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Mesopelagic fishes of the Arabian Sea: distribution, abundance and diet of *Chauliodus pammelas*, *Chauliodus sloani*, *Stomias affinis*, and *Stomias nebulosus*

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Abstract

Four species of predatory fishes – *Chauliodus pammelas*, *Chauliodus sloani*, *Stomias affinis* and *Stomias nebulosus* – were collected on two cruises to the Arabian Sea during 1995. We present data on the abundances, horizontal and vertical distributions, and diet of these fishes. We also discuss briefly the importance of the oxygen minimum zone and predation on myctophid fishes to the ecology of these mesopelagic predators. *Chauliodus pammelas* and *C. sloani* appear to have only partially overlapping horizontal distributions in the Arabian Sea, with *C. pammelas* more common to the north and *C. sloani* more common to the south. Our data support previous results suggesting that diel vertical migration is the norm for these species, with smaller individuals usually nearer to the surface and larger individuals tending to stay deeper. In contrast to *Chauliodus*, *Stomias affinis* and *S. nebulosus* appear to have largely overlapping horizontal distributions in the Arabian Sea. However, they may have slightly different vertical distributions, with *S. affinis* living slightly shallower (especially at night) than *S. nebulosus*. All four species spend most of their time in the oxygen minimum zone, entering the surface oxygenated waters (100–150 m) only at night (if at all). The diets of *C. pammelas*, *C. sloani*, and *S. affinis* consisted mainly of lanternfishes, Myctophidae, and other fishes. In contrast, *S. nebulosus*, the smaller of the two *Stomias* species, ate mostly copepods and other crustaceans. This differential feeding may allow the two *Stomias* species to co-occur. Three of these four stomiids appear to play an important role in predation on myctophid fish populations in the Arabian Sea. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Arabian Sea is an unusual ocean environment, due in large part to the influence of the region's monsoonal weather. The Southwest Monsoon (June–September) causes upwelling along the Somali coast, leading to a large seasonal phytoplankton bloom; and the Northeast Monsoon (December–February) produces strong surface convection in the northern Arabian Sea also producing phytoplankton blooms (US GLOBEC, 1993; Smith et al., 1998). These blooms result in large downward fluxes of organic material in the Arabian Sea. The microbial oxidation of this material contributes to a suboxic ($< 0.1 \text{ ml l}^{-1}$ oxygen) layer, which can range from the bottom of the photic zone (ca. 150 m) to depths greater than 1000 m (Wyrski, 1971; Olson et al., 1993).

Such low oxygen zones can have striking effects on zooplankton and fish distributions. For example, studies of zooplankton feeding and metabolism show some species of zooplankton avoid low oxygen waters, while others appear better equipped physiologically to live in these zones, at least for part of the time (Vinogradov and Voronina, 1961; Childress, 1975, 1977; Mincks et al., 2000). Some species of lanternfishes, Myctophidae, in the Arabian Sea migrate vertically to reside in the suboxic zone during the day, but come up into the oxygenated surface waters to feed at night (Kinzer et al., 1993; US GLOBEC, 1993). Diversity of myctophid species was reduced in regions with the most depressed oxygen levels (Kinzer et al., 1993).

Predatory mesopelagic fishes in the Arabian Sea have been poorly studied, in their ecology in general and their vertical migration and feeding in particular. Prior zoogeographic surveys have shown that *Chauliodus pammelas* (Gibbs and Hurwitz, 1967; Belyanina, 1976) and *Stomias affinis* (Gibbs, 1969; Belyanina, 1976) inhabit equatorial and more northern tropical waters of the Indian ocean and overlap with *C. sloani* (Gibbs and Hurwitz, 1967; Belyanina, 1976) and *S. nebulosus* (Gibbs, 1969; Belyanina, 1976), which have been collected only in a narrow equatorial region. These reports, however, used non-closing nets with no instrumentation, providing little information on the vertical distribution and diet of these fishes.

The available vertical distribution data present broad ranges of depth strata, do not specify time of capture, or estimate depth-of-tow only approximately (e.g., length of the wire out). For example, although Gibbs and Hurwitz (1967) presented interesting zoogeographical and morphological data showing *C. pammelas* and *C. sloani* to inhabit different regions of the Indian Ocean, they did not specify the depths from which the fish were sampled more precisely than “shallow fractions” (approximately 300 m to the surface) and “deep fractions”, which varied in depth. Haffner (1952) divided the water column into 200-m depth strata, but estimated sampling depths as half the length of the wire out, an estimate that was biased by towing speed or currents. Some general trends in vertical distribution are evident from previous studies: *Chauliodus* were generally collected at deeper maximum depths (2800 m maximum depth; Morrow, 1961) than *Stomias* (1000 m; Gibbs, 1969).

Dietary information on these species is limited, especially for the Indian Ocean. *Chauliodus* spp. and *Stomias* spp. collected in the Pacific Ocean and the northeastern Atlantic Ocean typically were found with little or no food in their stomachs (Clarke, 1974; Roe and Badcock, 1984). Borodulina (1972) found that on average only 12% of mesopelagic fishes sampled in the Atlantic, Pacific, and Indian Oceans had substantial amounts of food in their guts. The diet of *Chauliodus* appeared to be mainly fish (including myctophids) and crustaceans (Haffner, 1952; Grey, 1955; Borodulina, 1972; Merrett and Roe, 1974; Clarke, 1982). The diets of *Stomias affinis* and other *Stomias* species

consisted mainly of myctophids, other fish, and to a much lesser degree decapods (Borodulina, 1972; Sutton and Hopkins, 1996), but the data are limited due to small sample sizes. Referring to predatory mesopelagic fishes in general, Clarke (1982) wrote, “Little is known of the feeding habits of these fishes and, consequently, of their role and importance in the pelagic food web.”

