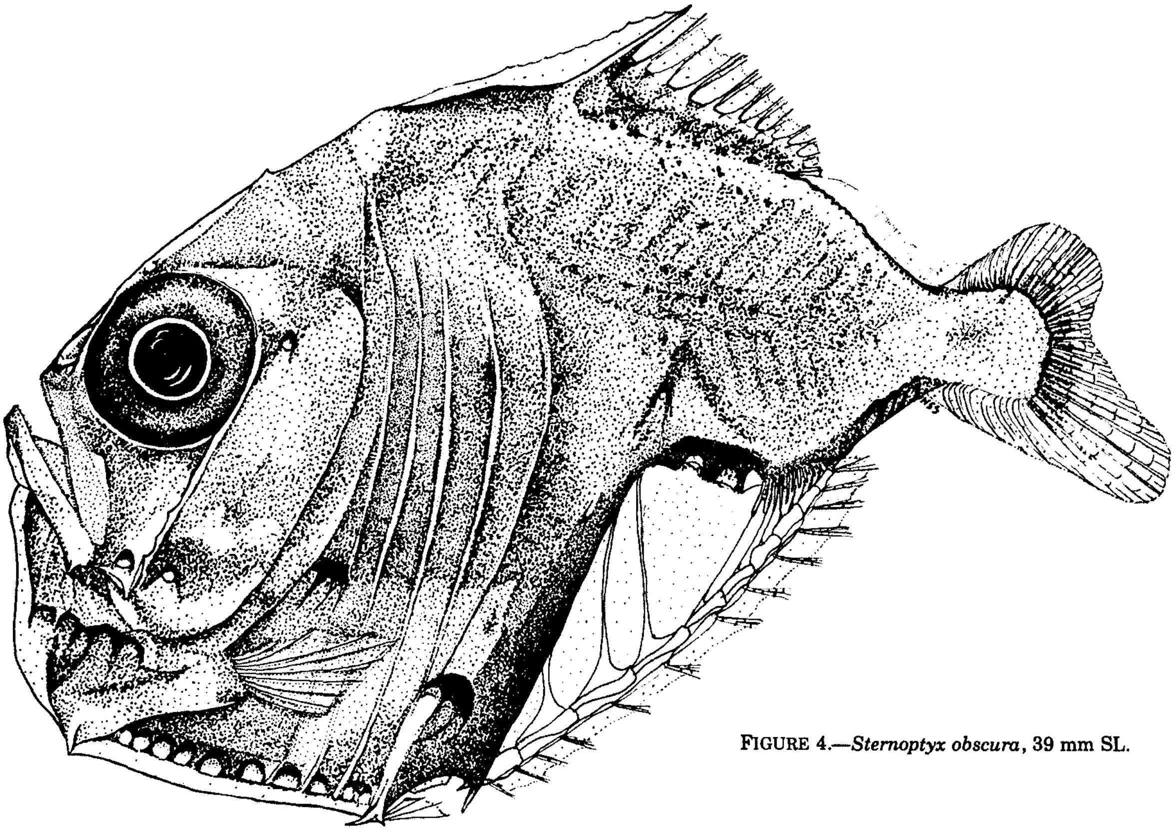

FIGURE 4.—*Sternoptyx obscura*, 39 mm SL.

TABLE 3.—Proportional measurements of *Sternoptyx* species for various size classes.

Item	11-16 mm SL[1] *S. diaphana* Mean	Range	*n*	17-47 mm SL *S. diaphana* Mean	Range	*n*	16-55 mm SL *S. pseudobscura* Mean	Range	*n*
Body depth[2]	85.2	80.8-90.0	7	87.1	75.7-96.7	74	87.4	73.2-96.2	52
AN length[2]	10.1	8.2-11.4	11	12.0	9.4-13.9	58	8.6	5.5-10.5	45
SC length[2]	5.5	4.2-6.4	6	7.3	5.9-11.2	55	5.3	3.8-6.7	41
SAN depth[2]	29.8	28.3-31.8	10	33.2	27.0-39.7	88	20.8	14.4-30.7	66
Trunk depth[2]	38.0	34.2.40.8	11	44.1	38.3-49.5	88	39.5	33.7-46.7	56
Trunk length[2]	36.1	34.2-38.2	11	36.1	32.0-43.8	86	35.6	27.0-41.5	54
Trunk depth/trunk length	1.05	1.00-1.12	11	1.21	0.94-1.37	86	1.12	0.95-1.33	64
Dorsal base/dorsal blade	—	—	—	0.76	0.56-1.00	72	0.79	0.56-0.94	19
Trunk depth/SAN height	4.4	3.8-6.0	11	3.8	2.9-6.1	86	2.0	1.6-2.5	56
Orbit diameter/suborbital length	0.89	0.83-0.95	11	1.03	0.89-1.21	57	0.85	0.72-1.04	37

Item	13-17 mm SL[1] *S. pseudodiaphana* Mean	Range	*n*	18-61 mm SL *S. pseudodiaphana* Mean	Range	*n*	15-40 mm SL *S. obscura* Mean	Range	*n*
Body depth[2]	78.6	70.1-89.4	27	80.8	70.5-92.6	131	74.9	68.4-82.1	18
AN length[2]	9.8	7.6-11.8	36	11.4	8.8-13.7	120	8.5	6.0-11.1	11
SC length[2]	6.3	5.3-7.6	19	7.6	5.0-11.7	120	5.1	4.0-7.7	11
SAN depth[2]	24.4	22.3-31.8	36	25.3	21.7-33.2	132	22.9	20.3-26.2	18
Trunk depth[2]	35.8	31.4-41.2	36	38.8	33.5-46.6	132	31.6	27.5-35.1	18
Trunk length[2]	37.4	32.9-43.8	36	37.7	33.2-43.4	132	37.7	32.5-42.2	18
Trunk depth/trunk length	0.95	0.83-1.11	34	1.03	0.86-1.24	131	0.83	0.75-0.94	26
Dorsal base/dorsal blade	—	—	—	0.90	0.65-1.12	51	1.14	1.03-1.43	14
Trunk depth/SAN height	2.8	2.3-3.4	32	2.7	2.1-3.4	132	3.6	2.6-5.1	18
Orbit diameter/suborbital length	1.06	0.96-1.21	36	1.07	0.92-1.45	108	1.05	0.89-1.30	10

[1]Subadults.
[2]Percent standard length.

pseudobscura (and indeed, all other species of *Sternoptyx*) by the narrow shape and configuration of the trunk and also the high dorsal fin base/dorsal blade ratio. The trunk is markedly longer than it is deep, while the dorsal blade height is usually much shorter than dorsal fin base length

