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Species Composition, Abundance, and Vertical Distribution of the Stomiid (Pisces: Stomiiformes) Fish Assemblage of the Gulf of Mexico

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SPECIES COMPOSITION, ABUNDANCE, AND VERTICAL
DISTRIBUTION OF THE STOMIID
(PISCES: STOMIIFORMES) FISH
ASSEMBLAGE OF THE GULF OF MEXICO

Tracey T. Sutton and Thomas L. Hopkins

ABSTRACT

Species composition, abundance, and vertical distribution of the stomiid fish assemblage were investigated in the eastern Gulf of Mexico, a low-latitude, oligotrophic oceanic ecosystem. Seventy-two described species, representing 18 genera, and one undescribed species were identified from 1155 trawl samples. With an additional 10 species reported elsewhere, the stomiid species number now known equals 83, making the Stomiidae the most diverse fish family in the Gulf of Mexico. The assemblage was dominated by three species, *Photostomias guernei*, *Chauliodus sloani* and *Stomias affinis*. These species, as well as four other common species, exhibited an asynchronous diel vertical migration pattern (450-900 m during day; 20-300, 550-900 m at night). The percentage of the populations of the three dominant species migrating daily ranged from 50-70%. Two other patterns occurred in less abundant species: synchronous migration (400-700 m during the day, 0-200 m at night); and, possible migration from the bathypelagial (>1000 m during day; 50-300 m at night). Minimum abundance and biomass estimates for the entire assemblage were 1.86×10^5 individuals and 35.3 kg DW·km⁻² in the upper 1000 m. Stomiids comprised approximately 10% of the micronekton standing stock in the eastern Gulf. Extrapolating eastern Gulf data to the world warm-water mesopelagial, abundance results suggest that stomiids are the dominant mesopelagic upper-trophic level predatory fishes, and as such may serve as key trophic mediators in the transfer of energy in these ecosystems.

The "black" stomioid fishes of the family Stomiidae, sensu Fink (1985), are among the most specialized for a predatory oceanic existence (Tchernavin, 1953; Marshall, 1954), with characters including elongate black bodies, highly distensible stomachs, and mental barbels which often bear elaborate bioluminescent organs. Faunal studies from the western tropical Pacific, Hawaii, and the eastern North Atlantic show that stomiid assemblages are extremely species-rich in warm-water mesopelagic ecosystems (Parin et al., 1977; Clarke, 1982; Craddock et al., 1987). Despite the potential importance of these fishes in midwater food webs, very little is known of their abundance, vertical and geographic distributions, and assemblage structure (Haffner, 1952; Gibbs, 1969; Backus et al., 1970; Clarke, 1974, 1982; Badcock and Merrett, 1977; Blackburn, 1981). In this first paper we describe the structure of the stomiid assemblage found in the upper 1000 m of the eastern Gulf of Mexico. In a subsequent paper we will describe the feeding ecology of the Stomiidae.

Hydrographic Setting.—Circulation in the eastern Gulf of Mexico is dominated by the flow of the Subtropical Undercurrent (Florida Loop Current), which enters the Gulf through the Yucatan Straits and exits through the Florida Straits (Leipper, 1970; Nowlin, 1971; Maul, 1977). The extent of intrusion into the Gulf is latitudinally and seasonally unpredictable. The sampling site (27°N 86°W), located east of the axis of the Loop Current, is predominantly occupied by residual eastern Gulf water, which can be differentiated from Loop Current water by the depth of the 22°C isotherm (Leipper, 1970; Jones, 1973). The only sampling period in which Loop Current water was known to be present in the area was March 1985. Temperature profiles from the area show a surface mixed layer with a depth

between 30 m and 50 m and warm-month temperatures between 27°C and 30°C. The thermocline extends from the bottom of the mixed layer to approximately 150 m, with temperatures at the lower depth between 15°C and 18°C. Temperatures decrease to about 4°C at 1000 m. The water column is well oxygenated, having a minimum concentration of 2.7 to 2.9 ml/liter between 400 and 500 m (Hopkins, unpubl. data; Nowlin, 1971).

