

Aspects of the ecology of the mesopelagic fish *Gonostoma elongatum* (Gonostomatidae, Stomiiformes) in the eastern Gulf of Mexico

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ABSTRACT: *Gonostoma elongatum* is an important mesopelagic fish found throughout the world at subtropical-tropical latitudes. This study examined its distribution, abundance and life history in the eastern Gulf of Mexico. The species was a strong diel migrator, found from 25 to 325 m at night and from 425 to 725 m during the day with small fish occurring shallower than large fish. Numerical abundance and biomass were high, rivalling the dominant species of myctophids in the Gulf of Mexico. There were no obvious seasonal fluctuations in population abundance. *G. elongatum* is a protandric hermaphrodite whose population breeds throughout the year and females probably once a lifetime. Growth rate, based on 'daily' ring counts from otoliths, was linear (0.34 mm d^{-1}) and the largest fish (225 mm Standard Length) was estimated to live less than 2 yr. *G. elongatum* feeds primarily on crustaceans, with copepods and ostracods dominating in early juvenile stages ($< 50 \text{ mm SL}$) and euphausiids in the larger sizes. Diet composition shows little apparent seasonal variation. Size selectivity in feeding occurs, with *G. elongatum* preferentially ingesting medium to large zooplankton, a trend which becomes stronger with age. Taxonomic selectivity occurs as well in that this species preferentially feeds on conchoecid ostracods and copepods *Pleuromamma* spp. There is an obvious selection against non-crustacean prey. A cyclic feeding pattern was observed with most active feeding occurring in the 25 to 250 m zone at night. While *G. elongatum* has relatively little predation impact on one of its principal foods (*Pleuromamma* spp.) over the entire zone of occurrence of this prey genus, predation is substantial on large *Pleuromamma* ($> 3 \text{ mm}$) in certain depth zones (150 to 200 m) at night.

INTRODUCTION

Gonostoma elongatum, a member of the mesopelagic fish family Gonostomatidae, is found throughout most of the world ocean (Mukhacheva 1972) with its maximum abundance in the circumglobal belt of tropical-subtropical waters (Badcock 1984). It has been placed among the top 3 numerically dominant stomiiform species, *Cyclothone* excluded, in the northern and equatorial Atlantic (Backus et al. 1970, Backus & Craddock 1982), the Gulf of Mexico (Hopkins & Lancraft 1984) and the central Pacific (Clarke 1974). It is a highly fecund protandric hermaphrodite (Fisher 1983). We report on its vertical distribution and abundance (diel and seasonally), and aspects of its growth and reproduction.

The present paper also describes the trophic ecology of *Gonostoma elongatum* including information on diet composition, changes in diet with ontogeny, prey selec-

tivity and feeding chronology. Our data are compared with the findings of others on the nutrition of *G. elongatum* (e.g. Clarke 1978, Gorelova 1981) and estimates of the predation impact of this species on its zooplankton food resources in the eastern Gulf are discussed.

METHODS

Gonostoma elongatum was collected during 11 cruises between June 1975 and March 1987 within a 20 mile radius of 27° N , 86° W in the eastern Gulf of Mexico. The first 3 cruises, on the RV 'Columbus Ise-lin', were made during the summers of 3 successive years (June 1975, June 1976, September 1977). The 8 remaining cruises were on the RV 'Suncoaster' from September 1984 to March 1987 (Table 1).

Three different opening-closing modified Tucker-type trawls (Hopkins & Baird 1975) were used: one