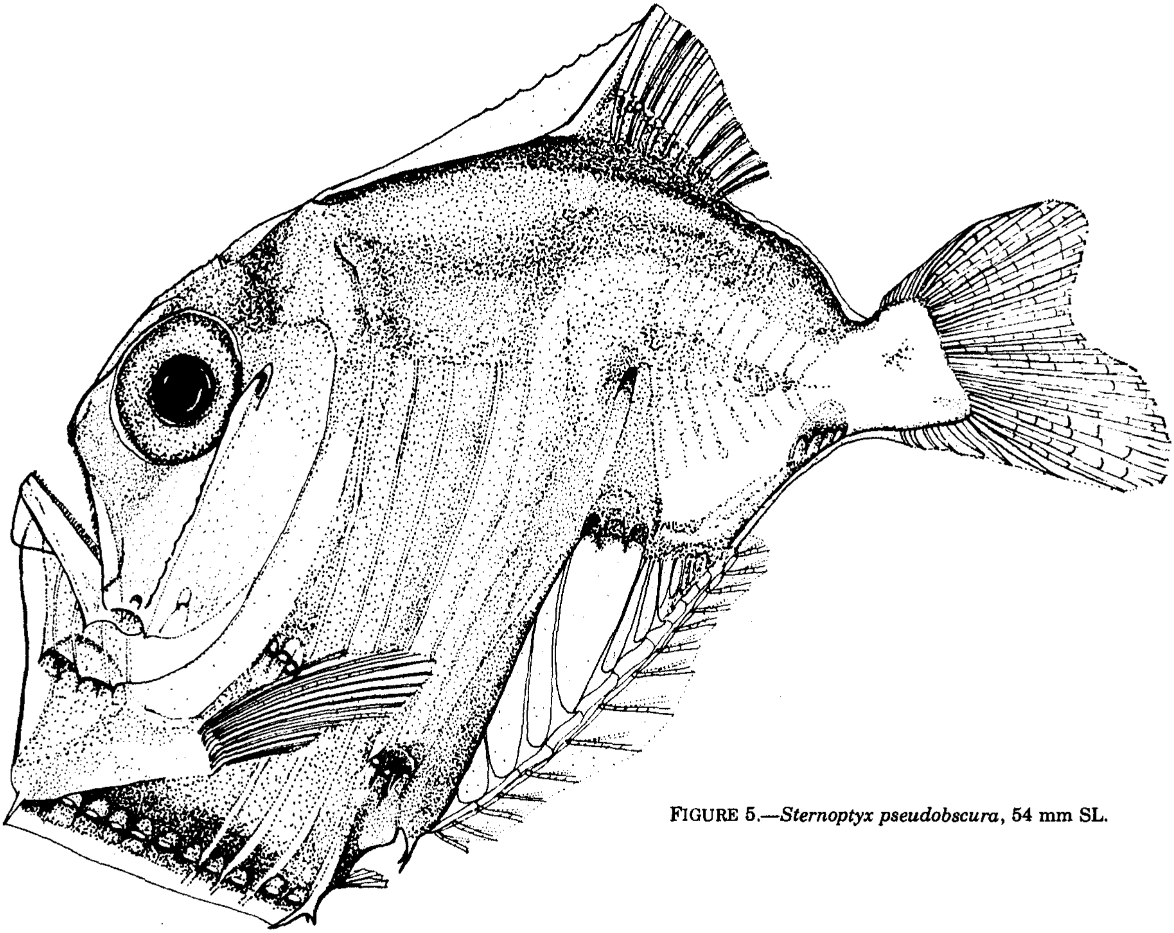

FIGURE 5.—*Sternoptyx pseudobscura*, 54 mm SL.

(Table 3). *Sternoptyx obscura* is further distinguished from *S. pseudobscura* by its lower placement of the photophore SAN and by uniformly dark pigment of body and trunk, as well as the presence of a dark corona along the caudal fin rays, radiating from the fin base.

Geographic Variation

The degree of genetic differentiation and nature of geographic variation in populations of midwater fishes have not been thoroughly explored, though evidence is now accumulating that such variation does exist and may be widespread in species with broad geographic ranges (e.g., Nafpaktitis 1968; Baird 1971; Pertseva-Ostroumova 1974; Karnella and Gibbs 1977). Baird (1971) was able to distinguish separate populations in several species of the related hatchetfish genus *Argyropelecus*. Populations tended to remain distinct over time and differences among populations were generally associated with zoogeographic boundaries. The present evidence indicates that similar patterns of geographic variation occur in species of *Sternoptyx*, the extent of which awaits more extensive investigation.

Geographic variation is apparent in both *S. pseudobscura* and *S. pseudodiaphana*. The systematic problems arising from such variation are illustrated in Figures 6 and 7. In addition to the indicated allometry, the suitability of the two character complexes (trunk depth/SAN photophore height and SAN photophore depth) for distinguishing species differs, depending on the populations being compared. Both characters are distinctive among the three species illustrated (*S. diaphana, S. pseudodiaphana,* and *S. pseudobscura*) for sympatric populations in the North Atlantic. However, where southeast Pacific populations of *S. pseudodiaphana* are compared with

TABLE 4.—Characters useful in differentiating species of the genus *Sternoptyx*.

Character	*S. pseudodiaphana*	*S. diaphana*	*S. obscura*	*S. pseudobscura*
Anal pterygiophore configuration	No appreciable pterygiophore extension posterior to anal photophores (>18 mm SL)	Similar to *S. pseudodiaphana* (>18 mm SL)	Extension posterior to anal photophores (see Haruta and Kawaguchi 1976)	Similar to *S. obscura* (see Haruta and Kawaguchi 1976)
SAN position	About 3 or less times in trunk depth; not more than 3½ times in subadults	More than 3 times in trunk depth: more than 4 times in subadults (<ca. 17 mm)	As in *S. diaphana*	About 1½ to 2½ times in trunk depth; raised to midtrunk line in Atlantic populations
Ratio dorsal base to dorsal blade	Dorsal base normally shorter than blade, occasionally about equal to or slightly longer	Dorsal base usually less than 0.9 of blade	Dorsal base longer than dorsal blade	As in *S. pseudodiaphana*
Trunk dimensions	Trunk depth about equal to trunk length; in subadults often less	Trunk depth conspicuously greater than trunk length; in subadults can be equal	Trunk depth conspicuously less than trunk length	Trunk width greater than trunk length
Trunk pigmentation	Dark bar above midline, little pigment near midline	Light in region of midline	Uniformly dark over whole trunk region	Nonuniform dark pigment in trunk region
Caudal fin pigmentation	Light pigment streaks at ventral outermost margin of caudal rays of larger adults (ca. 40 mm)	Little or no pigment on caudal rays	Corona of dark pigment spreading from base of caudal fin rays	Dark pigment restricted to innermost margin of caudal fin rays
Pectoral fin pigmentation	Absent in adults; present at ray bases in juveniles and subadults	Not present	Not present	Not present
Vertebral number	30-32, rarely 29	28, occasionally 27 or 29	30, occasionally 29	29, ocasionally 28 or 30
Anal rays	14-15, rarely 13	14-15, occasionally 13	12-13	13-15
Anal photophores	In adults: longer than peduncle depth; little horizontal extension of ventral body margin above anal fin	Similar to *S. pseudodiaphana*; anal photophores fill pterygiophore "gap"	Shorter than peduncle depth; body margin extends posteriorly above anal fin	Similar to *S. obscura*
Eye size	Orbit diameter greater than suborbital length; rarely less	Orbit diameter about equal to, often less than, suborbital length	Orbit diameter usually greater than suborbital length	Orbit diameter less than suborbital length, equal to it
Dorsal rays	9-13, usually 11-12	9-11, usually <11	9-11, usually <11	9-11
Maximum size (SL)	>60 mm	<50 mm	<45 mm	>55 mm

