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Deep-Sea Research I 52 (2005) 2065–2076

DEEP-SEA RESEARCH
PART I

www.elsevier.com/locate/dsr

Trophic ecology of the deep-sea fish *Malacosteus niger* (Pisces: Stomiidae): An enigmatic feeding ecology to facilitate a unique visual system?

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Received 24 November 2004; accepted 24 June 2005

Available online 18 August 2005

Abstract

The deep-sea fish *Malacosteus niger* belongs to a family of fishes, the dragonfishes (Order: Stomiiformes, Family: Stomiidae), that are among the top predators of the open ocean mesopelagic zone. *Malacosteus* typifies the morphological adaptation of this group for the taking of relatively large prey. These adaptations include huge fangs, an enormous gape, and the loss of gill rakers. Despite these adaptations, examination of specimens of this species from different ocean basins shows that zooplanktivory is a common feeding mode of the species, an extreme departure from its trophic lineage. Large calanoid copepods made up 69–83% of prey numbers and 9–47% of prey biomass in specimens from the North Atlantic, the Gulf of Mexico, and throughout the Pacific. As *M. niger* feeding observations have never been reported, the rationale for this enigmatic feeding ecology must be inferred from other aspects of its ecology. As presently known, *M. niger* is unique among all vertebrates in the possession of both a long-wave bioluminescence system and a bacteriochlorophyll-derived retinal photosensitizer that allows long-wave visual sensitivity. A two-part theory is presented to explain why *M. niger* radically diverges from its clade and preys on food it does not appear morphologically suited to eat: (1) the combination of long-wave bioluminescence and vision systems suggests that *M. niger* may search small volumes for food, and thus may sustain itself energetically by snacking on small parcels of food (copepods) in between rare encounters with large prey, and (2) *M. niger* may gain the raw material for its long-wave visual sensitivity, and thus its feeding mode, from the consumption of copepods.

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Keywords: Stomiidae; Prey selection; Plankton feeder; Bioluminescence; Photoreception; Visual pigments

1. Introduction

With respect to fish feeding ecology, the relative prey size preference of a species can, in most cases, be predicted from a study of its feeding morphology

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Table 1

Average diet and feeding morphology characteristics for 16 families (223 species) of mesopelagic fishes from the eastern Gulf of Mexico (ranges represent extrema within family)

Predator family	% Fish prey	Longest tooth length as % dentary length	No. teeth on right dentary	Gill raker length as % gill arch length ^a
Ceratiidae ^b	0	4.0–7.0	12	0
Melamphaidae	0.1	0.9	41–65	19.9
Bathylagidae	0.2	1.9	33	11.6
Myctophidae	0.1	0.6–1.8	154	17.5
Gonostomatidae	0.9	3.2–7.0	31–96	16.7
Bregmacerotidae	1.7	4.4	11	0
Phosichthyidae	0.9	4.5–9.8	24	14.3
Sternoptychidae	1.3	2.6–5.3	17–28	20.2
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Gempylidae	18.3	19.6	15	1.7
Omosudidae	22.2	36.5	10	0
Evermannellidae	47.7	37.5	13	0
Melanocetidae	50.0	31.0	17	0
Stomiidae	60.3	24.2–47.5	10–28	0
Scopelarchidae	72.2	23.7	23	0
Paralepididae ^b	70.8	4.4–17.1	6–21	0
Chiasmodontidae	92.3	8.0–33.0	14	0

The dashed line separates small item (above) and large item (below) predators. Specimens examined were near median size for each species, except where noted. Percent fish prey from Hopkins et al. (1996).

^aLongest gill raker on first right-side gill arch.

^bJuvenile specimens.

(e.g. mouth placement and relative size, dentition, branchial basket characteristics). Planktivores and other small-item predators generally have numerous but minute jaw teeth (or are edentate) and well-developed, closely spaced gill rakers. The intermeshing elements of the gill rakers are thought to determine the minimum prey size on which a fish can effectively feed (Nilsson, 1958; Ebeling and Cailliet, 1974; O'Brien, 1987, but see Drenner et al., 1987; Langeland and Nøst, 1995). Conversely, fishes that take relatively large prey usually have fewer but larger jaw teeth, recurved pharyngeal teeth to aid in swallowing large prey, reduced or no gill rakers, a non-restrictive pectoral girdle, and larger absolute mouth sizes. The latter determines the maximum prey size that can be swallowed whole. These stereotypical patterns are particularly evident among mesopelagic fishes, where prey type variability of a given fish species is minimal across major prey categories (Sutton et al., 1998). This can be demonstrated by ecomorphological data encompassing 223 species of mesopelagic fishes from the Gulf

of Mexico (Table 1, Hopkins and Sutton, unpublished data). Using an increase in percent fish prey biomass (from Hopkins et al., 1996) as a proxy for large prey size preference, the patterns demonstrated by predators on large prey (e.g., fewer, larger teeth and less conspicuous gill rakers) are unmistakable.