Table 1. Summary of sampling effort on 11 cruises conducted during the study

1975–1977 discrete depth tows				
Depth (m)	Day		Night	
	Vol. filt. (10 ⁴ m ³)	No. tows.	Vol. filt. (10 ⁴ m ³)	No. tows
50–100	0.8	1	5.4	3
100–150	9.1	5	16.0	9
150–200	3.2	2	1.4	1
200–250	1.6	1	4.3	3
275–325	5.5	3	9.4	5
325–375	1.0	1	1.4	1
375–425	3.0	2	3.7	3
425–475	5.9	4	4.3	3
475–525	4.2	4	4.1	3
525–575	5.2	4	6.2	4
575–625	9.1	4	5.8	2
625–675	1.0	1	–	–
675–725	4.6	2	2.4	1
775–825	3.6	2	3.8	2
900–1000	6.2	3	6.2	3
1000–1100	1.8	1	6.6	3
1100–1300	<u>1.9</u>	<u>1</u>	<u>1.8</u>	<u>1</u>
	67.7	41	82.8	47
1984–1987 series (night only)				
Month	Discrete depth tows (0–25 m, 25–50 m zones)		Oblique depth tows (0–200 m ± 25 m)	
	Vol. filt. (10 ⁴ m ³)	No. tows	Vol. filt. (10 ⁴ m ³)	No. tows
Sep 1984	2.9	1	22.2	14
Mar 1985	8.9	3	51.4	30
Jul 1985	1.8	2	37.3	23
Nov 1985	2.6	3	42.8	25
Jan 1986	1.3	1	43.7	24
May 1986	2.3	2	32.4	22
Jan 1987	–	–	36.6	24
Mar 1987	<u>1.4</u>	<u>1</u>	<u>36.8</u>	<u>23</u>
	21.2	13	303.2	185

with a 5.3 m² mouth opening (effective fishing area) with a main net constructed of 4 mm square mesh, one trawl with a 2.65 m² mouth area using 4 mm mesh, and one with a 2.65 m² mouth area trawl and 1.6 mm square mesh size. The latter trawl was used only on the 'Suncoaster' cruises, in conjunction with the other 2 trawls. All main nets tapered down to a plankton net (1 mm square mesh) and terminated in a 1 mm square mesh cod end net and bucket. The trawls were towed at an average speed of 2 knots. Each trawl was equipped with a collapsible 66 × 66 cm, 163 µm mesh plankton net nested within the main net (Hopkins & Baird 1975). The trawls were opened and closed with messenger or clock actuated release devices (Davies & Barham 1969). The volume of water filtered was recorded by dial-type flowmeters only when the net

was fishing (Hopkins & Baird 1975). Tow depth was monitored through wire angle measurements or an electronic depth transducer system and documented with a time-depth recorder. A fish catcher – a shallow-coned retaining net of 4 mm mesh located well ahead of the cod end net – was used to prevent fish from mixing with and feeding on the plankton in the trawl cod end. During the 'Suncoaster' cruises expendable bathythermograph (XBT) casts down to 900 m were conducted daily or more frequently within the study area.

The smaller (1.6 mm) mesh was used to estimate the effect of mesh size on catch abundances and insure capture of the smallest post-larval fish (23 mm standard length, SL; Loeb 1979). Assuming a 5:1 length:height ratio (Grey 1964) minimum cross-sectional diameter was greater than 4 mm for a 23 mm SL fish.

All fish were either preserved in buffered 10 % formaldehyde solution or blotted of excess water and frozen immediately after capture. Preserved specimens were subsequently transferred to 50 % isopropanol. Some specimens were measured before freezing, but all fish, frozen or preserved, were measured to the nearest millimeter standard length (mm SL) in the laboratory. Shrinkage due to freezing was negligible as lengths did not differ significantly (paired *t*-test, *t* > 0.5, *n* = 62) in those fish measured before and after freezing. Length-weight curves were generated using the least squares method for the frozen specimens. The length-wet weight relation based on 355 fish (± 0.001 g) is:

$$W = 4.0 \times 10^{-6} L^{2.984} \quad (r^2 = 0.99)$$

where *W* = g wet weight (WW); *L* = mm SL. The length-dry weight expression, determined by drying 27 fish to constant weight (± 0.001 g) at 60 °C is:

$$W = 2.3 \times 10^{-6} L^{2.628} \quad (r^2 = 0.99)$$

where *W* = g dry weight (DW).

The diel vertical distribution of *Gonostoma elongatum* was primarily determined from discrete horizontal tows between 50 and 1300 m using 4 mm mesh nets on the 'Columbus Iselin' cruises. Supplementary discrete tows from the 0 to 25 m and 25 to 50 m zones were made from the 'Suncoaster' cruises, making a total of 19 depth horizons fished. A summary of the number of tows and volume of water filtered from each discrete depth horizon is given in Table 1. The tows in the 0 to 25 m zone were conducted during all seasonal sampling periods. To make a clear separation between day and night, no fishing was done within 1½ h of dawn or dusk. Abundance values (numbers per 10⁴ m³) were determined by dividing the total number of fish collected by the volume filtered for each depth horizon. To determine biomass (mg DW per 10⁴ m³), the dry weight

of each fish was calculated using the length-dry weight expression, summed with the dry weight of all fish collected in that horizon, and then divided by the volume of water sampled.