Atlantic forms of *S. diaphana* the trunk depth character exhibits overlap particularly in smaller individuals. Likewise, while the SAN depth character is distinctive for *S. diaphana* and *S. pseudodiaphana*, there is considerable overlap when Pacific populations of *S. pseudobscura* are compared with *S. pseudodiaphana*. The lower position of the SAN photophore has been illustrated by Haruta and Kawaguchi (1976, figure 6) for western Pacific forms of *S. pseudobscura* and can be compared with the Atlantic form illustrated here (Figure 5). Differences in vertebral number between Pacific and tropical Atlantic forms of *S. pseudodiaphana* are indicated (Table 2) and the character should be useful in distinguishing the Pacific population from *S. obscura*.

Postlarval Development

Characters useful in distinguishing later life stages are often less suitable or ineffective for metamorphosing and postlarval stages or indeed small (<18 mm) subadults. Geographic variation and allometric growth further complicate identification. The present data, while substantiating the presence of both allometry and geographic variation (Table 3; Figure 7), cannot be considered comprehensive and intensive studies of collections from numerous geographic regions are yet to be done. The extension of the ventral trunk margin, size of AN photophore group, and elongate posterior pterygiophores appear to be neotenic characters established from mid- to late-metamorphic stages (Figures 8, 9) and are consequently less useful as species-distinctive characters for early life stages.

When present, the location of photophore SAN is diagnostic, though the placement tends to be somewhat lower on the body in postlarvae. SAN is closely associated with photophores AN in *S. diaphana* and not markedly raised in *S. obscura*. For *S. pseudodiaphana* and *S. pseudobscura* it is vertically separated from the AN group. In Atlantic populations of *S. pseudobscura* the photophore SAN is raised to the midtrunk line, distinguishing it from other congeners. The lower SAN position in Indo-Pacific populations of *S. pseudobscura* make this character less useful in separating it from *S. pseudodiaphana*. The smaller eye (noted by Günther 1887) in *S. pseudobscura* (Table 3) is

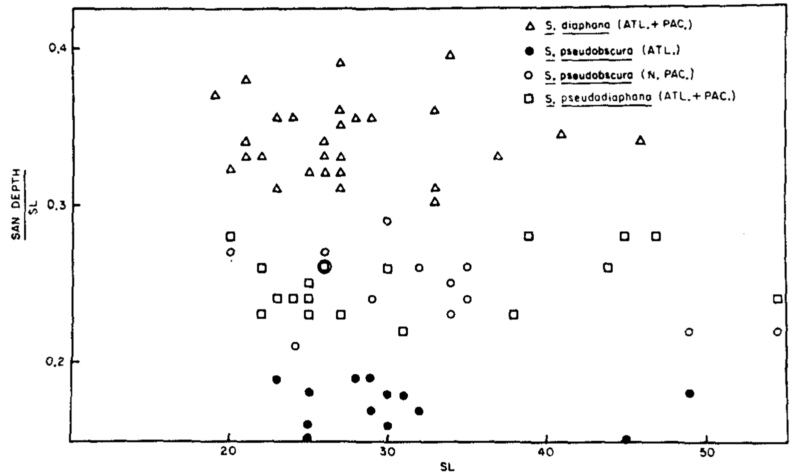

FIGURE 6.—Scattergram of ratio of SAN photophore depth/SL and SL (millimeters) for three species of *Sternoptyx*.

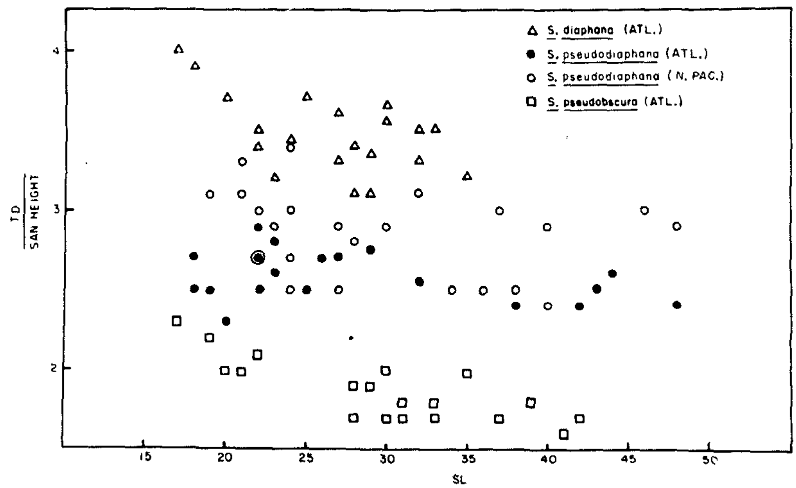

FIGURE 7.—Scattergram of ratio of trunk depth (TD)/SAN photophore height and SL (millimeters) for three species of *Sternoptyx*.

diagnostic while small individuals of the two species may be separated on the basis of pectoral fin ray pigment present in *S. pseudodiaphana*. The young of *S. obscura* are uniformly pigmented and have the characteristically narrow trunk at quite small sizes.

The sequence of numbered "stages" in which photophore groups appear and are completed is listed in Table 1 for *S. pseudodiaphana* and *S. diaphana*. The sequential pattern is identical in both species, and limited data suggest *S. pseudobscura* also conforms to this pattern though the early-metamorphic forms of these species are as yet undescribed. For ease of reference a sequence of stages based on the order of appearance of photophores during development is presented in Table 1. The brief account given below is intended primarily to outline the major anatomical landmarks during metamorphosis and to indicate some of the distinctions among species during postlarval development.