Primary productivity measurements indicate that the sampling area lies in oligotrophic waters, with an annual production of around 100 gC·y⁻¹ (El-Sayed and Turner, 1977). Residual eastern Gulf water, though oligotrophic, appears to be somewhat more productive than Loop Current water (Jones, 1973; Hopkins, 1982). It is estimated that mixing between the two water masses is only 10% (Passarella and Hopkins, 1991), allowing the development of a unique faunal community in eastern Gulf residual water (Michel and Foyo, 1976; Gartner et al., 1987; Passarella and Hopkins, 1991; Flock and Hopkins, 1992; Richards et al., 1993). The zooplankton standing stock of the upper 1000 m in the area has been estimated to be 1.2 gDW·m⁻² (Hopkins, 1982), which is within the range of values found for oligotrophic boundary currents (Vinogradov, 1970). The hydrography of the eastern Gulf of Mexico, then, is characteristic of non-upwelling, seasonally stable, vertically stratified, oligotrophic, subtropical-tropical oceanic waters (McGowan, 1974; Longhurst, 1976). This area should represent a reasonable analog to the low-latitude oceanic gyre systems. Trophic organization and energy transfer are thought to be relatively advanced (i.e., high transfer efficiency between trophic levels) in low-latitude gyre systems due to resource limitations and hydrographic stability (Ryther, 1969; Steele, 1974; Sheldon et al., 1977; McGowan, 1977), allowing the high diversity seen in tropical midwater faunas in general (Gibbs and Roper, 1970; Badcock, 1970) and in particular in the stomiid assemblage of the eastern Gulf.

METHODS

Specimens were sorted from 1,176 trawl samples taken on 24 cruises. These cruises occurred over an 19-year span and covered all four seasons (Table 1), though with most collections (71%) taken during the warm months between May and September. Sampling was centered within a 35 km radius of 27°N 86°W. This site has a depth greater than 3,000 m and is located far enough from the continental shelf that stragglers from "boundary communities" are rarely encountered (Hopkins et al., 1981; Reid et al., 1991; Hulley, 1992).

Sampling prior to August 1987 was conducted with mouth opening-closing Tucker trawls of 1.6 mm or 4.0 mm mesh netting and effective mouth areas of 2.6 m² or 5.3 m², based on a mouth angle of 35° from vertical (SCUBA observations) measured at a towing speed of 2 kn. The trawls were fitted with 0.33-, 0.5-, or 1-mm-mesh cod end plankton nets. Depth was monitored using a depth transducer/conducting cable system, excepting earlier cruises (Mizar I, Bellows I-III) where triangulation was used. A time-depth recorder attached to the trawl frame served as a back-up record on all tows. The trawls were opened and closed either by a messenger-operated double release mechanism (Hopkins et al., 1973) or by paired clock release mechanisms (Davies and Barham, 1969). The volume of water filtered was measured by a dial-type flow meter which recorded only when the trawl was fishing. The filtration efficiency for all volume calculations was assumed to be 100%. Expendable bathythermograph (XBT) and/or CTD casts were made on all cruises to determine the temperature profiles from 0-1,000 m.

Sampling after August 1987 was conducted with a seven-net 4-m² MOCNESS midwater trawl (Wiebe et al., 1976) towed at 2 to 4 kn. Physical data and volume sampled were recorded during sampling with a CTD and TSK flowmeter, respectively. These data were stored via conducting cable/microprocessor system.

Samples were fixed in 10% (v/v) buffered formalin and later transferred to 50% isopropanol or 70% ethanol. Stomiid specimens were identified according to the keys and revisions of Gibbs (1964a, 1964b), Morrow (1964a, 1964b, 1964c), Morrow and Gibbs (1964), Weitzman (1967), Barnett and Gibbs (1968), Goodyear and Gibbs (1969), Gibbs et al. (1983), Gomon and Gibbs (1985) and Fink and Fink (1986). The status of the familial classification of the barbeled stomioids has not reached

Table 1. Sampling data. All tows taken in the vicinity of 27°N 36°W

Cruise	Date	Sampling gear	No. tows
MIZAR I	Jun 1971	Tucker trawl	21
BELLOWS I	Aug 1972	Tucker trawl	25
BELLOWS II	Oct 1973	Tucker trawl	11
BELLOWS III	Aug 1974	Tucker trawl	15
COLUMBUS ISELIN I	Jun 1975	Tucker trawl	29
COLUMBUS ISELIN II	Jun 1976	Tucker trawl	133
BELLOWS IV	Jun 1977	Tucker trawl	52
COLUMBUS ISELIN III	Oct 1977	Tucker trawl	96
BELLOWS VII	Jun 1981	Tucker trawl	3
BELLOWS VIII	Aug 1981	Tucker trawl	66
BELLOWS IX	Jul 1982	Tucker trawl	62
BELLOWS X	Aug 1982	Tucker trawl	30
SUNCOASTER I	Aug 1984	Tucker trawl	52
SUNCOASTER II	Mar 1985	Tucker trawl	66
SUNCOASTER III	Jul 1985	Tucker trawl	59
SUNCOASTER IV	Nov 1985	Tucker trawl	49
SUNCOASTER V	Jan 1986	Tucker trawl	49
SUNCOASTER VI	May 1986	Tucker trawl	48
SUNCOASTER VII	Jan 1987	Tucker trawl	34
SUNCOASTER VIII	Mar 1987	Tucker trawl	30
SUNCOASTER IX	Aug 1987	MOCNESS	55
SUNCOASTER X	Sep 1987	MOCNESS	20
SUNCOASTER XI	Jul 1989	MOCNESS	99
SUNCOASTER XII	Jul 1990	MOCNESS	72
24	1971-1990		1,176