Numerical abundance and biomass were integrated down to 200 m and 1000 m for both day and night. This was done by multiplying the appropriate density or biomass concentration (adjusted to a m^3 basis) for each horizon by the depth range, in meters, of that horizon and then summing the products vertically.

Seasonal aspects of biomass, numerical abundance, and percentage composition of juveniles and mature adults were analysed by using the oblique 0 to 200 m (± 25 m) night tows taken during the 8 'Suncoaster' cruises (Table 1). These tows captured the complete size range of *Gonostoma elongatum* (see 'Results') but since the entire depth range was not sampled the biomass and abundance values were considered for seasonal comparisons and not for absolute estimates of total population abundance. Seasonal biomass values (mg DW m^{-2}) for *G. elongatum* were calculated by summing the dry weight of all fish from all of each cruise's 0 to 200 m tows, dividing by the total water filtered, and then multiplying by the depth of the sampled water column (200 m). Seasonal numerical abundances (number m^{-2}) were determined by calculating the quotient of total number of fish per water volume filtered for all 0 to 200 m tows in each cruise, and then multiplying by 200 m. Except for specimens from the July 1985 cruise, gonads were removed from all individuals 110 mm SL or larger and assigned a reproductive maturity state according to the criteria established by Fisher (1983). This size range contains gonads from most of the ripe males, all ripe females, and some hermaphrodites (Fisher 1983).

Growth rate was estimated by counting the 'daily rings' in sagittae (otoliths) which were removed from frozen or fresh fish after they had been measured and sexed. The otoliths were then cleaned, stored dry, and later mounted whole on microscope slides with a clear synthetic mounting medium. The number of increments were counted at high magnifications (400 to 1000 \times) under immersion oil using a microscope-video camera system. The video system magnified and enhanced the contrast of the increment image. To eliminate bias, each otolith was assigned an arbitrary number, without listing fish length or sex. The number of increments were counted twice by one observer (T.M.L.) on separate days and if the 2 counts varied by greater than 5% from a mean of the 2 then a third reading was performed. If the third reading was not within the percentage range then that otolith was discarded ($n = 3$). While the periodicity of primary zones is generally thought to be daily in nature (see 'Discussion') laboratory verification was impossible because

Gonostoma elongatum rarely survives more than a day after capture.

Kolmogorov-Smirnov 2-sample tests between mesh sizes and net mouth sizes for abundance of fish in 15 mm size class intervals (21 to 185 mm SL, 11 classes) for all 8 seasonal collections were performed to evaluate the catching abilities of the different net sizes and meshes. An ANOVA was used to test if median seasonal abundances varied relative to net mouth size.

Fishes used in diet analysis were measured (mm SL) before their digestive tracts were removed. The digestive tract was opened longitudinally with iris scissors and the contents removed to small watch glasses or microscope slides. All material was microscopically examined in water and separate records were kept for stomach and intestinal contents. The *Gonostoma elongatum* size classes considered for diet analysis were 20–29, 30–50, 51–79, 80–100, 110–130 and 131–150 mm SL. The numbers of fish examined for each size class were, respectively, 28, 114, 29, 121, 208 and 15.

Identification of food items was made to species, if possible. When whole prey animals were encountered, measurements were made of total length to the nearest 0.1 mm. The dimensions measured for each type of prey are described in Hopkins (1982). In cases of fragmented prey, key morphological features were measured which could be related to total size through regressions of these fragment dimensions versus total animal size (Hopkins 1987). The prey most commonly fragmented were ostracods, copepods and euphausiids. Linear regressions on total length were obtained for the most commonly occurring body parts of prey. The basal segment (length) of the second antennae and mandibles (width) were measured in ostracods. Mandibles (width) were used in copepods and, for *Pleuromamma*, the metasomal spot (diameter). Eyes (diameter) were measured in euphausiids. Analysis of the diet information indicated that 15 to 20 fish with food in their guts were enough for estimating within 5% the relative abundance of the dominant food taxa in a fish sample.

Feeding chronology was addressed by dividing the diel period into 7 time (local) intervals, 19:00 to 21:00, 21:00 to 23:00, 23:00 to 1:00, 1:00 to 3:00, 3:00 to 5:00, 7:00 to 13:00, and 13:00 to 18:00 h, then assigning the dietary data to the appropriate time of fish capture. Three size classes of *Gonostoma elongatum* were considered (30–50, 80–100 and 110–130 mm SL), and the information used was the total number of prey in the digestive tract.