In this paper we present data on the abundance, horizontal distribution, vertical distribution and diet of *C. pammelas*, *C. sloani*, *S. affinis* and *S. nebulosus*. Our data are mainly from two sites in the Arabian Sea where our sampling was most thorough: (1) along the upwelling areas of the Somali coast, and (2) in the central Arabian Sea around a long-term mooring (15.5°N 61.5°E; Weller et al., 1998), which we define here as our Mooring Site. We also discuss briefly the potential predation impact and general ecological significance of predatory mesopelagic fishes in Arabian Sea.

2. Materials and methods

Fish collections were made aboard the *R/V Malcolm Baldrige* during May 5–23, 1995 (Spring Intermonsoon) and July 31–August 19, 1995 (towards the end of the Southwest Monsoon). In May,

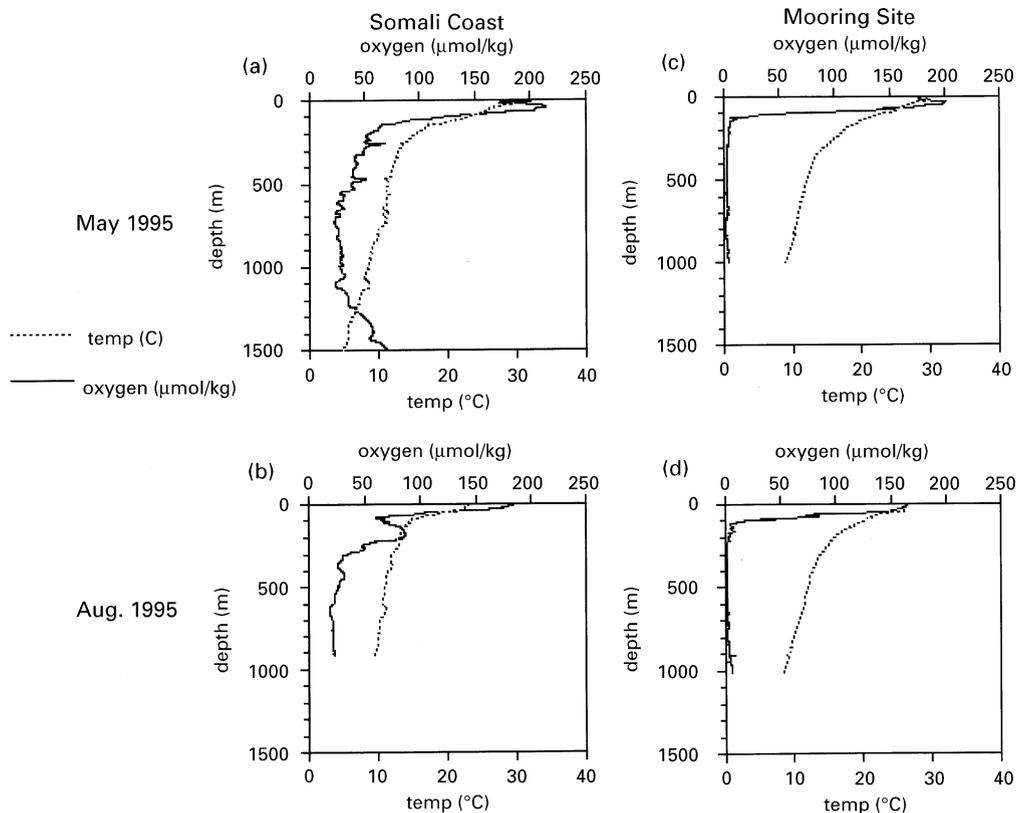


Fig. 1. Vertical profiles of temperature (dashed lines) and oxygen (solid lines); (a) off the Somali Coast in May, 1995; (b) off the Somali Coast in August, 1995; (c) at the Mooring Site in May, 1995; and (d) at the Mooring Site in August, 1995.

Table 1

10 m² MOCNESS hauls taken at two sites (Somali Coast and Mooring Site) in the Arabian Sea aboard the *R/V Malcolm Baldrige* in 1995. See text and figures for locations of other stations in the Arabian Sea

Tow #	Date (1995)	Latitude N	Longitude E	Depth Sampled (m)	Start time (GMT + 4)
Somali Coast					
1	May 5	05°13'	49°08'	0–1430	0215
2	May 5	05°36'	49°22'	0–1420	1016
3	May 7	08°41'	51°11'	0–938	0305
4	May 8	10°00'	52°00'	0–1500	0219
5	May 8	10°11'	51°58'	0–1503	0937
6	May 9	10°11'	52°02'	0–1512	0226
7	May 9	10°02'	52°04'	0–1511	0836
52	Aug. 11	10°41'	51°51'	0–900	1344
53	Aug. 11	10°42'	51°49'	0–900	2144
54	Aug. 12	10°45'	51°53'	0–900	1044
55	Aug. 13	10°45'	51°52'	0–900	0150
Mooring					
11	May 13	15°30'	61°19'	0–1000	1808
12	May 13	15°32'	61°20'	0–1000	2226
14	May 14	15°31'	61°21'	0–1000	0650
15	May 14	15°32'	61°21'	0–1000	1230
16	May 14	15°31'	61°21'	0–1000	1638
17	May 14	15°37'	61°23'	0–1000	2149
18	May 15	15°34'	61°22'	0–1000	0211
19	May 15	15°31'	61°23'	0–1000	0644
58	Aug. 17	15°21'	61°34'	0–1000	0248
59	Aug. 17	15°20'	61°33'	0–1000	1012
60	Aug. 17	15°21'	61°33'	0–1000	1529
61	Aug. 17	15°21'	61°36'	0–1000	2103
62	Aug. 18	15°21'	61°35'	0–1000	0227
63	Aug. 18	15°20'	61°33'	0–1000	1001