universal agreement; some workers favor the single family (Stomiidae) scheme of Fink (1985) (Gibbs and McKinney, 1988; Nelson, 1994), while others have opted for the six family scheme listed in Weitzman (1974) (Eschmeyer, 1990; Reid et al., 1991). The single family classification scheme (Fink, 1985) is followed here with acceptance of the subfamilies Astronesthinae, Idiacanthinae, Malacosteinae, Melanostomiinae, and Stomiinae (Nelson, 1994).

Specimens were measured to the nearest millimeter standard length (SL). Corrections for shrinkage due to preservation were not attempted because no fresh specimens were available for comparison. Shrinkage has been estimated to be 5% SL of preserved melanostomiines (Beebe and Crane, 1939) and 12% SL of preserved myctophids (Gartner et al., 1987). Biomass was estimated via individual length-dry weight (weight after 24 h at 60°C) regressions for dominant species and pooled length-dry weight regressions for rare species to minimize destruction of specimens. The latter regressions were pooled according to similarity of morphology (e.g., ratio of head depth in length), which resulted in three groupings of species. These groups are defined as: Group 1, elongate melanostomiines; Group 2, short-bodied melanostomiines and malacosteines; and Group 3, short- and thick-bodied astronesthines. Regressions were generated by weighing only those specimens which did not appear to contain prey, as stomiids often take prey equal to their own weight (Sutton, unpubl. data). The appropriate regressions were then used to estimate the biomass of all stomiid specimens, with the resulting estimates being unbiased by prey weights. Stomiid biomass was prorated to volume of water filtered from 0-1,000 m.

Diel vertical distributions were determined using 258 trawl samples from the three R/V COLUMBUS ISELIN cruises, 171 trawl samples from two R/V SUNCOASTER cruises (1989, 1990), and 21 trawl samples from the USNV MIZAR I cruise. These samples covered discrete-depth horizons with 30-m intervals in the upper 200 m, 50-m intervals from 200-600 m, and 100-m intervals from 600-1,000 m. Discrete-depth data for the majority of stomiid species were sparse, with many species being collected in oblique tows only. Therefore, vertical distribution analyses were conducted only on those species with adequate sample size, arbitrarily chosen as >10 individuals from discrete-depth samples.

Preliminary analysis of vertical distribution results revealed that stomiids were captured at a higher rate at night. Therefore, abundance estimates were based on nighttime samples only. Data from 450 nighttime 0-200 m oblique biomass tows were integrated with discrete depth data to maximize sample size with respect to rare species. Abundance values were prorated to volume of water filtered.

Sampler avoidance may be the largest source of error in abundance estimation. Tucker tows operated at 2 kn have been shown to sample smaller fishes more effectively than larger, more mobile

fishes (Clarke, 1969; Badcock and Merrett, 1976, 1977; Kashkin and Parin, 1983). Possible evidence of stomiid avoidance is seen in the study by Clarke (1974) in which few or no sexually mature specimens of many Pacific stomiids were captured by midwater trawling. This is also true of eastern Gulf stomiids (Sutton, unpubl. data). Also, given the relatively small cross-sectional area of most stomiids, losses by escapement through trawl meshes are possible for the smaller size classes (<3 cm, see Gartner et al., 1989). Therefore, the abundance estimates generated should be considered minimal. It is likely that an extensive trawling survey with larger trawls may result in higher estimates of abundance and biomass.

RESULTS

Assemblage Composition.—The stomiid assemblage in the Gulf of Mexico (referred to hereafter as Gulf) is comprised of 83 species referable to 18 genera (Table 2). Seventy-three of these species have been captured in the eastern Gulf and 10 other species have been reported for the Gulf in the literature. Thirty-six species are new records for the gulf, and one of the 73 species from the eastern Gulf (*Eustomias* sp. 1) appears to be an undescribed form (description in progress). The genus *Eustomias* contributed the most species (27) to the Gulf assemblage and includes the only described mesopelagic fish unique to the Gulf, *Eustomias hypopsilus* (Gomon and Gibbs, 1985). The majority of the remaining species are divided among six genera: *Photonectes* (8 species); *Astronesthes* (8 species); *Bathophilus* (7 species); *Melanostomias* (7 species); *Leptostomias* (6 species); and *Aristostomias* (5 species). The remaining 11 genera have three or less species (Table 2), but include the dominant species.