Sternoptyx pseudodiaphana

The least developed specimen observed of *S. pseudodiaphana* from the Atlantic (10.2 mm SL) is elongate, with the head about 25% of SL. Dorsal and pelvic fins are undeveloped, while the pectoral fin has six and the anal seven rays developing. The caudal has 19 rays. The postlarva is relatively transparent and pigment is restricted to certain areas: a symphysial pair of spots, two isthmus spots, the pectoral fin, and a caudal peduncle spot. Internally, the swim bladder is pigmented dorsad, as is the posterior part of the stomach. Meningeal pigment is present both as a melanophore in the

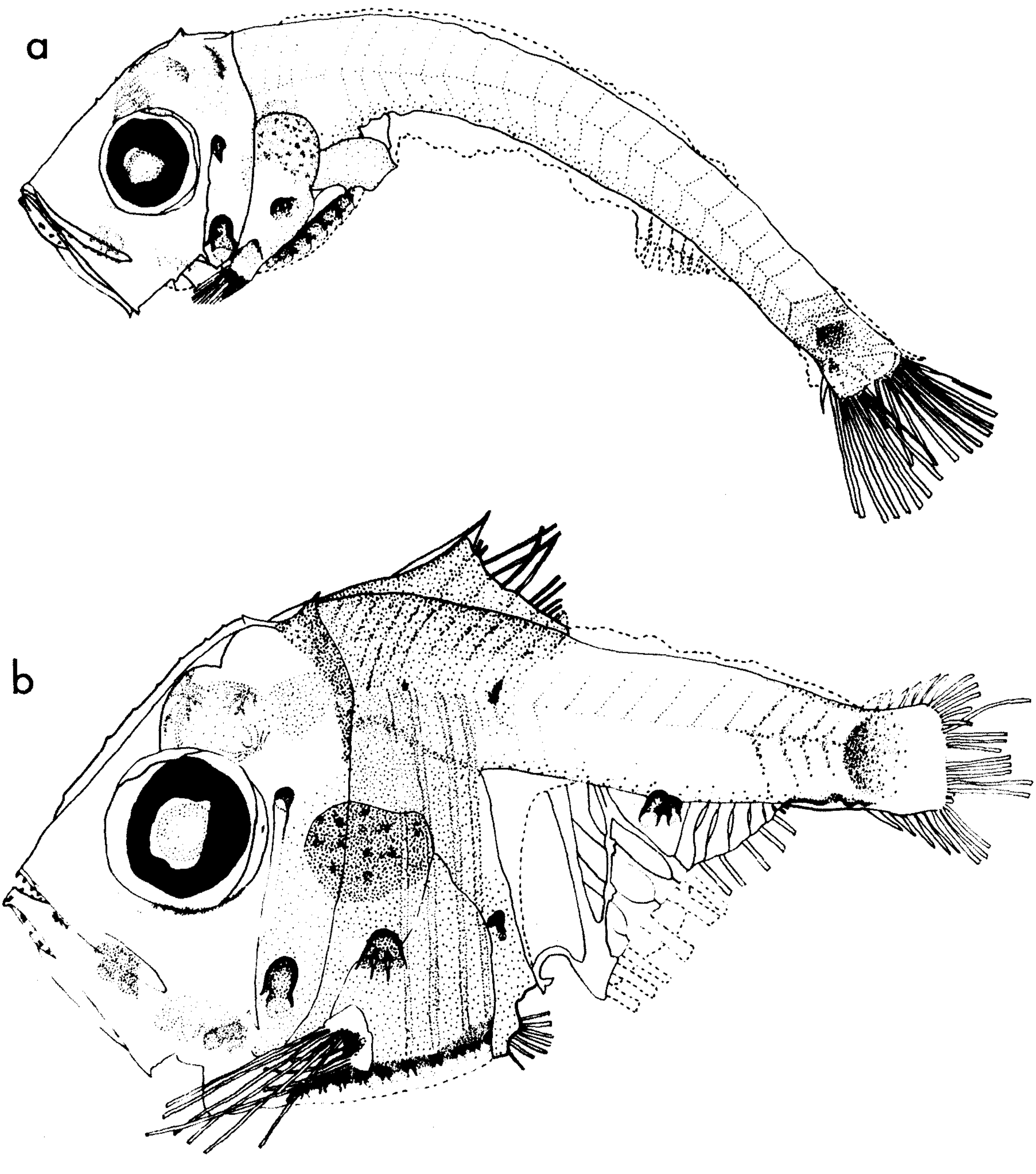

FIGURE 8.—Development of *Sternoptyx pseudodiaphana*: (a) Stage 1, 10.0 mm SL; (b) Stage 4, 8.9 mm SL.

pineal region and as scattered melanophores posterior to it. In the most advanced Stage 1 specimen (Figure 8a) additional pigment occurs anterior to the stomach. Stomach pigmentation is completed by Stage 3 and during this stage new pigment sites develop along the ventral margin of the orbit, in the opercular region, and along the predorsal crest. Light abdominal pigmentation appears during Stage 4 and the caudal pigment extends anteriorly along the dorsum (Figure 8b), reaching the dorsal fin base later in this stage. As development progresses, pigmentation spreads and intensifies