the ship track originated in Sri Lanka and headed west to the coast of Africa, then north along the coast of Somalia, then east to the Central Mooring Site, and finally northwest to Oman. In August, the ship originated in Oman and headed south along the Omani coast, into the Gulf of Aden, south along the coast of Somalia, and finally finished sampling at the Central Mooring Site. A total of 60 trawl collections were made along these two cruise tracks. Whenever possible, both daytime and nighttime trawls were collected at the same or near-by stations. Station information from two sites (Somali Coast and the Mooring Site) from which we have the most complete data is given in Table 1.

Fish and macrozooplankton were collected using a Multiple Opening–Closing Net/Environmental Sensing System (MOCNESS; Wiebe et al., 1985) trawl, with five, 3-mm knotless mesh nets

attached to a 10-m² frame (MOC-10). The MOC-10, opened and closed by electronic command from the surface, sampled one oblique haul to 1000–1500 m during descent, and four discrete depth intervals during ascent. Volumes filtered during ascent averaged 41,790 m³, with a minimum of 12,063 m³ and a maximum of 71,304 m³. The trawl was towed at approximately 2 knots for 2–5 h, while sensors on the net frame provided continuous data on depth, temperature, salinity, flow through the net, frame angle, and oxygen concentration.

All fish were placed in ice-chilled sorting trays immediately upon retrieval of the trawl, an initial inventory was taken, and then the fish were preserved in 5% formalin, usually within 5–15 min of being brought on-board.

Final species identifications were done in the laboratory. *Chauliodus pammelas* were identified as having 23 or fewer VAV photophores (those photophores located from between pelvic insertions to before anal origin) (Gibbs, 1969), and *Chauliodus sloani* were identified as having 24 or greater VAV photophores (Morrow, 1961; Gibbs and Hurwitz, 1967). *Stomias affinis* and *S. nebulosus* were differentiated by jaw morphology as described by Borodulina (1988). The relative size and color of *Stomias* stomachs also were used in species identification: *Stomias affinis* stomachs were 75% of the fish's standard body length and were caramel colored with white spots, whereas *S. nebulosus* stomachs spanned less than 50% of the body and were black (Ege, 1934).

Each specimen was measured for standard length, displacement volume and wet weight, and then the stomach and intestines were removed. Stomach and intestine contents were separated, blotted, weighed and preserved in ethanol for further analysis. Standard lengths of the fish prey also were taken if possible. The few prey found in the mouths of predators were noted, but not included

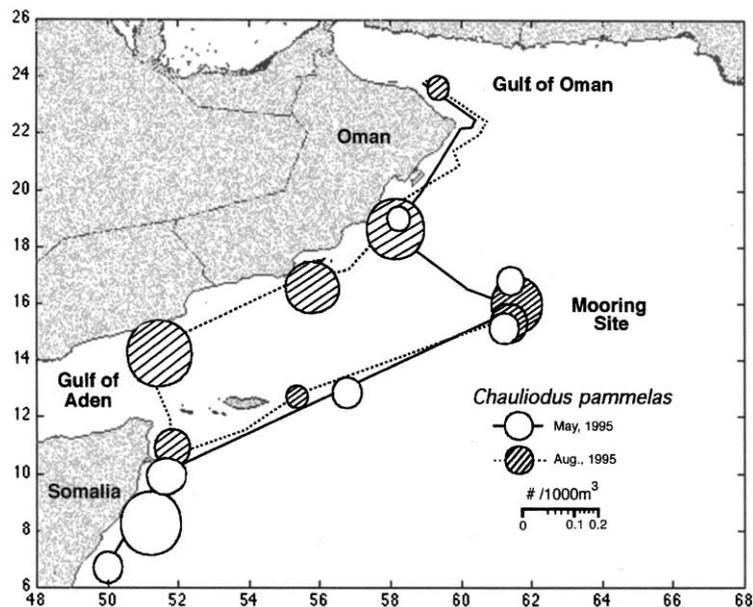


Fig. 2. Horizontal distribution of *Chauliodus pammelas* in the Arabian Sea. Open circles with solid cruise track represent abundances measured in May 1995; hatched circles with dashed cruise track represent abundances measured in August 1995.