Abundance and Biomass.—The stomiid assemblage in the eastern Gulf was dominated numerically by three species, in order of abundance, *Photostomias guernei*, *Chauliodus sloani*, and *Stomias affinis* (Table 2). These three species comprised 56.1% of the specimens collected during the sampling period. The moderately common stomiids were *Astronesthes macropogon*, *Bathophilus pawneeii*, and *Leptostomias bilobatus*, each comprising approximately 3% of the total specimens. The occasionally sampled stomiids, defined here as those species which comprised at least 1% of the total specimens included, in order of abundance, *Astronesthes similis*, *Astronesthes niger*, *Malacosteus niger*, *Aristostomias xenostoma*, *Astronesthes micropogon*, *Aristostomias polydactylus*, *Echiostoma barbatum*, *Eustomias schmidtii*, and *Idiacanthus fasciola*. The remaining 57 species (78% of the total species number from the eastern Gulf) made up the balance (19%) of the specimens collected.

Abundance and biomass estimates indicated that *Photostomias guernei* (Table 3) was the most commonly collected stomiid of the eastern Gulf while *Stomias affinis* contributed the most biomass due to its larger average length and weight. Numerically, *S. affinis* and *Chauliodus sloani* were approximately equal. The pooled elongate melanostomiine genera (Group 1) were the next most abundant fraction of the assemblage, due mainly to the diversity of these genera and not abundance per species. The pooled short-bodied melanostomiine and malacosteine genera (Group 2) contributed little to the abundance or biomass of the assemblage due to their rarity and small average size. The pooled astronesthine genera (Group 3), while least abundant numerically, were significant contributors to the total assemblage biomass. Abundance and biomass minimum estimates for the total stomiid assemblage were 1.86×10^5 fish and 35.3 kg DW·km⁻² of ocean surface between 0–1,000 m.

Vertical Distribution.—The three dominant stomiids of the eastern Gulf displayed an asynchronous vertical migration pattern (Fig. 1). This pattern is characterized by residence deep within the mesopelagic zone during daylight and divided res-

Table 2. Dragonfishes of the Gulf of Mexico. Species listed in bold type not captured during eastern Gulf sampling, but listed for gulf in literature (source). N = total no. specimens captured in eastern Gulf, C = circumglobal, A = Atlantic, G = Gulf of Mexico.

Species	N	Range	Species	N	Range
<i>Aristostomias grimaldii</i>	10	C	<i>Eustomias parvibulbus*</i>	1	A
<i>Aristostomias lunifer*</i>	6	C	<i>Eustomias polyaster</i> (5)		A
<i>Aristostomias polydactylus</i>	21	C	<i>Eustomias schmidti*</i>	16	C
<i>Aristostomias titmanni</i>	11	A	<i>Eustomias variabilis</i>	1	A
<i>Aristostomias xenostoma</i>	24	C	<i>Eustomias xenobolus</i>	1	A
<i>Aristostomias</i> sp.‡	2	—	<i>Eustomias</i> sp. 1*†	1	G
			<i>Eustomias</i> sp.‡	22	—
<i>Astronesthes cyclophotus</i>	3	A			
<i>Astronesthes gemmifer</i> (1)		A	<i>Flagellostomias boureei</i>	1	C
<i>Astronesthes indicus</i>	10	C			
<i>Astronesthes macropogon</i>	42	A	<i>Grammatostomias circularis</i>	1	A
<i>Astronesthes micropogon</i>	21	A	<i>Grammatostomias</i> sp.‡	3	—
<i>Astronesthes niger</i>	36	A			
<i>Astronesthes richardsoni</i>	9	A	<i>Heterophotus ophistoma</i>	2	C
<i>Astronesthes similis</i>	43	A			
			<i>Idiacanthus fasciola</i>	18	C
<i>Bathophilus altipinnis*</i>	1	A			
<i>Bathophilus digitatus*</i>	8	C	<i>Leptostomias analis*</i>	1	A
<i>Bathophilus longipinnis</i>	6	C	<i>Leptostomias bermudensis*</i>	6	A
<i>Bathophilus nigerrimus</i>	3	C	<i>Leptostomias bilobatus</i>	48	A
<i>Bathophilus pawneeii</i>	46	C	<i>Leptostomias gladiator</i>	7	C
<i>Bathophilus proximus*</i>	4	A	<i>Leptostomias haplocaulus*</i>	1	C
<i>Bathophilus schizochirus*</i>	3	C	<i>Leptostomias leptobolus*</i>	4	C
<i>Bathophilus</i> sp.‡	6	—	<i>Leptostomias</i> sp.‡	13	—
<i>Borostomias elucens</i>	2	C	<i>Malacosteus niger</i>	26	C
<i>Borostomias mononema</i>	4	C			
			<i>Melanostomias biseriatus*</i>	2	C
<i>Chauliodus danae</i>	2	C	<i>Melanostomias macrophotus</i> (7)		C
<i>Chauliodus sloani</i>	271	C	<i>Melanostomias margaritifera*</i>	1	A
			<i>Melanostomias melanopogon*</i>	1	A
<i>Echistoma barbatum</i>	20	C	<i>Melanostomias melanops</i>	1	A
			<i>Melanostomias tentaculatus*</i>	8	C
<i>Eustomias acinosus*</i>	7	A	<i>Melanostomias valdiviae</i>	3	C
<i>Eustomias arborifer</i> (2)		A	<i>Melanostomias</i> sp.‡	4	—
<i>Eustomias bibulbosus*</i>	1	A			
<i>Eustomias bigelowi*</i>	4	C	<i>Pachystomias microdon*</i>	8	C
<i>Eustomias binghami*</i>	1	A			
<i>Eustomias braueri</i> (7)		A	<i>Photonectes achirus*</i>	1	A
<i>Eustomias brevibarbatu</i>	12	A	<i>Photonectes braueri</i> (6)		A
<i>Eustomias</i> cf. <i>chabanaudi*</i>	1	A	<i>Photonectes dinema</i> (7)		A
<i>Eustomias dendriticus*</i>	6	A	<i>Photonectes leucospilus*</i>	2	A
<i>Eustomias enbarbatus*</i>	1	C	<i>Photonectes margarita</i>	6	C
<i>Eustomias filifer*</i>	5	A	<i>Photonectes mirabilis*</i>	1	A
<i>Eustomias fissibarbis</i>	11	C	<i>Photonectes parvimanus*</i>	1	A
<i>Eustomias hypopsilus</i>	5	G	<i>Photonectes phylloporogon*</i>	2	A
<i>Eustomias kreffti*</i>	1	A	<i>Photonectes</i> sp.‡	1	—
<i>Eustomias leptobolus</i> (3)		A			
<i>Eustomias lipochirus*</i>	2	A	<i>Photostomias quernei</i>	339	C
<i>Eustomias longibarba</i> (4)		A			
<i>Eustomias macrophthalmus</i> (5)		A	<i>Stomias affinis</i>	168	C
<i>Eustomias macrurus*</i>	2	C	<i>Stomias brevibarbatu</i>	1	A
<i>Eustomias melanostigma*</i>	1	A	<i>Stomias longibarbatu</i>	1	C
<i>Eustomias micraster</i>	2	A			