There are notable exceptions to this feeding morphology/prey preference paradigm. One of these, exhibited by the mesopelagic fish *Malacosteus niger*, is the subject of this paper. The fish family to which this species belongs, the Stomiidae (sensu Fink, 1985), is known to feed on relatively large prey, at times taking items greater in weight than themselves (Sutton and Hopkins, 1996a). The feeding morphology of stomiids reflects this, and no species appears more suited to this feeding mode than *M. niger*. It has one of the largest relative gapes (Fig. 1A and D) of any fish, with the lower jaw being approximately one-quarter of the fish's standard length (SL). It has enlarged fangs (Fig. 1B), as well as large, recurved gullet (basibranchial and pharyngobranchial) teeth

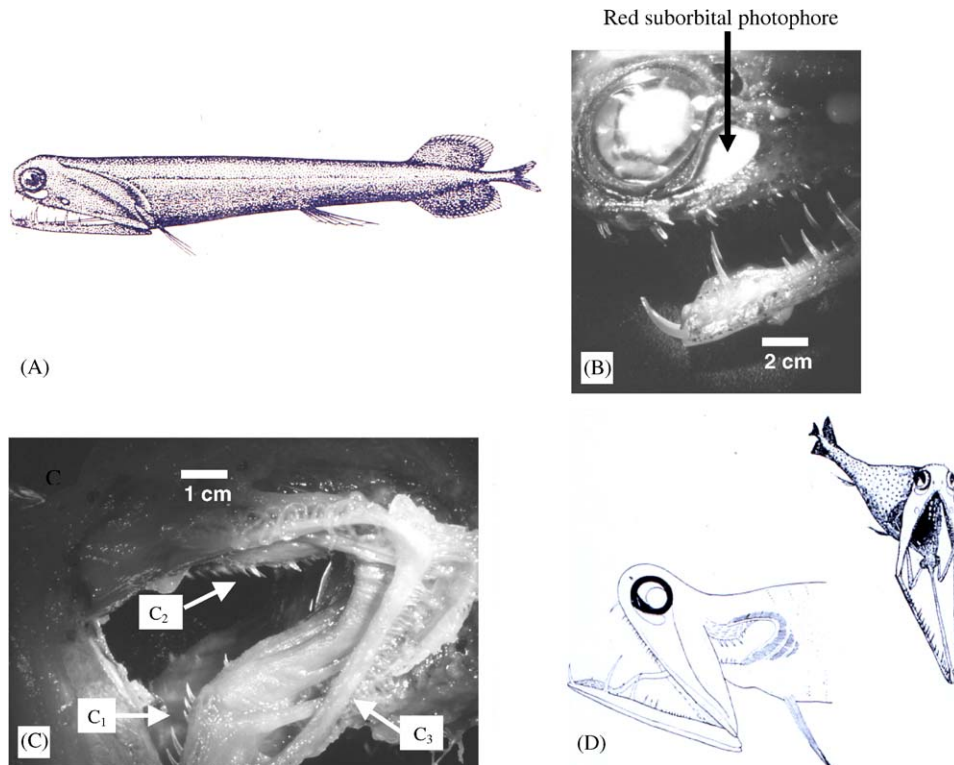


Fig. 1. Morphological characteristics of *M. niger*: (A) whole specimen, approximately 150 mm SL; (B) jaw dentition; (C) branchial basket and hyoid, orientation of fish as in A [C₁, basibranchial teeth; C₂, pharyngobranchial teeth; C₃, gill arch]; (D) diagrammatic representation of gape demonstrating lack of ethmoid membrane [floor of mouth]. A, drawn by Shirley G. Hartman; D, after Marshall, 1954 [left], and Günther and Deckert, 1959 [right].

(Fig. 1C). It has no gill rakers, gill teeth, or any other element on the buccal surface of the gill arches (Fig. 1C). The anterior vertebrae are unossified, ostensibly to allow the fish to ‘throw back its head’ to take large prey (Regan and Trewavas, 1930). And lastly, *M. niger*, along with the closely related genera *Aristostomias* and *Photostomias*, lacks an ethmoid membrane; i.e., there is no ‘floor’ in its mouth (Fig. 1D). Thus, retention of small particles by *M. niger* would seem problematic.