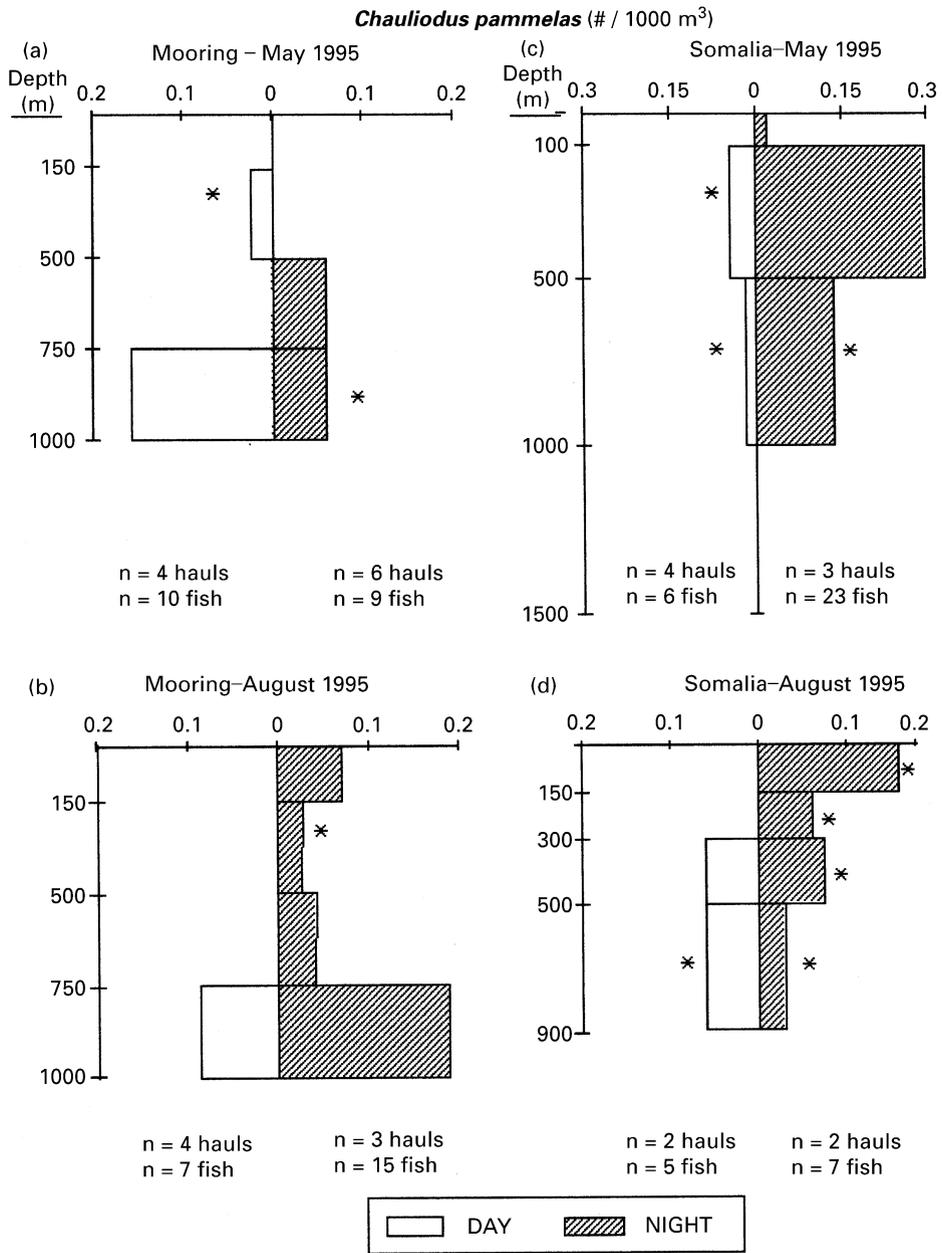


Fig. 3. Mean daytime (open) and nighttime (hatched) vertical distributions of *Chauliodus pammelas*; n = number of MOC-10 hauls (vertically stratified trawls) taken (day/night) and the total number of fish caught (day/night). Stars represent depths that contained animals with prey in their stomachs.

in the analysis that follows, as these items were likely the result of net or cod-end feeding. All material is deposited in the Museum of Comparative Zoology, Harvard University. Many other species of fish and macrozooplankton were collected during our sampling with the MOC-10; these results are reported in Madin et al. (in prep.).

3. Results

Physical properties at the two primary sites were as follows. Near the Somali Coast in May the surface temperature was nearly 30°C, and the low oxygen zone (≤ 1 ml/l) extended from about 175 m down to 1350 m (Fig. 1a). In August at this site, the sea-surface temperature was much cooler, 23°C, and the low oxygen (≤ 1 ml/l) zone was deeper, beginning around 300 m and extending at least to 900 m (the maximum depth of our sampling for this haul) (Fig. 1b). At the Mooring Site, the surface temperatures were similar to those found at the Somali Coast in both May and August. However, the oxygen levels were substantially lower; we could detect no oxygen below 125 m in May (Fig. 1c) and 200 m in August (Fig. 1d).

Abundances and distributions of the four species of mesopelagic fishes were as follows. *Chauliodus pammelas* was the most abundant and widely distributed of the four species. In May, the highest abundances occurred off the coast of Somalia (Fig. 2). They were generally more abundant in August, especially north of Somalia, off the coast of Oman and near the Mooring Site. With regard to vertical distribution, *C. pammelas* were most abundant between 750 and 1000 m during the day, and more broadly distributed at night (Fig. 3). Smaller specimens (20–70 mm) in particular tended to be found above 150 m at night.