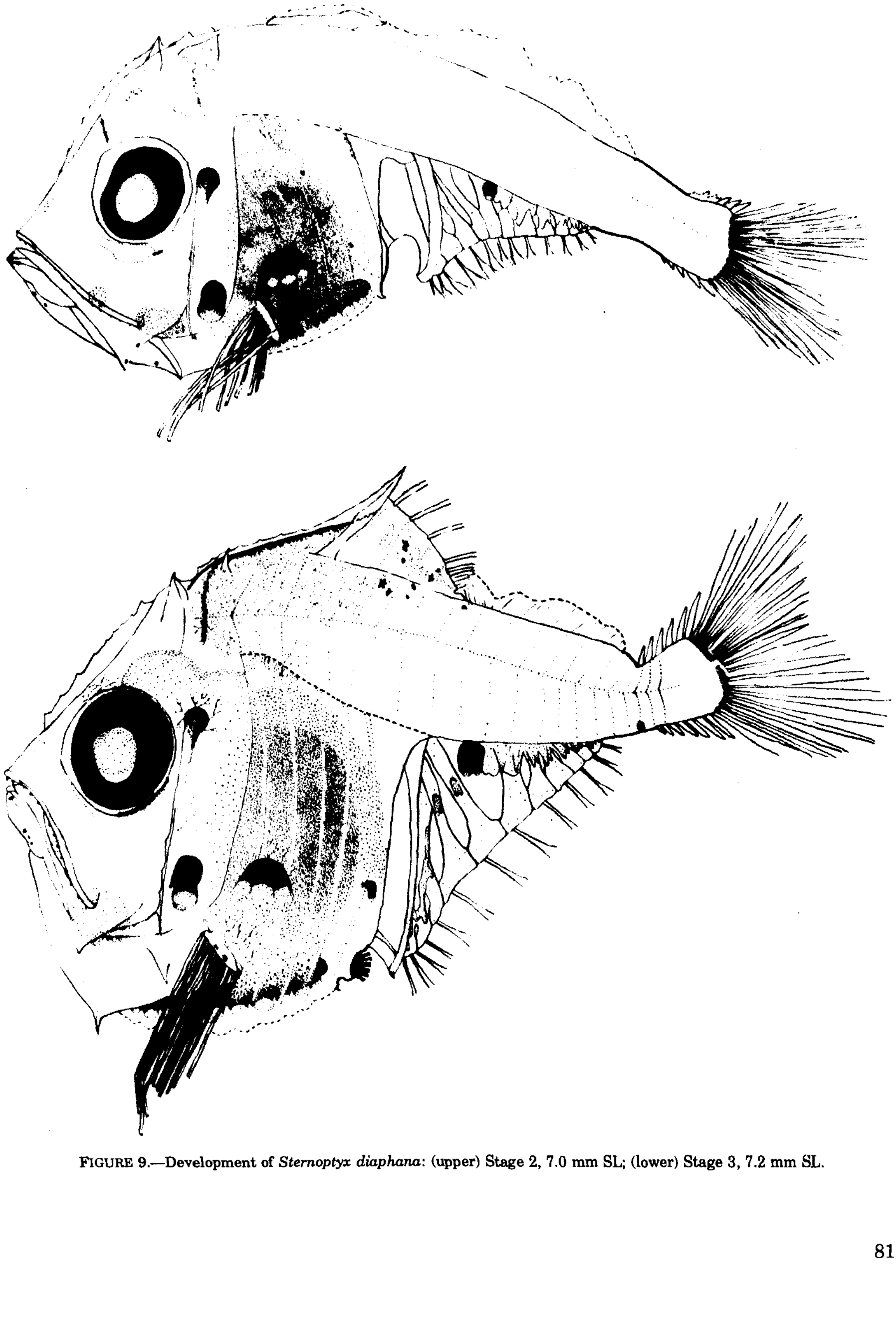

FIGURE 9.—Development of *Sternoptyx diaphana*: (upper) Stage 2, 7.0 mm SL; (lower) Stage 3, 7.2 mm SL.

leading to the adult condition. The rays of the dorsal fin first develop during Stage 3; the rays of the pelvic fin first appear in Stage 4.

A series of *S. pseudodiaphana* taken from the southeastern Pacific (lat. 33°-39° S, long. 80°-120° W) show a similarity in morphology and pattern of development to North Atlantic forms. The data indicate that the sequences of both appearance and completion of the various photophore groups are similar, although the relative timing of completion for certain groups may differ slightly. For example, while the completion of PV in North Atlantic forms apparently occurs prior to the initiation of SC, in southeastern Pacific forms it occurs afterwards (Table 1). Pigmentation in specimens from these two populations is essentially alike, but a small pigment spot located near the posterior end of the dentary in Pacific forms was not noted in the Atlantic material. As in the adults, differences between postlarvae from the two areas, then, does occur.

Slight differences in larval characteristics between populations of the same species have been shown for certain lanternfishes (Pertseva-Ostroumova 1974) and do occur in the genus *Sternoptyx*, differences which we suspect, based on *Argyropelecus*, may be more extensive than indicated here. They can render species differentiation difficult in certain areas. Early-metamorphic individuals of *S. diaphana* and *S. pseudobscura* are superficially similar and in tropical Atlantic collections only late-metamorphic stages can be separated with certainty. Metamorphic individuals of *S. pseudodiaphana*, on the other hand, are highly distinctive. A series of *S. diaphana* taken off Bermuda, an area where *S. pseudobscura* is apparently rare, allowed for some comparison between the midmetamorphic forms of this species and *S. pseudodiaphana*.

The caudal spot so conspicuous in the young of *S. pseudodiaphana* at Stage 1 (Table 1) is found neither in *S. diaphana* nor *S. pseudobscura* prior to completion of photophore development. Pigmentation of the pectoral fin rays has been found in *S. diaphana,* although not consistently, up to Stage 3. At any given stage, *S. diaphana* appears to be in a more advanced state both morphologically and in terms of pigmentation. Thus the configuration of the anal fin pterygiophores attains the juvenile appearance during Stage 3, appearing in Stage 4 in *S. pseudodiaphana*; the pelvic fins differentiate earlier (Stage 3 versus 4), as does the pigmentation of *S. diaphana* in general (Figure 9). Even so, the pigmentation of *S. pseudodiaphana* tends to be denser in the more advanced specimens, which are conspicuous by the dark color of the dorsum. Elbert H. Ahlstrom[4] recognizes three forms of postlarval *Sternoptyx* spp. in his North Pacific collections, none of which bear a caudal melanophore. As populations of *S. pseudodiaphana* are unknown north of the Equator in the Pacific, then, tentatively, postlarval *S. obscura* also lack caudal pigment. *Sternoptyx pseudodiaphana* may, therefore, be distinguished from congeners by this character.

General Comments

During metamorphosis postlarval *Sternoptyx* (ca. 6-14 mm) undergo extensive change from an elongate premetamorphic form to a deep-bodied juvenile. In earlier stages, metamorphic individuals are somewhat shorter than premetamorphic forms, a pattern of apparent loss in length also observed in the related hatchetfish genus *Argyropelecus* (e.g., Brauer 1906; Jespersen 1915; and others). While the sequential pattern of photophore addition appears identical among the species examined, timetables for the differentiation of other external characters do not necessarily coincide. As indicated, *S. diaphana* appears in a more advanced state of morphological differentiation and development than *S. pseudodiaphana* at comparable photophore stages. A similar pattern has been observed by Baird (unpubl. data) among species of *Argyropelecus*. Geographic variation both among and within species is apparent. It appears that there can be appreciable flexibility among species in the timing of photophore addition in relation to the development of other morphological characters, though the adaptive significance of these observations is presently unclear. Growth rate, the functional significance of photophore presence at a given size, and broader ecological considerations such as predation or resource availability, are likely complexly related to patterns of photophore development.

GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION OF *STERNOPTYX* SPECIES

The genus is widespread, occurring in all oceans

[4]E. H. Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. November 1975.

and apparently excluded only from polar seas and the Mediterranean (Jespersen 1915; Geistdoerfer et al. 1970; Baird 1971; Haruta and Kawaguchi 1976; Borodulina 1978). The geographic distributions of the species are presented in Figures 10 and 11 and, when coupled with the recent Russian data (Borodulina 1978), exhibit certain distinct patterns. The species tend to be limited to areas with hydrographically similar characteristics (sensu Baird 1971) and often exhibit mutually exclusive distributions. The horizontal distributions conform in general to zoogeographically distinct regions in the oceans (e.g., Baird 1971; McGowan 1977; Backus and Craddock 1977), the nature and limits of which are only generally defined. From the limited number of observations of vertical distribution in areas of sympatry, species which share the water column tend to have separate depths of maximum abundance.