* New record for Gulf of Mexico, † Undescribed species, ‡ Damaged specimens. Sources: (1) Gibbs, 1964; (2) Gibbs et al., 1983; (3) Morrow and Gibbs, 1964; (4) Gibbs et al., 1983; (5) Gomon and Gibbs, 1985; (6) Murdy et al., 1983; (7) Backus and Craddock, unpub.)

Table 3. Stomiid abundance and biomass estimates for the upper 1,000 m in the eastern Gulf of Mexico (Length/dry weight regressions in parentheses)

Species	No./10,000 m ⁻³	gDW/10,000 m ⁻³ (regression)	
<i>Photostomias guernei</i>	0.74	0.067	(DW = 3.889E ⁻⁷ (SL) ^{2.94})
<i>Stomias affinis</i>	0.40	0.130	(DW = 2.019E ⁻⁷ (SL) ^{3.07})
<i>Chauliodus sloani</i>	0.39	0.130	(DW = 2.38E ⁻⁶ (SL) ^{2.54})
Group 1:	0.14	0.016	(DW = 5.0E ⁻⁷ (SL) ^{2.74})
<i>Leptostomias</i> spp.			
<i>Eustomias</i> spp.			
<i>Idiacanthus fasciola</i>			
<i>Melanostomias</i> spp.			
<i>Echistoma barbatum</i>			
<i>Flagellostomias boureei</i>			
Group 2:	0.10	0.009	(DW = 4.24E ⁻⁷ (SL) ^{3.03})
<i>Bathophilus</i> spp.			
<i>Photonectes</i> spp.			
<i>Aristostomias</i> spp.			
<i>Pachystomias microdon</i>			
<i>Grammatostomias</i> spp.			
<i>Malacosteus niger</i>			
Group 3:	0.09	0.032	(DW = 1.04E ⁻⁶ (SL) ^{3.04})
<i>Astronesthes</i> spp.			
<i>Heterophotus ophistoma</i>			
<i>Borostomias</i> spp.			
Total stomiids	1.86	0.353	

idence at night, with some individuals migrating upwards and some individuals remaining at daytime depths. *Photostomias guernei* had a daytime depth distribution between 650–850 m, while at night approximately 50% of the population migrated above 200 m. *Stomias affinis* exhibited the same general distribution as *P. guernei*, with the exceptions of having a greater fraction of the population above 650 m during daylight and a slightly higher percentage of the population (60%) undergoing vertical migration on a diel basis. *Chauliodus sloani* differed