Given these characteristics, it would be expected that *M. niger* would feed primarily on large items. However, the scant data available suggest that small prey items, namely copepods, are a diet component of this species (Clarke, 1982; Sutton and Hopkins, 1996a). Unfortunately, small sample sizes in these studies precluded an adequate

description of the trophic ecology of *M. niger*. In the present study additional specimens were analyzed to address this seemingly enigmatic feeding mode. The goals were to determine if zooplanktivory was the exception or the rule, to quantify the dietary contribution of zooplankton prey, and to apply available ecological and physiological information about *M. niger* to propose an explanation for this potential departure from the classic form/function paradigm.

2. Methods

Specimens from various museum collections provided the basis for this study. These collections included: the Museum of Comparative Zoology, Harvard University (MCZ); the Scripps

Institution of Oceanography Marine Vertebrates Collection (SIO); the Peabody Museum, Yale University (YPM); and the Natural History Museum and Institute, Chiba, Japan (CBM). This assortment minimized the possibility of regional bias in this study, as the collection locations for the specimen pool spanned the known biogeographical range of *M. niger* (Sutton, 2003). The material examined (Table 2) included specimens from western North Atlantic Slope Water (MCZ), the Northern Sargasso Sea (MCZ), the eastern tropical Pacific (SIO), the central equatorial Pacific (SIO, CBM), the North and South Central Pacific Gyres (SIO), the western Pacific (YPM), and the Coral Sea (SIO). Data from the eastern Gulf of Mexico were reported elsewhere (Sutton and Hopkins, 1996a), and have been incorporated here for comparison. Sampling was conducted with a variety of open or opening/closing mid-water trawls (Table 2). Most samples were oblique (0–1000 m), but some specimens were taken during discrete-depth sampling (strata between 500 and 1250 m). Times of capture were not included in the archived data sets, so vertical migration patterns could not be addressed directly (see Discussion).

Diet analysis methods followed those of Sutton and Hopkins (1996a). Briefly, the entire digestive tract was removed and dissected. Diet items in the mouth or esophagus were not counted to avoid possible bias due to post-capture ingestion ('net

feeding'). Diet items removed from the stomach and intestines were identified to the lowest taxonomic level possible. For prey biomass determination, individual diet items were measured to the nearest 0.1 mm (total length for fish, metasomal length for copepods, carapace length for shrimp). Prey measurements were converted to estimates of dry organic weight of undigested prey (DW) using procedures described in Hopkins et al. (1996) and Sutton and Hopkins (1996a). This methodology compensated for variance in prey biomass estimation due to state of digestion and/or water content. Dry weights of prey items identifiable only to major prey type were determined using hard part length/DW regressions (e.g. eye lens diameter) appropriate for the taxon.

3. Results

Gut content analysis results revealed that *M. niger* was zooplanktivorous throughout its range, with large calanoid copepods as its most numerous prey (Tables 3–5, Fig. 2). Copepods made up 69–83% of prey numbers and 9–47% of prey biomass of specimens from different ocean basins. Of the 62 *M. niger* specimens containing prey, 43 (69%) contained copepods and 19 (31%) contained only copepods. The mean copepod prey number per fish was 1.2, with a maximum of 5 in

Table 2
Sample data

Oceanic region	Approximate location	Years sampled	Sampling gear	<i>N</i>
Eastern Gulf of Mexico	27°N86°W	1971–1990	RMT, MOCNESS	30
N. Atlantic Slope Water	37–41°N63–74°W	1974–1982	RMT, MOCNESS	16
Northern Sargasso Sea	32–35°N60–76°W	1972–1979	RMT, MOCNESS	19
Eastern tropical Pacific	12°S70°W	1965	IKMT	1
Central equatorial Pacific	3–7°N113–155°W	1960–1990	RMT, IKMT	12
N. Pacific Central Gyre	20–28°N154–156°W	1960–1974	RMT, IKMT	5
S. Pacific Central Gyre	25°S155°W	1972	IKMT	1
Coral Sea	14°S151°W	1975	IKMT	2
Western Pacific	15–17°N123–124°W	1995	30-m OT	5
			Total	91

RMT, rectangular midwater trawl; MOCNESS, multiple opening-closing net and environmental sampling system (Wiebe et al., 1976); IKMT, Isaacs-Kidd midwater trawl (see Friedl, 1971); OT, otter trawl.