Information on the principal zooplankton prey of *Gonostoma elongatum* comes from 2 sets of samples. One set, reported in Hopkins (1982), was taken during the RV 'Columbus Iselin' cruises (Table 1). These col-

lections provided averaged data for summer on vertical distribution of major food taxa in the day and night zones of occurrence of *G. elongatum*. Also, the data used in the discussion on the vertical distribution and abundance of various species and size classes of the copepod genus *Pleuromamma* comes from a master's thesis (Bennett 1986) based on these collections. The second set, providing seasonal data, comes from the RV 'Suncoaster' cruises (Table 1). Six samples were analyzed from each cruise with these being taken in the period 21:30 to 4:00 h, 3 from pre-midnight and 3 from post-midnight. Four aliquots were examined from each sample using the procedures detailed in Hopkins (1982) and the results of the aliquot analyses ($n = 24$) for each cruise were averaged.

RESULTS

XBT data

Winter and summer temperature profiles represent the maximum seasonal variation during all cruises from our sampling site (Fig. 1). The mixed layer ranged from 20 to 40 m but generally occurred at less than 25 m throughout the year.

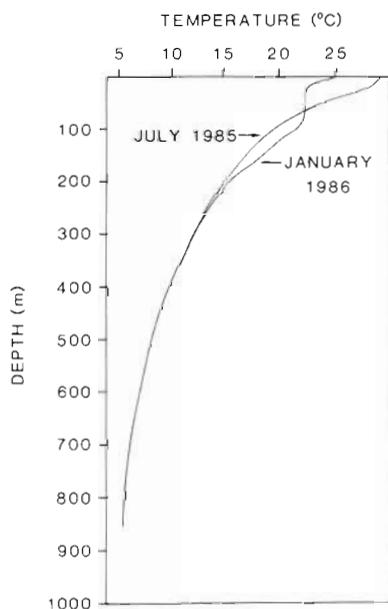


Fig. 1. Winter and summer temperature profiles from the eastern Gulf of Mexico (27°N, 86°W)

Net comparisons

Comparison of abundances of fish in all size categories between different mesh sizes (1.6 vs 4 mm square) for all 8 seasonal collections showed no mesh-

related, statistically different catches (Kolmogorov-Smirnov 2-sample tests, all 8 cruises, $p > 0.05$). Using 0 to 200 m tows ($n = 185$) a comparison (ANOVA, $p > 0.3$) of the median seasonal abundances between net mouth sizes (5.3 vs 2.65 m²) showed no significant differences in catch abundances related to net mouth size for any sampling period. Additionally, there were no differences in abundances of all size categories between net mouth sizes for any cruise (Kolmogorov-Smirnov tests, $p > 0.05$). This data indicated that our 4 m mesh nets were adequate for sampling the entire post-metamorphic population of *Gonostoma elongatum*. Therefore, all tows were grouped to determine seasonal numerical abundances and biomasses.

Diel vertical distribution and abundance

A total of 275 specimens ranging from 21 to 162 mm SL were collected in the horizontal discrete tow series (Table 1). *Gonostoma elongatum* was a strong diel migrator with the entire population moving from nighttime depths of 25 to 325 m to daytime depths of 425 to 725 m (Fig. 2). Night-time and daytime abundance peaks were at 200 and 600 m, respectively. Despite the intensive night-time trawling program, no fish were

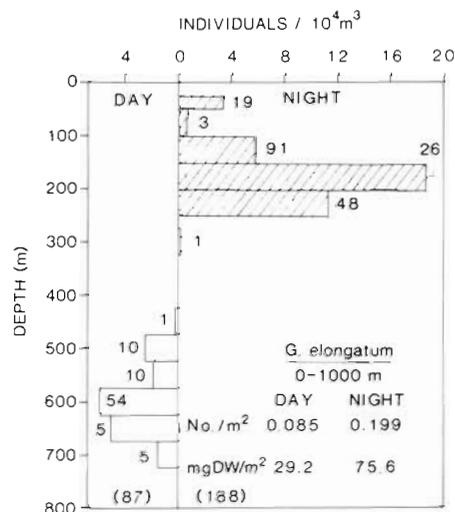


Fig. 2. *Gonostoma elongatum*. Diel vertical distribution. Numbers beside bars are sample sizes; totals are in parentheses. Diel integrated 0 to 1000 m abundance and biomass values also presented

captured from the upper 25 m (mixed layer) from any cruise. Larger fish lived and migrated in deeper depth horizons than did smaller fish (Fig. 3).