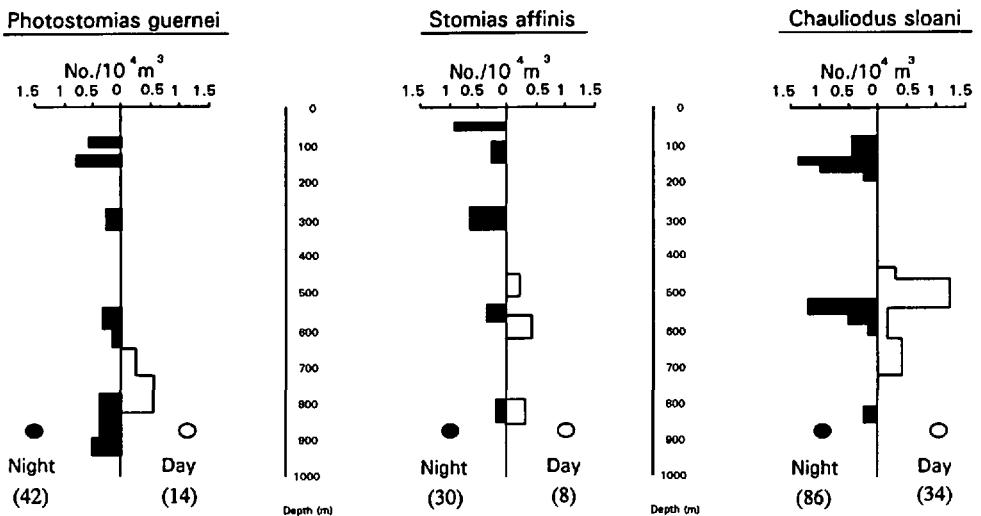


Figure 1. Diel vertical distribution of the three dominant stomiids of the eastern Gulf of Mexico. Sample size in parentheses.

from the preceding two species in having a shallower daytime distribution (450–700 m), with approximately 70% of the individuals vertically migrating over the diel cycle. Analysis of the size-depth distribution of these three species revealed no significant differences in the lengths of individuals above and below 200 m at night. This suggests that the divided nighttime depth distribution observed was ethological in nature and not the result of ontogenetic descent, as has been reported for several mesopelagic fishes (Badcock, 1970; Clarke, 1973; Gartner et al., 1987).

Four additional stomiid species also appear to migrate with non-diel periodicity (Fig. 2). *Aristostomias polydactylus* has nighttime centers of abundance between 0–300 m and 700–800 m, and a daytime center of abundance between 300–700 m. *Bathophilus pawneeii*, *Eustomias schmidti* and *Astronesthes similis* exhibited overlapping vertical distributions, with nighttime centers of abundance between 0–200 m and 500–700 m, and a daytime center of abundance between 500–700 m.

Four stomiid species displayed a synchronous diel vertical migration pattern (Fig. 2). *Aristostomias xenostoma*, *Astronesthes micropogon*, *Astronesthes macropogon*, and *Astronesthes similis* shared a common nighttime center of abundance between 0–200 m. Daytime centers of abundance for these species ranged from 400–700 m, but interspecific variation in depth ranges could not be discerned due to small sample size.

Discrete-depth data of two stomiid species suggested the possibility of a bathy- to epipelagic vertical migration (Fig. 3). *Echiosstoma barbatum* and *Leptostomias bilobatus* were both sampled between 0–300 m at night, but were not sampled within the upper 1,000 m during the day. While positive discrete-depth captures definitively prove the occurrence of a species in a particular depth stratum, the absence of captures does not prove exclusion, especially in rare species such as these. Although these species apparently do not possess any morphological characteristics (e.g., larger size) that would endow a greater avoidance ability than those species captured within the mesopelagial, increased daytime sampler avoidance (Clarke, 1974) cannot be ruled out as causative factor in the observed distribution. Unfortunately, there are no reports of the daytime vertical distribution of either species for comparison. Krueger and Gibbs (1966) reported *E. barbatum* captures shallower than 1,000 m in the northern Gulf, but the time of capture was not indicated.

While sample sizes from discrete-depth tows of the remaining species were too small for accurate determination of vertical distribution, the available data are presented here due to the paucity of information in the literature regarding the vertical distribution of these species. Four *Malacosteus niger* specimens were taken during the day between 600–700 m and two specimens were taken at night between 500–700 m, suggesting non-migration. Five rare species appeared to be vertical migrators: two specimens each of *Grammatostomias* cf. *circularis* and *Photoneustes margarita* were caught between 100–130 m at night; two female *Idiacanthus fasciola* were caught above 200 m at night; four *Pachystomias microdon* specimens were caught above 250 m at night; and one *Heterophotus ophistoma* was taken between 125–150 m. *Flagellostomias boureei* and *Borostomias* spp. were only taken in 0–900 m oblique trawls during daylight. Consequently, little can be inferred regarding their vertical distribution.