Table 3

Prey composition of *M. niger* from the eastern Gulf of Mexico ($n = 30$; positive guts = 21)

Prey item	% O	% B
Copepoda	83.3	46.9
Aetideidae	36.1	17.7
<i>Chirundina streetsi</i>	13.8	6.5
<i>Gaetanus kruppil</i>	2.8	1.3
<i>Gaetanus tenuispinus</i>	2.8	1.3
<i>Euchirella maxima</i>	2.8	2.8
<i>Euchirella venusta</i>	2.8	1.9
aetideid copepod	11.1	3.9
Euchaetidae	5.6	7.2
<i>Paraeuchaeta gracilis</i>	2.8	3.6
<i>Paraeuchaeta hanseni</i>	2.8	3.6
Others	11.2	7.0
<i>Pleuromamma xiphias</i>	2.8	1.9
<i>Amalothrix emarginata</i>	2.8	0.7
<i>Scaphocalanus magnus</i>	2.8	0.8
<i>Heterostylites</i> spp.	2.8	3.6
Calanoid copepod	30.4	15.0
Pisces	8.3	> 11.6 ^a
Myctophidae	2.8	11.6
Fish (unidentified)	5.5	ND
Decapoda	5.6	36.7
<i>Gemadas</i> spp.	2.8	15.1
Penaidea (unidentified)	2.8	21.6
Euphausiacea	2.8	4.8
<i>Euphausia gibboides</i>	2.8	4.8

% O, percent occurrence; % B, percent biomass (DW); ND (not determined), biomass determination not possible due to advanced state of digestion. Table ordered by % occurrence of higher taxa.

^aAdvanced state of digestion resulted in underestimation of prey biomass.

two specimens. Notably prominent among the copepod prey were the families Aetideidae and Euchaetidae, which together accounted for 79%, 83%, and 90% of all copepod prey identifiable to family from the Gulf of Mexico, western North Atlantic, and Pacific, respectively. The copepods taken by *M. niger* were large, averaging around 4.5 mm metasomal length. No predator size/copepod prey abundance relationship was apparent for *M. niger*, as the larger specimens contained the same proportions of copepod prey as did the smaller. Other than a single chaetognath in the intestine of one specimen, small euphausiids were the only other zooplanktonic prey found in the

Table 4

Prey composition of *M. niger* from the western North Atlantic ($n = 35$; positive guts = 23); % O, percent occurrence; % B, percent biomass (DW)

Prey item	% O	% B
Copepoda	70.2	9.3
Euchaetidae	42.5	6.3
<i>Paraeuchaeta norvegica</i>	29.6	5.3
<i>Paraeuchaeta barbata</i>	2.3	0.4
Euchaetid copepod	10.6	0.6
Aetideidae	10.6	1.2
<i>Gaetanus kruppil</i>	2.9	0.3
<i>Gaetanus</i> spp.	1.3	0.2
<i>Chirundina streetsi</i>	2.1	0.3
<i>Euchirella</i> spp.	2.1	0.2
Aetideid copepod	2.2	0.2
Others	10.5	1.5
<i>Calanus</i> spp.	4.2	0.3
<i>Eucalanus</i> spp.	4.2	1.1
<i>Scaphocalanus magnus</i>	2.1	0.1
Calanoid copepod	6.6	0.3
Decapoda	8.5	60.1
Sergestidae	2.1	15.0
decapod (unidentified)	6.4	45.1
Euphausiacea	8.5	0.3
Pisces	6.4	0.8 ^a
Mysidacea	4.2	29.7
<i>Eucopia</i> spp.	4.2	29.7
Chaetognatha	4.2	0.1

^aAdvanced state of digestion resulted in underestimation of prey biomass.

diet of *M. niger*, accounting for 3–9% of prey numbers and 0.3–5% of prey biomass.

Larger micronekton accounted for a substantial, even dominant, proportion of prey biomass, despite the numerical dominance of copepod prey. In total, larger micronekton accounted for 48%, 67% and 90% of prey biomass from the Gulf of Mexico, Pacific, and western North Atlantic, respectively. These numbers likely underestimated the prey biomass contribution of larger prey, as the advanced state of digestion of fish prey occasionally prevented accurate biomass determination. In specimens from the Gulf of Mexico and the Pacific, decapod shrimps, primarily Sergestidae and Aristeidae, contributed about one-third of prey biomass, while in the western North Atlantic, decapods contributed 60% and larger mysids contributed ~30%. Fish made up the remainder

Table 5
Prey composition of *M. niger* from the Pacific ($n = 26$; positive guts = 18)

Prey item	% O	% B
Copepoda	68.6	31.1
Euchaetidae	17.1	11.4
<i>Euchaeta/Paraeuchaeta</i> spp.	17.1	11.4
Aetideidae	8.6	2.1
<i>Euchirella</i> spp.	2.9	1.0
aetideid copepod	5.7	1.1
Others	2.9	0.5
<i>Scottocalanus</i> spp.	2.9	0.5
Calanoid copepod	40.0	17.1
Pisces	11.4	> 34.7 ^a
<i>Howella sherborni</i>	2.3	8.9
<i>Cyclothone</i> spp.	2.3	3.6
Myctophidae	4.5	22.2
Fish (unidentified)	2.3	ND
Decapoda	11.4	32.1
Sergestidae	6.8	32.1
Decapod (unidentified)	4.6	ND
Euphausiacea	8.6	2.1
<i>Euphausia</i> spp.	4.3	1.1
<i>Stylocheiron</i> spp.	2.6	0.6
Euphausiid (unidentified)	1.7	0.4

% O, percent occurrence; % B, percent biomass (DW); ND (not determined), biomass determination not possible due to advanced state of digestion.