Chauliodus sloani was found only in May along the Somali Coast (Fig. 4). These fish were collected between 100 and 1500 m, with smaller (20–150 mm) individuals near the surface (100–500 m) and larger fish (150–210 mm) deeper (than 500 m). However, the small sample size

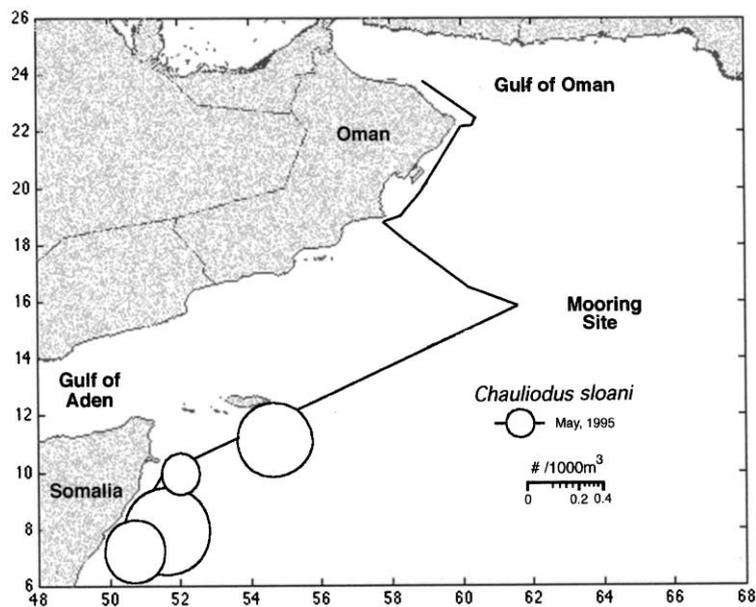


Fig. 4. Horizontal distribution of *Chauliodus sloani* in the Arabian Sea. Open circles with solid cruise track represent abundances measured in May 1995; hatched circles with dashed cruise track represent abundances measured in August 1995.

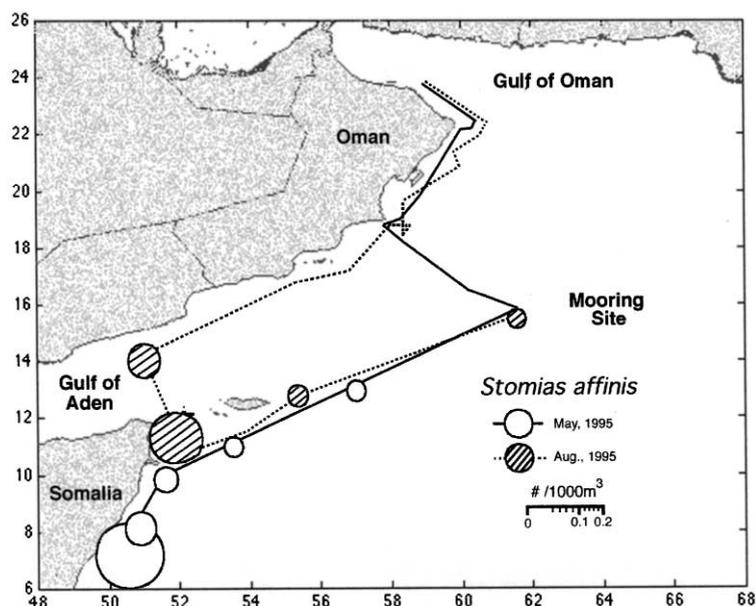


Fig. 5. Horizontal distribution of *Stomias affinis* in the Arabian Sea. Open circles with solid cruise track represent abundances measured in May 1995; hatched circles with dashed cruise track represent abundances measured in August 1995.

($n = 6$) precludes our saying anything else about vertical distribution or migration of this species.

Stomias affinis was found mostly along the northeast coast of Africa, especially near the entrance to the Gulf of Aden, around Socotra, and further south along the Somali Coast (Fig. 5). Distributions appear to be somewhat more southerly in May compared to August, although this may be due to a seasonal difference in sampling sites. Vertical distributions of *S. affinis* off the Somali Coast ranged from 100 to 1000 m during the day and from 900 m to the surface during the night.

Stomias nebulosus were only abundant around 7°N (northeast tip of Somalia) in May (Fig. 6). These fish were captured between 100 and 1000 m both day and night, with larger (60–120 mm) individuals below 500 m and smaller (40–90 mm) fish above 500 m.

With respect to diet, a total of 126 fish from the Somali Coast and Mooring Site were examined for stomach contents. However, the percentage of empty stomachs was quite high, ranging from a low of 57% (*S. affinis*; May) to a high of 84% (*C. pammelas*; August). Five prey types were identified: myctophid fishes, unidentified fishes, copepods, other crustaceans (decapods and euphausiids), and unidentified material. Of the stomachs that contained identifiable material, fish (including several species of myctophids which were relatively rare in comparison to those caught in the MOC-10, Madin et al., in prep.) made up the bulk of the diet of *Chauliodus pammelas*, *C. sloani*, and *Stomias affinis* at both sites during both seasons (Tables 2 and 3, Fig. 7). In contrast, *S. nebulosus* stomachs contained predominantly crustaceans (including several species of euphausiids, copepods, and shrimp) in May and August (Tables 2 and 3).