Sternoptyx obscura is confined to the Indo-Pacific. In the eastern Pacific and Indian equatorial regions, it is the sole representative of the genus. In the periphery of its distribution, it can be relatively abundant (e.g., basins off southern California) and can occur in sympatry with *S. diaphana* and *S. pseudobscura* (Figures 10, 11). In general the geographic distribution resembles that of a number of other species, e.g., *Myctophum aurolanternatum, Cyclothone acclinidens, Scopelarchoides signifer, Rosenblattichthys alatus* (Nafpaktitis and Nafpaktitis 1969; Parin et al. 1973; Johnson 1974; Mukhacheva 1974; Quero 1974; Becker and Borodulina 1976), that are apparent equatorial Indo-Pacific endemics.

Sternoptyx diaphana and *S. pseudobscura* occur in the Atlantic and Indo-Pacific and overlap for much of their ranges (Figures 10, 11). *Sternoptyx pseudobscura*, however, is apparently uncommon in the western North Atlantic and the Caribbean, where *S. diaphana* is abundant, yet it is well represented in the Gulf of Mexico. The occurrence of all three species in Indonesian basin regions is indicative of the zoogeographic complexity of the mesopelagic ichthyofauna of that area.

Sternoptyx pseudodiaphana is widely distributed in the Southern Ocean (see also Borodulina 1978) and associated boundary currents in the Southern Hemisphere (Figure 11). Evidence from other studies (e.g., Alvarino 1965; Gibbs 1968; Krefft and Parin 1972; Nafpaktitis 1973; Mayer 1975; Bertelsen et al. 1976) has indicated that the subtropical convergence area, at least in the South Pacific, is a distinct zoogeographic region with a number of endemic or characteristic species. The occurrence of *S. pseudodiaphana* off South Australia, in the Indian Ocean, and across the South Atlantic between lat. 32°-40° S reinforces the concept that many elements of the subtropical con-

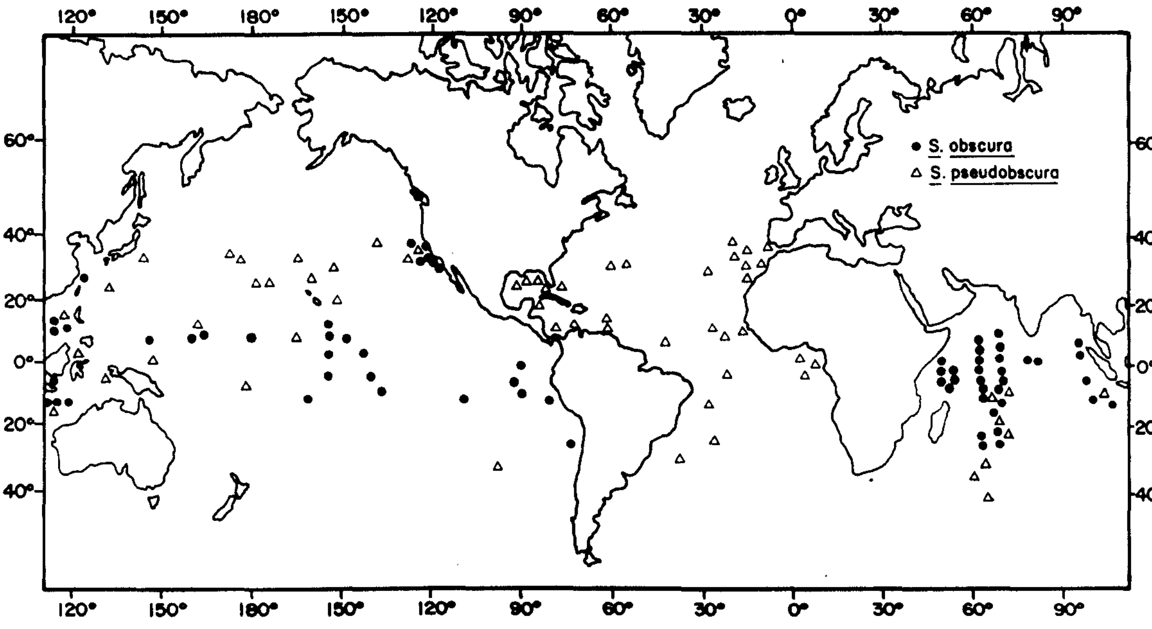

FIGURE 10.—Distribution of *Sternoptyx obscura* and *S. pseudobscura* (also from Baird 1971; Haruta and Kawaguchi 1976).

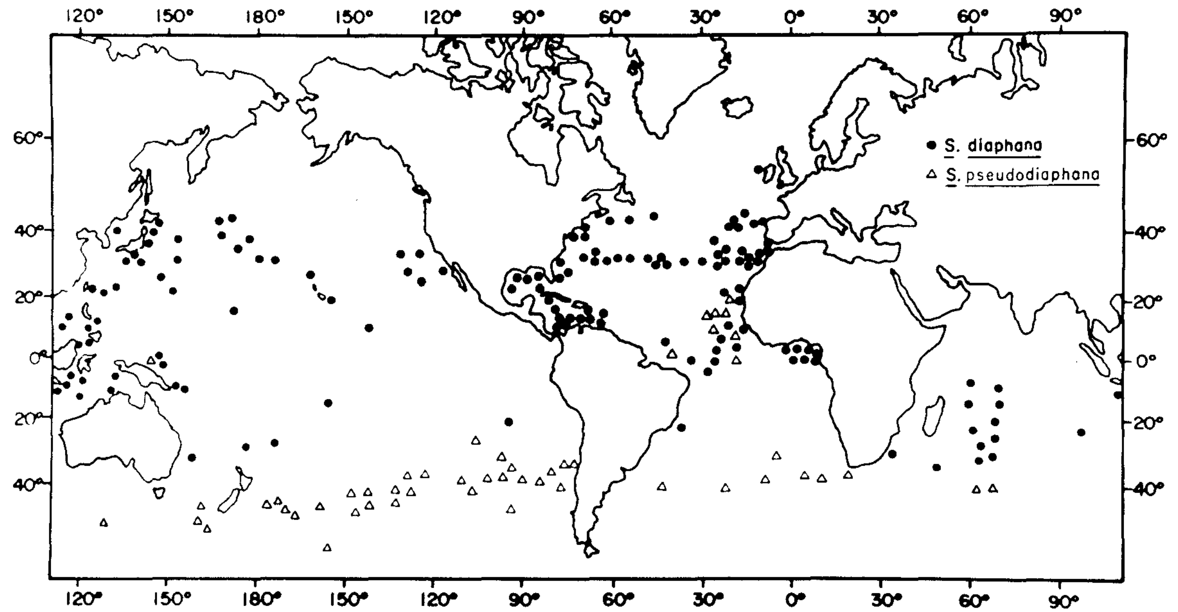

FIGURE 11.—Distribution of *Sternoptyx diaphana* and *S. pseudodiaphana* (also from Baird 1971; Haruta and Kawaguchi 1976).