^aAdvanced state of digestion resulted in underestimation of prey biomass.

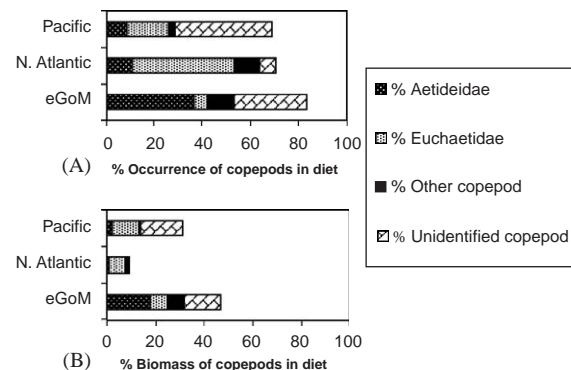


Fig. 2. Percent composition of copepods in the diet of *M. niger*: (A) percent occurrence; and (B) percent biomass. eGoM = eastern Gulf of Mexico.

of the micronekton prey biomass, with Myctophidae, Gonostomatidae (*Cyclothone*) and Perichthyidae (*Howella*) identified as prey.

4. Discussion

The numerical dominance of calanoid copepods in the guts of *M. niger* specimens suggests that while large items provide a substantial fraction of prey biomass, zooplanktivory is a common feeding mode of this species despite its apparent morphological adaptations for the consumption of relatively large prey. Integrating results from this study, copepods have been found as prey in 60 of the 191 *M. niger* specimens (31%) reported from diet analysis (Clarke, 1982; Sutton and Hopkins, 1996a).

4.1. Elements of bias

The counter-intuitive nature of this result warrants an investigation of the potential elements of bias. The foremost element of bias in deep-sea fish trophic studies is small sample size (see Gartner et al., 1997), due in most cases to the paucity of specimens and to the frequent low proportion of specimens containing prey. Ninety-one specimens were examined in this study. While analysis of additional specimens would allow for a more robust quantitative estimation, it is unlikely that this would change the overall conclusion that copepods are an integral component of the diet of *M. niger*. The similarity between data from specimens collected from different ocean basins suggests that copepod prey abundances were not anomalously high in any one region. If we accept that the finding of copepods in the guts of this species is not an anomaly, then we can further investigate other potential sources of bias.

Postcapture ingestion of prey items, or “net feeding,” is also a consideration in deep-sea fish trophic studies (Hopkins and Baird, 1975; Lancraft and Robison, 1980; Balanov et al., 1994). Trawl cod-ends are often crowded with potential prey, and fishes may voluntarily (active feeding) or involuntarily (reflexive gulping) ingest items that might not be a ‘normal’ component of their diets. In this study, 84% of the copepod prey was found in the intestines and showed signs of digestion (Fig. 3), suggesting longer-term gut residence, and therefore precapture ingestion. Another factor arguing against net feeding is that



Fig. 3. Prey items (*Paraeuchaeta norvegica*) from the intestine of a North Atlantic *M. niger* specimen showing various states of digestion. Most prey items identified in this study were similar to the bottom (most digested) prey carcass.

most trawl-caught *M. niger* specimens have broken necks (Sutton, unpublished observations), probably sustained on contact between the fish's fangs and the trawl mesh. Specimens in this condition also contain copepods.