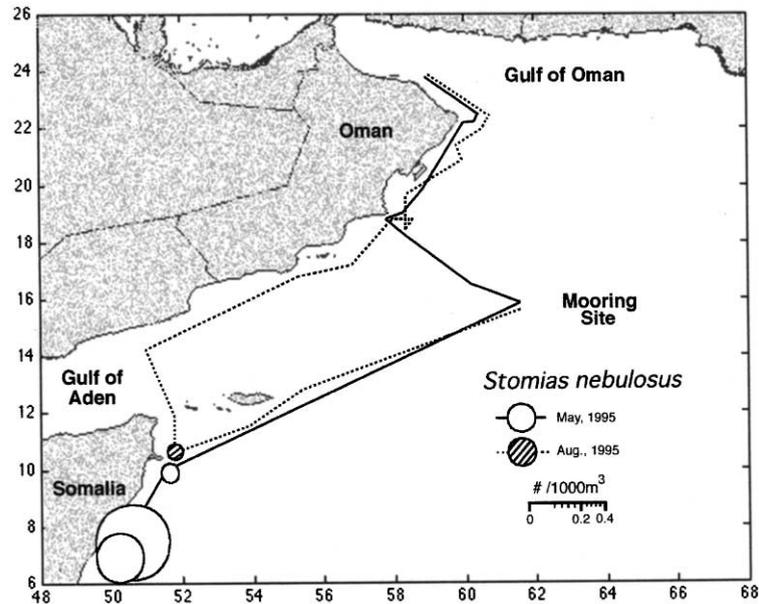


Fig. 6. Horizontal distribution of *Stomias nebulosus* in the Arabian Sea. Open circles with solid cruise track represent abundances measured in May 1995; hatched circles with dashed cruise track represent abundances measured in August 1995.

4. Discussion

The horizontal distributions of *Chauliodus* spp. that we observed on these two cruises agreed with those reported by other investigators (Gibbs and Hurwitz, 1967; Gibbs, 1969; Belyanina, 1976). They found *Chauliodus pammelas* and *C. sloani* to have partially overlapping geographical distributions in the Arabian Sea, with *C. pammelas* north of 5°N, *C. sloani* south of 10°N, and an area of overlap occurring between 5°N and 10°N (Gibbs and Hurwitz, 1967). Our Somali coast station is between 5°N and 10°N, and we found both species in May. We collected no *C. sloani* in August, but our coastal sampling did not extend as far south in August as it did in May.

Kinzer et al. (1993) found that the number of species of myctophids decreased along a transect running north from the equator. Similarly, Goodyear and Gibbs (1969) found reduced species diversity of stomiatooids in the Arabian Sea compared to that found in adjacent waters of the Equatorial or Central Indian Ocean. Specifically, they looked at the families Chauliodontidae, Stomiidae, Melanostomiidae, and Malacosteidae, all of which are today classified in the Stomiidae (Fink, 1985; Harold and Weitzman, 1996). Our data showed lower oxygen levels at the more northerly Mooring Site than at the Somali Coast (Fig. 1). Other northern stations along the Omani Coast and in the Omani basin also had subsurface oxygen concentrations too low to detect. *Chauliodus pammelas* was the only species taken in substantial numbers at these low oxygen sites; *C. sloani* and both *Stomias* species were apparently restricted to the higher oxygen regions of the Somali Coast, Gulf of Aden and Socotra regions. Possibly, the greater gill development in *C. pammelas* makes it better adapted for living in low oxygen zones (Gibbs and Hurwitz, 1967).

Table 2
Detailed list of prey items found in stomachs of *Chauliodus* and *Stomias*

Fish	Size (mm)	Prey item	Station/date	
<i>Chauliodus pammelas</i>	60	Fish remains (eye and vertebrae)	Somali/May 1995	
	170	<i>Diaphus regani</i>	Somali/May 1995	
	152	Unidentified digested material	Somali/May 1995	
	63	Digested fish	Somali/May 1995	
	59	Digested fish	Somali/May 1995	
	62	Unidentified digested material	Somali/May 1995	
	120	Unidentified digested material	Mooring/May 1995	
	174	Unidentified digested material	Mooring/May 1995	
	99	Digested fish	Mooring/May 1995	
	150	Unidentified digested material	Mooring/May 1995	
	162	Unidentified digested material and 1 chaetognath	Mooring/May 1995	
	87	Unidentified digested material	Somali/Aug. 1995	
	151	<i>Diaphus regani</i>	Somali/Aug. 1995	
	178	Unidentified digested material	Somali/Aug. 1995	
	145	Unidentified digested fish	Mooring/Aug. 1995	
	145	Cyclothone (found in mouth)	Mooring/Aug. 1995	
	157	Unidentified digested material	Mooring/Aug. 1995	
	146	Shrimp (found in mouth)	Mooring/Aug. 1995	
	45	Unidentified digested material	Mooring/Aug. 1995	
	<i>Chauliodus sloani</i>	51	Digested fish	Somali/May 1995
<i>Stomias nebulosus</i>	95	3 copepods, 1 caridean shrimp	Somali/May 1995	
	114	<i>Gennadas incertus</i>	Somali/May 1995	
	74	Unidentified digested material, 3 copepods	Somali/May 1995	
	125	1 copepod, 1 caridean shrimp	Somali/May 1995	
	91	3 copepods	Somali/May 1995	
	77	13 copepods, 3 pairs of euphausiid eyes	Somali/May 1995	
	43	Unidentified material	Somali/May 1995	
	84	<i>Nematoscelis</i> sp.	Somali/May 1995	
	100	Unidentified digested material	Somali/May 1995	
	89	Unidentified digested material	Somali/May 1995	
	90	<i>Stylocheiron maximum</i>	Somali/May 1995	
	67	2 copepods, 3 euphausiids (at least one <i>Euphausia diomedea</i>)	Somali/Aug. 1995	
	<i>Stomias affinis</i>	81	<i>Diaphus signatus</i>	Somali/May 1995
		66	Unidentified fish (recently swallowed)	Somali/May 1995
		196	<i>Sergestes</i> sp. (<i>edwardsii</i> group)	Somali/Aug. 1995
128		<i>Diaphus regani</i>	Somali/Aug. 1995	
109		Digested fish	Somali/Aug. 1995	
116		<i>Diaphus regani</i>	Somali/Aug. 1995	
140		Unidentified myctophid	Somali/Aug. 1995	
114		<i>Diogenichthys panurgus</i> , <i>Benthosema fibulatum</i>	Somali/Aug. 1995	