DISCUSSION

With the addition of the 36 new records from this study, the Stomiidae represent the most species diverse oceanic or neritic fish family known to date in the Gulf

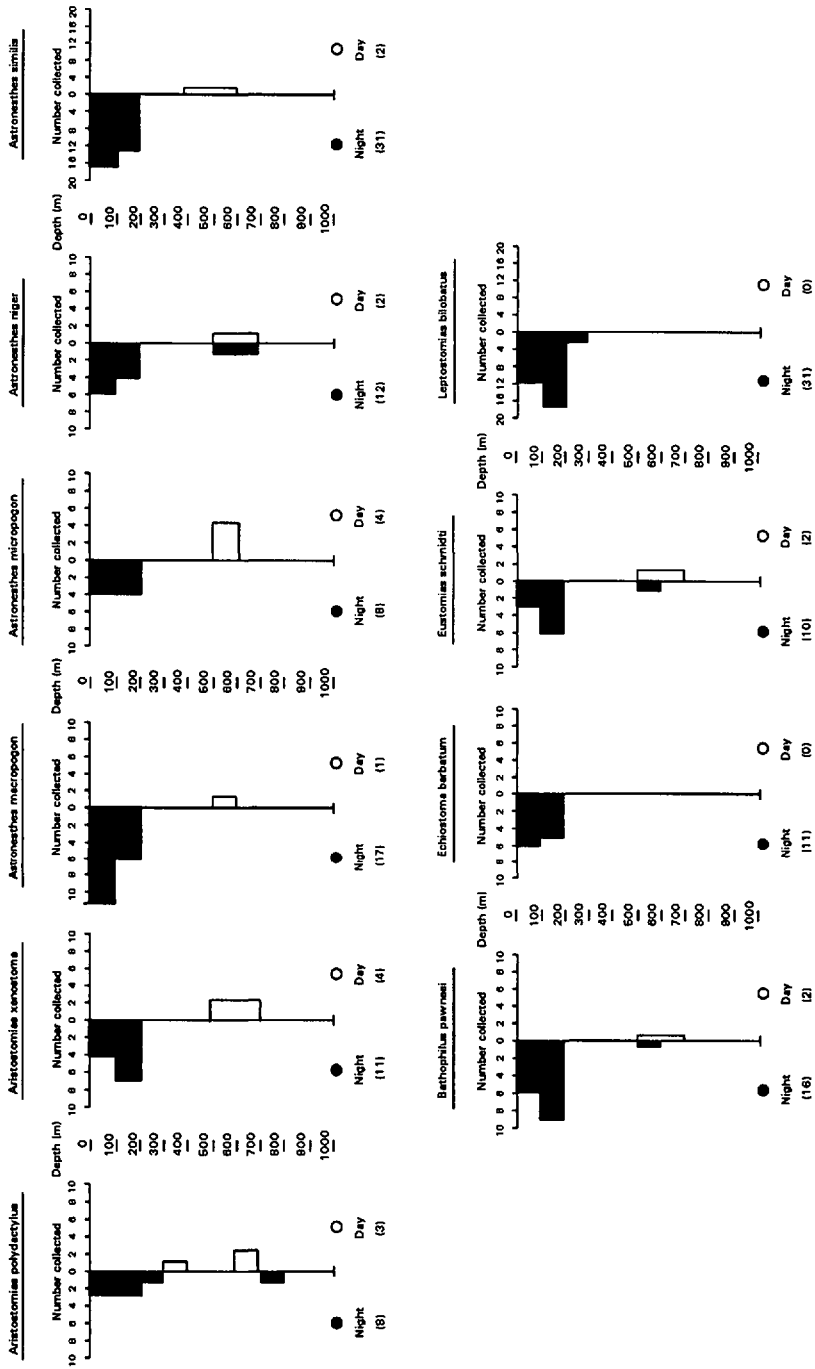


Figure 2. Diel vertical distribution of common stomiids with adequate sample size (>10, in parentheses).

of Mexico (Gartner et al., 1987; Robins et al., 1991). In deference to the alternate stomiid classification scheme (six families—see Methods), these new records would make the Melanostomiidae the most species diverse fish family known to date in the Gulf (59 species). Further, the Gulf stomiid assemblage is the most diversified known to date from a single biogeographic province, outnumbering the stomiid number reported by Parin et al., (1977) for the western tropical Pacific. The higher level of diversity in the Gulf is likely the result of tropical/subtropical location and sampling intensity. Higher faunal diversity is characteristic of low-latitude ecosystems and has been hypothesized to be a result of the age and stability of these ecosystems (Fischer, 1960; Marshall, 1963). With respect to sampling intensity it appears that the relationship between stomiid species richness and sample size is asymptotic; a moderate sample size (100's of trawls) will identify the core group of species, but an immense sample size (>1000 trawls) is necessary to identify the rare species.