Planktivory is at times a function of ontogeny, with juveniles feeding on microcrustacea before switching to an adult diet (e.g., euphausiid predation by *Chauliodus sloani* juveniles before switching to piscivory; see Sutton and Hopkins, 1996a). This does not appear to be the case with *M. niger* because the larger specimens examined in this study were near the maximum size known for the species (~240 mm), and many of these contained copepods. Another potentially confounding problem in trophic studies is the differential digestion rates of various prey taxa. The digestion time of crustacean prey is generally greater than that for similar sized fish prey (Pandian, 1967), and thus may have a longer residence time in a digestive tract. This could potentially inflate the importance of crustacean prey in a fish's diet, particularly when intestines are examined. This argument likely does not hold for microcrustacea relative to fish prey. Zooplanktivorous mesopelagic fishes are capable of completely clearing their digestive tracts within a diel cycle, as evidenced by the change in gut fullness from nighttime (near full) to afternoon (near empty), a phenomenon often used to describe a

species' feeding chronology (Dewitt and Cailliet, 1972; Baird et al., 1975; Gorelova, 1980; Tyler and Percy, 1975; Ozawa et al., 1977; Hopkins and Baird, 1981; Cailliet and Ebeling, 1990). Further, the lack of diel feeding periodicity in the stomiid species known to take fish prey (e.g. *C. sloani*, *Stomias affinis*; Sutton and Hopkins, 1996a) suggests that these predators may take several days to digest their prey. Thus, it would be more likely that copepods would be passed faster, not more slowly than fish prey, and if anything, fish occurrence in the diet of *M. niger* may be overestimated by a longer gut residence time. Given these considerations, it is reasonable to conclude that the results reported here represent the natural feeding ecology of this species and not artificial bias.

4.2. Ecological background

If it is accepted that this feeding pattern is confirmed, then two questions can be asked: (1) how, and (2) why, does *M. niger* prey on something it does not appear morphologically suited to eat? As for (1) how, the feeding mechanics of *M. niger* are unknown, as there are no reported observations of its feeding. Morphologically, the lack of an ethmoid membrane (Fig. 1D) would seem to be the most serious impediment to small particle retention. It is likely that *M. niger* would need to keep both sides of the lower jaw together medially to prevent the loss of prey items through the open floor of the buccal cavity. The lack of gill rakers would also seem problematic, though it has been shown that not all fishes require gill rakers for small particle retention (Drenner et al., 1987), and that those with gill rakers sometimes take prey smaller than would be predicted using a passive straining model (Langeland and Nøst, 1995). The presence of copepods in its diet suggests that *M. niger* has overcome these obstacles through some undetermined feeding mechanism. The copepod species comprising the diet of *M. niger* are among the largest found in its habitat, so there does appear to be some form of size selectivity. Hopkins and Sutton (1998) found that prey size, more than taxon-specificity per se, accounted for greater niche separation of Gulf of Mexico mesopelagic

fishes and shrimps. Whether selectivity occurs prior to attack or is a function of retention is unknown. As for (2) why *M. niger* eats copepods, an integration of the known biology of this species, including recent discoveries of its visual ecology, provides a possible explanation.

M. niger is a circumglobally distributed fish with a known vertical distribution between 500 and 1000 m (Morrow, 1964; Goodyear, 1990; Sutton, 2003). There is one congeneric species, *M. indicus*, which, if valid, is apparently restricted to the western Central Pacific. Almost nothing is known of this species, as there is only a single documented capture (1952, off Galapagos Islands, SIO 52-404) after its initial description (Günther, 1878). A potential third *Malacosteus* species, *M. danae*, is a junior synonym of *M. niger* (Goodyear, 1990). Unlike the other 220+ species in its family, *Malacosteus* spp. apparently do not vertically migrate (Regan and Trewavas, 1930; Clarke, 1974; Sutton and Hopkins, 1996b). This suggests a mode of feeding that differs from other stomiids, most of which vertically migrate into the near-surface (<200 m) waters to feed nocturnally (Sutton and Hopkins, 1996a). The copepods on which *M. niger* is known to prey can be classified as large, adult or near-adult (CV) life stages of deep-meso/bathypelagic calanoids, some of which vertically migrate (Raymont, 1983). For example, *Chirundina streetsi*, one of the most commonly taken prey species, occurs at depths between 450 and 1000 m (Grice and Hulsemann, 1965; Roe, 1972; Deevey and Brooks, 1977). *Gaetanus tenuispinus* occurs between 250 and 2850 m (Grice and Hulsemann, 1965; Roe, 1972; Park, 1975), while *Euchirella* spp. generally occur between 500 and 1000 m (Grice and Hulsemann, 1965; Park, 1976; Deevey and Brooks, 1977). *Gaetanus kruppii*, one of the most abundant bathypelagic copepods, can live at considerable depths (more than 2000 m), but usually occurs between 500 and 1000 m (Raymont, 1983). Park (1975) found this species between 500 and 2000 m in the Gulf of Mexico. *Paraeuchaeta*, *Scaphocalanus* and *Amallothrix* are also deep-living genera (Raymont, 1983; Park, 1994), with species most common between 500 and 2000 m. Thus, the copepods preyed upon by *M. niger* are among the most abundant large calanoid

taxa within *M. niger*'s depth domain (Raymont, 1983; Park, 1994, 1995).