Previous studies of vertical distribution of *Chauliodus* suggest they are vertical migrators. Roe and Badcock (1984) found that most individuals of this genus in the northeastern Atlantic Ocean lived between 400 and 600 m by day, with the majority migrating upwards to around 100 m at night

Table 3

Summary data on the diet of the four species of fish collected at the two sites aboard the *R/V Malcolm Baldrige* in 1995

Site	Diet Composition												
	Myctophids		Unidentified Fish		Copepods		Euphausiids and Decapod Shrimp		Unidentified		B(g) = Average biomass in non-empty stomachs % = % stomachs found empty		
	% by no.	% by wt	% by no.	% by wt	% by no.	% by wt	% by no.	% by wt	% by no.	% by wt	B	%	
Mooring													
<i>C. pammelas</i>													
May (21)	0	0	29	66	0	0	0	0	0	71	34	0.009	67
August (19)	0	0	33	100	0	0	0	0	0	67	< 1	0.003	84
Somali													
<i>C. pammelas</i>													
May (15)	17	99	50	< 1	0	0	0	0	0	33	1	0.167	60
August (12)	33	100	0	0	0	0	0	0	0	67	< 1	0.158	75
<i>C. sloani</i>													
May (5)	0	0	100	100	0	0	0	0	0	0	0	0.007	60
<i>S. affinis</i>													
May (8)	50	88	50	12	0	0	0	0	0	0	0	0.137	75
August (14)	14	94	71	6	0	0	14	0	0	0	0	0.340	57
<i>S. nebulosus</i>													
May (30)	0	0	0	0	66	6	23	93	11	2	0.021	60	
August (2)	0	0	0	0	50	2	50	98	0	0	0.027	50	

and only a small proportion remaining at depth. Our data for *Chauliodus* in the Arabian Sea also suggest diel vertical migration, but these distributions are based on numbers of specimens too small to be compared statistically between day and night. Ontogenetic (size) differences in vertical distribution are also suggested by our data. This is in agreement with previous reports that smaller individuals are found at shallower depths and larger individuals reside in deeper waters (Morrow, 1961; Gibbs and Hurwitz, 1967; Goodyear and Gibbs, 1969; Roe and Badcock, 1984).

The horizontal distributions of *S. nebulosus* and *S. affinis* in our collections did not differ markedly between species. Gibbs (1969) found that these two species occur sympatrically in a narrow band between southern Africa and Sri Lanka, and south of the Indonesian Islands and the South China Sea. Because of their similar horizontal distributions, Gibbs (1969) suggested that

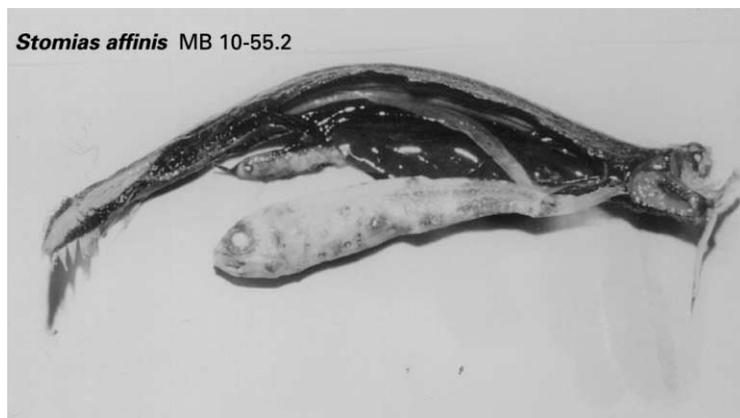


Fig. 7. A single specimen of *Stomias affinis* and its gut contents (2 myctophids) collected from the Somali Coast in August, 1995. Note the very large size of the prey relative to the predator.

the two species may generally differ in their vertical distributions, noting that *S. affinis* occurs shallower than *S. nebulosus*, but with considerable overlap. Our data generally support this, i.e., similar daytime distributions but slightly shallower nighttime distribution for *S. affinis*. However, again, our small sample sizes preclude statistical comparisons between species or dates.

Our data show that the four fish we examined generally spend much of their time in the suboxic zone, only coming above 150 m at night, most likely to forage. This behavior is similar to that of the myctophids studied by Kinzer et al. (1993), which were found to “migrate in a diel pattern, residing during daytime at depths of extremely low oxygen levels ($< 0.1 \text{ ml O}_2 \text{ l}^{-1}$) and foraging in the oxygen-rich surface layer at night.” Of course, possible daytime gear avoidance can complicate the interpretation of these results (e.g., Davis et al., 1990; Marschoff et al., 1998).