vergence fauna in the Pacific have circum-Southern Ocean distributions (Craddock and Mead 1970). McGinnis (1974) has presented evidence in support of counterclockwise circulation in the Pacific subantarctic with observed endemism in mesopelagic fishes resulting from zoogeographic isolation of that region. *Sternoptyx pseudodiaphana* from this area can be distinguished from Atlantic forms and the evidence presented here is not in conflict with the McGinnis hypothesis. In the tropical eastern North Atlantic *S. pseudodiaphana* extends as far north as lat. 20° N, long. 21° W (where it exists in sympatry with *S. diaphana*) and it is not unlikely that it occurs in the Gulf of Guinea (Figure 11). Although some specimens have been taken in the Benguela Current area, the general paucity of material at present available from the South Atlantic precludes judgment as to whether a link exists between the North Atlantic and Subtropical Convergence populations. A potentially disjunct distribution, in a manner less extreme than is expressed by *Stomias boa boa* (Gibbs 1969), is given some tentative support by the apparent differences observed between postlarvae from the North Atlantic and South Pacific. Thus it is possible that the North Atlantic population of *S. pseudodiaphana* is a diverging form of the Subtropical Convergence stock. Finally, mention should be made of the single specimen apparently caught near the Philippines. There is no obvious mistake in the station labelling for this individual (*Challenger* Stn. 218). The species range extends considerably northward in the Atlantic and future studies may also confirm a more complex distribution pattern in the Pacific than present data would indicate.

The species of *Sternoptyx* are the deepest dwelling of the marine hatchetfishes and do not exhibit marked diel vertical migration. There are few capture records from opening/closing nets but new data are provided from recent comprehensive surveys (0-2,000 m) at three locations, in the eastern North Atlantic and Gulf of Mexico, where discrete-depth trawls were taken (Hopkins and Baird 1973; Badcock and Merrett 1976). *Sternoptyx diaphana* and *S. pseudobscura* occur sympatrically at all three locations. *Sternoptyx pseudodiaphana* was found only at the eastern Atlantic stations where it was the least abundant species at lat. 18° N but more common at lat. 11° N. Individuals of all species were taken over a broad depth range (ca. 500-2,000 m) but were only abundant over a much more restricted depth zone (Table 5). Thus, *S. diaphana* and *S. pseudobscura*, which have broad areas of sympatry, tend to have distinctly separate zones of maximum abundance while *S. pseudodiaphana*, at the limits of its distribution, is somewhat intermediate and overlaps

TABLE 5.—Range of depths of maximum abundance of species of *Sternoptyx* in sympatry at three locations (subadults and adults) (Hopkins and Baird 1973; Badcock and Merrett 1976).

Species	Lat. 27° N, long. 86° W	Lat. 18° N, long. 25° W	Lat. 11° N, long. 20° W
S. diaphana	600-750 m	600-800 m	500-700 m
S. pseudobscura	850-1,000 m	800-1,500 m	800-1,000 m
S. pseudodiaphana	Not present	600-1,500 m	600-1,000 m

both congeners (Table 5). The shoaling of *Sternoptyx* spp. between lat. 18° N and 11° N is not a function of developmental state and is a feature shown by many species of midwater fishes (Badcock and Merrett 1977).

In other areas of the eastern North Atlantic and also in the Gulf of Mexico where *S. pseudobscura* and *S. diaphana* share the water column, populations of *S. pseudobscura* are always centered below those of *S. diaphana*. Data presented by Baird (1971) indicated that *S. pseudodiaphana* is usually taken in 800-1,200 m depth in the Southern Ocean. Evidence from recent collections from the South Atlantic imply a similar pattern of vertical distribution.[5] In general, then, *S. pseudodiaphana* and *S. pseudobscura* may be regarded as deeper dwelling species of *Sternoptyx* while *S. diaphana* is a shallower living form. In certain areas of the Atlantic, discrete sampling has shown *S. diaphana* to be centered deeper than indicated above (Badcock 1970; Badcock and Merrett 1976; Roper et al.[6]). *Sternoptyx pseudobscura* has been shown to be of low abundance in these areas but the deepening of *S. diaphana* is likely to be a consequence of the sinking of isotherms relative to other areas. The role of competitive interactions among these species is yet undocumented and these may also exert an effect on geographic patterns of vertical distribution. Data on *S. obscura* are not comprehensive, but a preliminary survey of maximum depth of open trawl collections indicate a depth range similar to *S. diaphana* (500-1,000 m) in basins off southern California.

An analysis of the vertical distribution of mid- and late-metamorphic stages in the eastern North Atlantic was possible only for *S. pseudodiaphana* because of the problems in distinguishing between such individuals of the other two species examined. As with subadults and adults, individuals of like developmental stage lay shallower in the water column at lat. 11° N, long. 20° W than at lat. 18° N, long. 25° W (400-800 m versus 500-900 m depth). Although the data are sparse, there is evidence for ontogenetic vertical stratification among metamorphic stages. At lat. 11° N, long. 20° W, Stages 1-3 occurred only in 400-500 m depth; Stage 4 in 400-600 m; Stage 5 in 500-700 m; and Stage 6 in 500-800 m. A similar relationship is implied for metamorphic stages from lat. 18° N, long. 25° W, although stratification occurred deeper in the water column.

[5]G. Krefft, Instutit für Seefischerei, Hamburg, West Germany, pers. commun. 1976.

[6]Roper, C. F. E., R. H. Gibbs, Jr., and W. Aron. 1970. Ocean acre: an interim report. Report to the U.S. Navy Underwater Sound Laboratory. Contract No. N00140-69-C-0166. Smithson. Inst., Wash., D.C., 22 p.

CONCLUSIONS

The evidence presented shows *Sternoptyx* to contain four closely related species. Morphological distinctions between them are relatively slight, but are consistent among the populations examined. The four species have broad geographic ranges and the limited data indicate the occurrence of geographic variation in *S. pseudobscura* and *S. pseudodiaphana* at adult and postlarval levels. Thus systematic difficulties arise in that certain characters useful in distinguishing species in sympatry may overlap when measurements from other populations are included.

Characters subject to allometric growth similarly present systematic problems. Nevertheless, most of the morphological criteria used here to separate species are maintained irrespective of population or developmental state. When found in sympatry, distinctions are clear and species consistently separable by many characters.

While we distinguish two species pairs on the basis of anal fin pterygiophore configuration, no hypothesis of cladistic relationship among the species is advanced. Considering the highly specialized and peculiar morphology of the genus (Baird 1971; Baird and Eckhardt 1972; Weitzman 1974; for discussion of family relationships), the most parsimonious hypothesis advanced is that a single ancestral species evolved which diverged considerably from a more generalized hatchetfish stock. Subsequent speciation in the genus probably involved the isolation of populations which now show very slight morphological divergence, exhibit various degrees of geographic variation, and have distinct horizontal and vertical patterns of distribution.