The character that makes *Malacosteus* unique among fishes, and all known vertebrates for that matter, is the combination of long-wave bioluminescence and a unique visual system utilizing a retinal photosensitizer. Presently this combination is known only for *M. niger*. Its congener, *M. indicus*, may also share this trait, but this species has not been examined for the presence of this photosensitizer. With respect to *M. niger*, it has been proposed that such a coupled system would be advantageous for intraspecific communication (i.e., sexual selection, etc.) and/or prey detection (Partridge and Douglas, 1995; Douglas et al., 2000). This system provides a possible explanation for the enigmatic feeding ecology of *M. niger*.

The production of long-wave bioluminescence makes *M. niger* one of the oddities of the biological world. Only two other closely related genera of fishes, *Aristostomias* and *Pachystomias*, and one genus of beetle, *Phrixothrix*, are known to produce long-wave bioluminescence (Denton et al., 1970, 1985; Widder et al., 1984). *M. niger* emits far-red (beyond 700 nm) bioluminescence from a large sub-orbital photophore (Fig. 1B and D). This long-wave bioluminescence would be useless without the ability to detect it, which is another unique feature of the fish genera with long-wave bioluminescence, as all other species of deep-sea fishes studied to date have visual sensitivities attuned to shorter (450–500 nm) wavelength regions of the spectrum (Partridge et al., 1988, 1989). The fishes with long-wave bioluminescence all possess long-wave-shifted visual pigments (O'Day and Fernandez, 1974; Bowmaker et al., 1988; Partridge et al., 1989; Crescitelli 1989, 1991; Douglas et al., 2000). *Aristostomias* and *Pachystomias*, both piscivores (Sutton and Hopkins, 1996a), possess at least three long-wave-shifted (wavelength of maximum absorption around 515, 550 and 590 nm) visual pigments (Douglas et al., 2000). The long-wave sensitivity of *M. niger*, which lacks the longest wavelength-shifted pigment found in the previous two genera, is enhanced with a bacteriochlorophyll-like photosensitizer (Douglas et al., 1998, 1999). Since vertebrates are not capable of synthesizing such a

photosensitizer, a dietary origin is suggested, as discussed below. In addition to these visual pigments, *M. niger* has yellow eye lenses with peak absorbance at 425 and 460 nm (Somiya, 1982), the blue region of the spectrum. Thus, not only can *M. niger* see long-wave light, it appears to have reduced visual sensitivity to the dominant light field (short-wave), perhaps affording the species more long-wave acuity and visual contrast.

4.3. Theory of why *M. niger* eats copepods

With this information in mind, it is possible to construct a theory of why *M. niger* takes food it does not appear morphologically suited to eat. First, *M. niger* likely searches small volumes for food. The rapid attenuation of long-wave light in seawater supports this (Denton et al., 1970), as do some aspects of *M. niger*'s morphology. The cranial osteology of *M. niger*, for example, may lend circumstantial evidence for this assertion (Fig. 4); the eyes are placed in a manner that may facilitate binocular vision in the forward-looking

field. While the actual visual field of *Malacosteus* is presently unknown, the eye placement condition of the two species is unique among the 220+ members of its family. A correlation may exist between the atypical eye placement and the atypical feeding strategy of this genus. If *M. niger* indeed searches small volumes for food, then large prey would be a very rare event at the depths in which it resides. Prey abundance data at the depths that *M. niger* resides in the eastern Gulf of Mexico indicate that large calanoid copepods are three orders of magnitude more abundant than either fish or shrimp (Table 6). Integrating these factors, it could be proposed that *M. niger* uses long-wave bioluminescence to illuminate a small search area (within 2 m of the fish, see Denton et al., 1985), and sustains itself by snacking on copepod prey in between infrequent encounters with larger prey items.

If bioenergetics were the sole reason for the atypical feeding ecology of this species relative to its confamilials, then why do not other species show the same pattern? In a treatment of the