The diet of *Chauliodus* and *Stomias* has been examined by several investigators (Borodulina, 1972; Clarke, 1974; Merrett and Roe, 1974; Clarke, 1982; Roe and Badcock, 1984), and fish are the most frequently reported prey, but euphausiids, copepods, and other crustaceans also have been taken. With large, heavily-toothed mouths, these fishes are well adapted for consuming larger, rarer prey items such as myctophids (Tchernavin, 1953; Merrett and Roe, 1974; Roe and Badcock, 1984). Diet appears to vary with the size of the predators. *Chauliodus* greater than 120 mm were found by Roe and Badcock (1984) to be exclusively piscivorous, whereas smaller specimens also consumed euphausiids. Our specimens (45–178 mm) consumed nearly all myctophids or unidentified fishes; and often the prey items were quite large relative to the predators (Fig. 7). Other reports have shown that *C. sloani* is able to consume fish up to 63% of its own standard length (Clarke, 1982).

While our data and previous reports indicate that the most common prey of these fish was other fish, including myctophids, the gut contents of *Stomias nebulosus* from 67 to 125 mm in length were crustaceans (89% in May and 100% in August). These specimens were smaller than the other species considered here, and perhaps larger individuals might feed on fishes rather than crustaceans, as has been found for *C. sloani* (Clarke, 1982). The maximum lengths for these two *Stomias* species differ substantially: for *S. nebulosus*, females measured 176 mm and males measured 93 mm; and for *S. affinis*, females measured 204 mm and males measured 130 mm (Gibbs, 1969). This size

differential was evident in our data as well, with the largest *S. affinis* measuring 196 mm and the largest *S. nebulosus* 125 mm. These two species may partition their habitat both by vertical separation (Gibbs, 1969; our data) and by different feeding preferences, i.e., the smaller *S. nebulosus* consume mainly crustaceans and the larger *S. affinis* feed more commonly on fish. Interpretation of our results, as well as those from most other studies relying on trawl collections, can be confounded by possible cod-end feeding and/or regurgitation (e.g., Baier et al., 1997), but examination of this was beyond the scope of the current study.

During our sampling there was considerable overlap in the distributions of *Chauliodus* and *Stomias* (our data) and of myctophids (Madin et al., in prep.), and thus a large potential for predation to occur. For example, at the Somali Coast site in August there was about 1.0 myctophid per 1000 m³ (average of day and night) between 300 and 500 m (Madin et al., in prep.), and about one-tenth this number of *C. pammelas* and *S. affinis*. Our data (Table 2) show about one-third of the predators had fish in their stomachs, and Clarke (1982) states that the time required to evacuate the stomach of fishes such as these is not longer than four days and probably less. This suggests that each predator eats at least one myctophid every 12 days, which would translate into slightly less than 1% removal rate per day. This estimate is comparable with that made by Sutton and Hopkins (1996), who estimated a 2% daily removal rate of myctophids by all 69 species of stomiids they caught in the eastern Gulf of Mexico.

Over the course of several months, such a removal rate could have a very large impact on the adult population of myctophid prey, even if they are short-lived (6 months) species, as has been suggested by Kinzer et al. (1993). At other sites and other depths, however, the effects may not be quite so dramatic. For example, at the Mooring Site in August, myctophids overlap with these piscivores only at night, and might therefore be expected to be impacted to a lesser degree. Nevertheless, these examples show that piscivores potentially can have very significant impacts on myctophid populations. Similarly, Clarke (1982) calculated that the impact of stomiatoids (stomioids) on their myctophid prey could be large. Using a gut passage time of 4 days, he calculated the annual consumption to be 57.5% of the average standing crop of myctophid prey, whereas a gut passage time of only one day would result in consumption of 2.3 times the standing crop. Sutton and Hopkins (1996) assumed a gastric evacuation rate of 2 days, with feeding occurring every 8 days, and thereby approximated an 89% annual removal of the myctophid standing stock. Of course, other predators such as other mesopelagic fish, epipelagic fish (e.g., tuna and mackerel), squid, whales, dolphins and birds also may be important. To assess more fully the potential predatory impact of the piscivorous fishes (or any other predator) on a given prey population of course, would require that all loss (other mortality) and gain (recruitment) terms in the population dynamics of the prey species be identified and quantified (e.g., Bollens, 1988).

In summary, we have found that *Chauliodus pammelas* and *C. sloani* appear to have only partially overlapping horizontal distributions in the Arabian Sea, with *C. pammelas* more common to the north and *C. sloani* more common to the south. Our data support previous results suggesting that diel vertical migration is the norm for these species, with smaller individuals usually nearer to the surface and larger individuals tending to stay deeper. In contrast to *Chauliodus*, *Stomias affinis* and *S. nebulosus* appear to have largely overlapping horizontal distributions in the Arabian Sea. However, they may have slightly different vertical distributions, with *S. affinis* living slightly shallower (especially at night) than *S. nebulosus*. *Chauliodus pammelas*, *C. sloani*, and *S. affinis* all fed predominantly on myctophids and other fishes, whereas *S. nebulosus*' diet consisted primarily of

crustaceans, suggesting a separate feeding niche. The vertical distribution of the most commonly consumed prey item, myctophid fishes, overlaps substantially with that of the predators. Conservative estimates of gut passage times, together with the proportion of full guts, leads us to conclude that these piscivores are major predators of myctophids in the Arabian Sea.

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