The Gulf of Mexico zoogeographic province is characterized as similar to the Atlantic Tropical Region, but with significant winter cooling (Backus et al., 1977). Significant differences are seen in the stomiid assemblages reported for the eastern Gulf and western tropical Atlantic (Beebe and Crane, 1939; Gibbs et al., 1983), both in species number and relative abundance. One possible explanation is that eastern Gulf residual mesopelagic water is cooler (5.5–9.5°C, Hopkins and Lancraft, 1984) than tropical Atlantic mesopelagic water (11.5–17°C, Donaldson, 1975), which may affect reproduction and recruitment. Faunal differences have also been reported for the eastern Gulf and tropical Atlantic myctophid assemblages (Gartner et al., 1987; Karnella, 1987), while Hopkins et al. (1989) and Flock and Hopkins (1992) found the caridean and sergestid assemblages of the two regions to be similar, possibly suggesting differences in the evolutionary ecologies of mesopelagic shrimps and fishes.

Beebe and Crane (1939) reported a single specimen for 12 of the 32 melanostomiine species collected off Bermuda. Twenty-three of the 73 species collected in this study are also represented by a single specimen. Possible explanations for this phenomenon are: (1) small sample size resulting from a biased sampling strategy; (2) species are actually subspecific morphs that are not temporally stable; (3) rare species are expatriates from other regions; and (4) the species normally occur in low numbers ("rare" strategy). The midwater trawl collections sorted for this study represents one of the largest in existence for a single location, and while it is possible that continued sampling and/or larger trawl gear would reduce the number of species with single specimens, we believe that this strategy would not significantly affect the relative abundance of these species.

Assuming that similar-sized melanostomiine fishes have similar avoidance capabilities, the most likely explanations for the extremely low abundances in the Gulf of many of these species are expatriation and a "rare" species strategy. The presence of "rare" stomiid species in the Gulf is possibly due to horizontal advection from the Caribbean Sea via the Loop Current. If conditions in the eastern Gulf (e.g., winter cooling) lie outside the reproductively acceptable parameters for these species, then their population densities may remain too low for establishment. This does not imply that these species are necessarily abundant in nearby provinces. Many oceanic species are never sampled in abundance anywhere within their range (e.g., *Heterophotus ophistoma* [Clarke, 1982]). A "rare" strategy of existence is likely a key factor in the maintenance of high diversity in resource-limited environments such as low-latitude ecosystems.

Possible underestimation of abundance notwithstanding, stomiid biomass in the eastern Gulf is approximately 10% (9.7) of the combined dominant midwater

biomass components (myctophids, gonostomatids, sternoptychids, decapod shrimps, and large euphausiids; Hopkins and Lancraft, 1984). These estimates indicate that stomiids are the dominant mesopelagic upper-trophic level predatory fishes of the Gulf, outnumbering the second-most abundant predator group, the pelagic Aulopiformes (Eschmeyer, 1990), by at least a factor of 10 (Sutton, unpubl. data). Using the oligotrophic eastern Gulf as an analog to the central water masses of the world ocean, the stomiids are likely the dominant group of midwater predatory fishes feeding on large prey.

The asynchronous migratory pattern seen in the three most abundant eastern Gulf stomiids has been reported for these species elsewhere (Gibbs, 1969; Clarke, 1974; Badcock and Merrett, 1976; Bailey and Robison, 1986). Since these species apparently do not respond synchronously to diel variations in light intensity, then the next most likely cause of this variable migration pattern would ostensibly be related to feeding. If vertical migration of stomiids is driven by feeding, then perhaps only that part of the population that is hungry undergoes this migration.

Clarke (1974), with a larger sample size, reported *Malacosteus niger* to be the only non-migrating stomioid in Hawaiian waters. Discrete depth sample size for this species was inadequate to describe its vertical distribution in the eastern Gulf, but those data that are available do not contradict a non-migratory pattern. Given the available knowledge of stomiid vertical distributions, non-migration by this species may represent a marked divergence in stomiid evolution.

In summation, the stomiid assemblage of the Gulf of Mexico is extremely species rich and constitutes a significant portion of the total biomass of the mesopelagic fauna. This assemblage regularly undertakes migrations from the lower mesopelagial to the epipelagial, presumably to feed. Therefore, it would be expected that this assemblage plays an important role in the oceanic food web of the Gulf of Mexico, and, in turn, the world's warm-water mesopelagial.

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