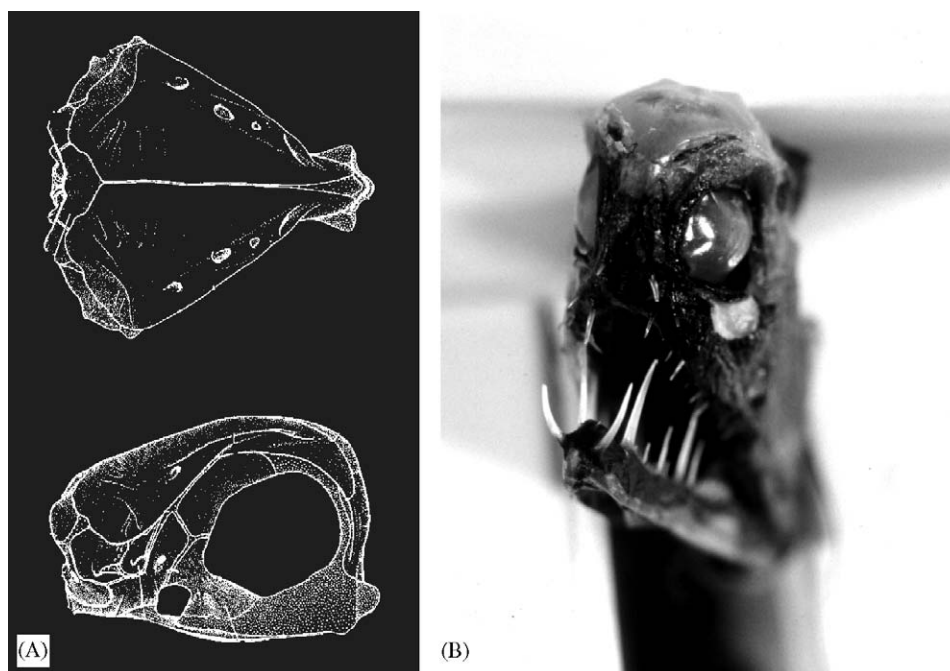


Fig. 4. (A) Cranial osteology of *M. niger*, dorsal (top) and right lateral (bottom) views (after Fink, 1985). (B) Frontal view of preserved specimen.

Table 6

The prey field of various prey taxa at the depths at which *M. niger* resides (500–1000 m) in the eastern Gulf of Mexico

Prey taxon	No. m ⁻³
Large copepods ^a	1.02 ^b
Decapods and mysids	0.0032 ^c
Fish	<0.0032 ^c

^aGreater than 2 mm metasomal length.

^bData from 136 plankton net (44 × 44-m² or 66 × 66-m² area, 162-μm mesh) samples (see Hopkins, 1982).

^cData from 1155 rectangular midwater trawl (4-m² or 8.3-m² area, 4-mm mesh) samples (see Hopkins and Sutton, 1998).

trophic ecology of the Stomiidae of the eastern Gulf of Mexico, Sutton and Hopkins (1996a) examined over 1200 specimens representing 63 species and 16 genera. Copepods were not found in any gut contents other than *M. niger*. In essence, those species morphologically adapted to take relatively large prey generally only take large prey. So why is *M. niger* divergent? The difference may lie in the unique retinal photosensitizer of *M. niger* previously mentioned. Douglas et al. (2000) have shown that the photosensitizer is a mixture of bacteriochlorophyll derivatives, most similar to *Chlorobium* pheophorbides. Since there is no known case of a chlorophyll derivative being synthesized by a vertebrate, it is reasonable to suppose that these pigments might be modified products of diet-derived chlorophyll. Using the preliminary trophic ecology data from eastern Gulf of Mexico *M. niger* (Sutton and Hopkins, 1996a), Douglas et al. (2000) also examined the fluorescent excitation and emission spectra of homogenates and methanol extracts of whole copepods (*Paraeuchaeta* spp.) and found that these spectra were very similar to those of the photosensitizer. Thus, while the dietary origin of this photosensitizer could not be proven conclusively, the fluorescence spectra suggest this as the most likely source. Copepods, through their access to phytoplankton, or to animals that feed directly on phytoplankton, may serve as a vector providing this photosensitizer that cannot be synthesized by *M. niger*.

In summary, *M. niger* appears to be a highly derived, aberrant deep-pelagic fish that has

diverged from the vertically migrating, feast-or-famine feeding scheme of its lineage. Instead, *M. niger* appears to utilize a feeding scheme that allows it to stay at depth and search small volumes closely for smaller food parcels in addition to the rarer, larger prey items for which it appears morphologically suited to eat. The smaller food parcels, in this case copepods, may provide both maintenance calories as well as a unique photosensitizer that facilitates the feeding scheme. In a sense, it appears to resemble a ‘chicken-or-the-egg’ scenario; *M. niger* eats large copepods at depth to acquire the visual sensitivity it needs to eat large copepods at depth.

Acknowledgements

This work was made possible by the loan arrangements and other courtesies of Karsten Hartel (MCZ), H.J. Walker (SIO), Masaki Miya (CBM), and Jon Moore (FAU). Drs. Tom Hopkins, Ron Douglas, Tamara Frank, Julian Partridge, Lita Proctor and Edith Widder provided much useful insight and commentary. Drs. Tom Hopkins and Taisoo Park kindly verified or provided identifications for several copepod prey items.

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