In the horizontal tow series twice as many specimens (188 vs 87) and higher standardized abundances were collected at night than during the day. Because day-

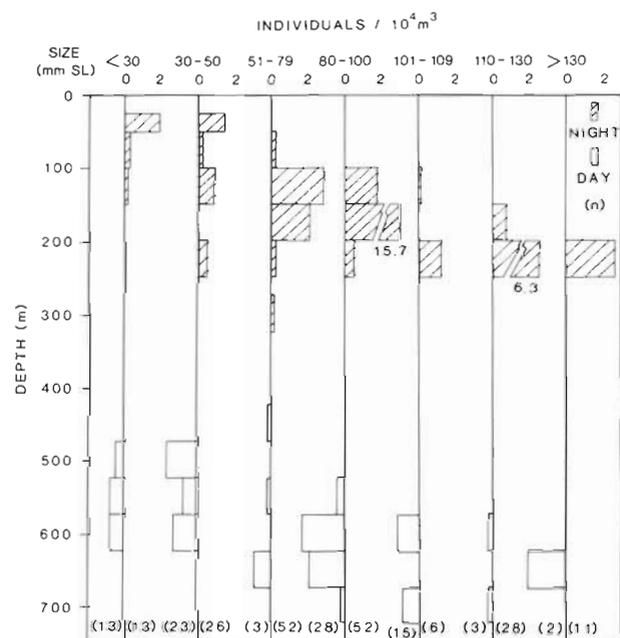


Fig. 3. *Gonostoma elongatum*. Diel depth distribution for each size class (mm SL)

time net avoidance seemed likely, night-time values were taken as the most accurate estimates of abundance and biomass. Night-time integrated 0 to 1000 m values for abundance and biomass were $0.199 \text{ fish m}^{-2}$ and $75.6 \text{ mg DW m}^{-2}$, respectively (Fig. 2).

Seasonal abundance and reproduction

A total of 1698 fish (22 to 225 mm SL) were collected in 185 night-time oblique tows (0 to 200 m) during the 8 seasonal cruises. Mean abundance for all seasons combined was $0.109 \text{ fish m}^{-2}$ in the upper 200 m (Fig. 4A) and mean biomass was $28.7 \text{ mg DW m}^{-2}$ (Fig. 4B).

No major seasonal reproductive patterns were present as post-larval juveniles (21–50 mm SL) were abundant almost all year around (Fig. 4C) and reproductively mature individuals of both sexes were found during all collection periods (Fig. 4D). Post-larval juveniles averaged nearly 40 % of the sampled population in most seasons. A total of 179 (14.4 %) ripe gonads were found in the 1247 fish collected (July 1985 excluded; sample destroyed). Ripe males accounted for 9.9 % of all fish and ripe females accounted for 4.5 %. The median sizes of ripe males ($n = 123$) and females ($n = 56$) were 115 mm SL (110–134 mm SL) and 161 mm SL (135–225 mm SL), respectively. All fish greater than 163 mm SL were ripe females. Only 6 females (about 10 % of the ripe females) were greater than 180 mm, the mid-range