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APPENDIX TABLE 1.—Materials and their sources of *Sternoptyx* spp.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
S. pseudodiaphana	1	BMNH	H.M.S. *Challenger*	159	47°25′ S, 130°22′ E	BMNH 87.12.7.151
	1			218	02°33′ S, 144°04′ E	BMNH 87.12.7.157
	6		RRS *Discovery II*	81	32°45′ S, 08°47′ W	BMNH 1930.1.12.43035
	1			85	33°08′ S, 04°30′ E	BMNH 1930.1.12.441
	3			86	33°25′ S, 06°39′ E	BMNH 1930.1.12.552-5
	2			256	34°14′ S, 06°49′ E	BMNH 1930.1.12.411-12
	4			269	15°55′ S, 10°35′ E	BMNH 1930.1.12.413-15
	15		RRS *Discovery* (45)	7824	11°01′ N, 20°11′ W	BMNH 1977.6.14.1-15
	1	IFS	*Walther Herwig*	30/68	36°37′ S, 43°30′ W	
	8			427/71	33°00′ S, 07°50′ E	
	50	IOS	RRS *Discovery* (31)	6662	10°58′ N, 20°00′ W	
	18			7089	17°50′ N, 25°25′ W	
	22			7803	17°50′ N, 25°00′ W	
	48			7824	10°50′ N, 20°00′ W	
	21	LACM	*Eltannin*	1781	39°42′ S, 130°11′ W	
	41			1812	36°38′ S, 87°09′ W	
	27			1835	42°23′ S, 160°14′ E	
	1	MCZ	*Anton Bruun* (3)	160	40°53′ S, 60°01′ E	
	1		(6)	7351	40°51′ S, 64°49′ E	
	1		(13)	5	34°26′ S, 73°28′ W	
	11			6	32°57′ S, 74°57′ W	
	3			10	33°32′ S, 77°56′ W	
	3			16	33°36′ S, 79°32′ W	
	2			20	34°01′ S, 84°58′ W	
	2			41	33°31′ S, 77°29′ W	
	1		*Chain* (35)	962	05°24′ N, 39°55′ W	

APPENDIX TABLE 1.—Continued.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
	2	USNM	*Eltannin* (21)	3	34°00′ S, 80°36′ W	207241
	19			5	33°06′ S, 83°57′ W	207243
	18			6	33°04′ S, 85°49′ W	207234;207235
	5			8	33°00′ S, 89°38′ W	207236
	7			11	37°12′ S, 94°24′ W	207233
	7			11A	38°35′ S, 95°39′ W	207227
	4			13	39°54′ S, 107°36′ W	207240
	3			15	44°03′ S, 120°17′ W	207239
S. diaphana	2	BMNH	H.M.S. *Challenger*	171	28°33′ S, 177°50′ W	BMNH 87.12.7.152-3
	1			214	04°33′ N, 127°06′ E	BMNH 87.12.7.155
	1	CAS	*Te Vega*	548	35°39′ N, 131°53′ W	
	13	IOS	RRS *Discovery* (21)	6662	10°58′ N, 20°22′ W	
	18		RRS *Discovery* (45)	7803	17°50′ N, 25°00′ W	
	35			7824	10°55′ N, 20°00′ W	
	51		RRS *Discovery* (52)	8281	32° N, 64° W	
	1	LACM	*Valero*	11360	33°20′ N, 118°45′ W	
	1	MCZ	*Anton Bruun* (6)	7247	07°56′ S, 65°14′ E	
	2			7298	22°48′ S, 64°55′ E	
	2			7305	24°22′ S, 64°50′ E	
	1			7352	29°45′ S, 64°58′ E	
	5		(19)	824	19°01′ N, 79°02′ W	
	2			829	19°21′ N, 85°31′ W	
	1		*Chain* (26)	505	12°00′ N, 65°00′ W	
	4		*Delaware* (63-4)	31	NW Atlantic	
	6	MSI	*Bellows* (1)	147	27°00′ N, 86°00′ W	
	3		*Mizar* (3)	166	27°36′ N, 88°40′ W	
S. obscura	1	BMNH	H.M.S. *Challenger*	214	04°33′ N, 127°06′ E	BMNH 87.12.7.156
	1	CAS	*Te Vega*	532	36°40′ N, 122°04′ W	
	1			620	32°48′ N, 118°16′ W	
	1	IOS	*Manihine* (226)		W. Equatorial Indian Ocean	
	3	LACM	*Eltannin*	34	07°47′ S, 81°23′ W	10203
	1		*Valero*		33°20′ N, 118°45′ W	11360
	10	MCZ	*Anton Bruun* (6)	7194	03°27′ N, 65°07′ E	
	10	UANM	*Eltannin* (31)	7A	10°57′ N, 149°19′ W	
	20	SIO	*Monsoon*		11°00′ N, 163°00′ E	
	11		*Tethys*		07°00′ S, 135°00′ W	
	25	ZMUC	*Galathea*		10°24′ S, 114°07′ E	
S. pseudobscura	1	BMNH	H.M.S. *Challenger*	214	04°33′ S, 177°06′ E	BMNH 87.12.7.154
	1			235	37°07′ N, 138°00′ E	BMNH 87.12.7.158
	7	IOS	RRS *Discovery* (21)	6662	10°58′ N, 20°00′ W	
	5		(45)	7803	17°50′ N, 25°00′ W	
	20			7824	10°55′ N, 20°00′ W	
	2		*Manihine* (226)		W. Equatorial Indian Ocean	
S. pseudobscura	1	MCZ	*Anton Bruun* (6)	7237	05°55′ S, 65°10′ E	
	5			7303	24°03′ S, 64°50′ E	
	1		(13)	24	33°48′ S, 90°19′ W	
	13			829	21°25′ N, 85°30′ W	
	1		*Chain* (35)	978	20°00′ S, 28°04′ W	
	3		*Delaware* (63-4)	15	NW Atlantic	
	17	MSI	*Bellows* (1)	142	27°00′ N, 86°00′ W	
	7	SIO	*Horizon*	51375	31°53′ N, 152°21′ W	
	6		*Monsoon*	56133	12°40′ N, 165°09′ W	

[1]BMNH—British Museum of Natural History, London; CAS—California Academy of Sciences, San Francisco; IFS—Institut für Seefischerei, Hamburg; IOS—Institute of Oceanographic Science, Wormley, Surrey; LACM—Los Angeles County Museum, Los Angeles, Calif.; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MSI—Department of Marine Science, University of South Florida, St. Petersburg, Fla.; USNM—National Museum of National History, Smithsonian Institution, Washington, D.C.; SIO—Scripps Institute of Oceanography, La Jolla, Calif.; ZMUC—Zoologiske Museum Copenhagen, University of Copenhagen, Copenhagen.