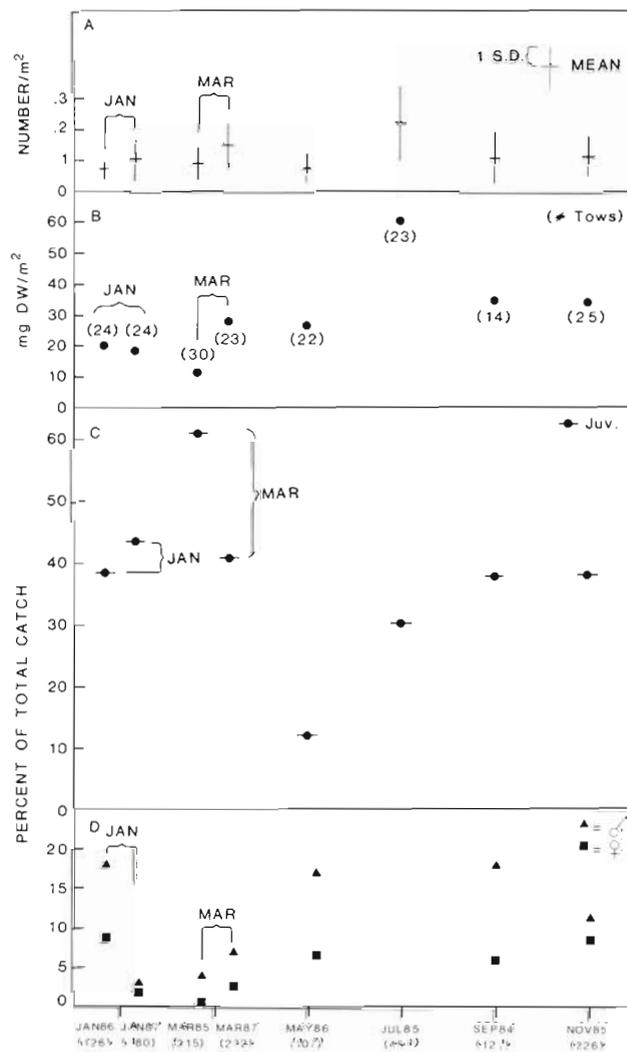


Fig. 4. *Gonostoma elongatum*. (A) Seasonal population abundance, and (B) biomass; (C) seasonal juvenile (21–50 mm SL) abundance, and (D) sexually mature adult abundance. Data taken from 1984 to 1987 oblique 0 to 200 m tow series

point. The occurrence of ripe males may have been underestimated since males smaller than 110 mm SL were not examined but this did not affect the observed absence of seasonality of reproduction. Gravid females rarely ($n = 3$) carried more than one size class of eggs and no spent ovaries were observed.

Growth

The otoliths of *Gonostoma elongatum* were small (< 3 mm in diameter), only slightly concave, and nearly transparent so whole otoliths could be mounted and examined without further treatment. The rings were distinct though narrow (1 to 3 μm) allowing for generally good readability. The numbers of increments

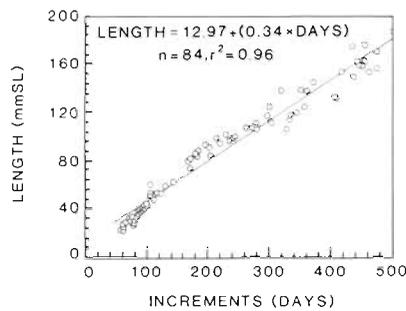


Fig. 5. *Gonostoma elongatum*. Growth rate (length, mm SL) in the eastern Gulf of Mexico

counted in 84 otoliths taken from fish ranging from 23 to 187 mm SL were regressed against fish length (Fig. 5) using a variety of models with the best fit resulting in the linear growth rate expression of:

$$\text{Length} = 12.97 + (0.34 \times \text{Increments}) \quad (r^2 = 0.96),$$

where length is in mm SL and increments are assumed to be days. The growth rate averaged over the entire size range was 0.34 mm d^{-1} . Using this growth rate, onset of sexual maturity for males (110 mm SL) and females (135 mm SL) began at 9 and 12 mo, respectively. The median sized ripe female lived to 15 mo; after this period female abundance dropped rapidly so only 10 % of the females survived over 16 mo (180 mm SL). The maximum calculated age for females at the largest observed size (225 mm SL) was 21 mo.

Increments near the center of the otolith were the widest and most distinct but they narrowed abruptly at a point 51 to 67 increments (mean = 57.3) from the center. The total number of increments counted in otoliths from four 23 mm SL recently metamorphosed fish ranged from 56 to 63 and averaged 60 increments, suggesting a 2 mo pre-metamorphic period.

Feeding

The diets of 3 size classes of *Gonostoma elongatum* from July 1985 collections are listed in Table 2. The diet of *G. elongatum* was composed overwhelmingly of Crustacea, with this group constituting 92 to 98 % of the food items identified. Food was taxonomically diverse and copepods accounted for most of the diversity and numbers of prey eaten. *Pleuromamma* was the obviously predominant genus. Two other important prey groups were conchoecid ostracods and euphausiids, particularly representatives of the genera *Nematoscelis* and *Stylocheiron*.

Size-related changes in diet were apparent. The data in Fig. 6 show a relative decrease in biomass contribution of copepods and ostracods and a corresponding

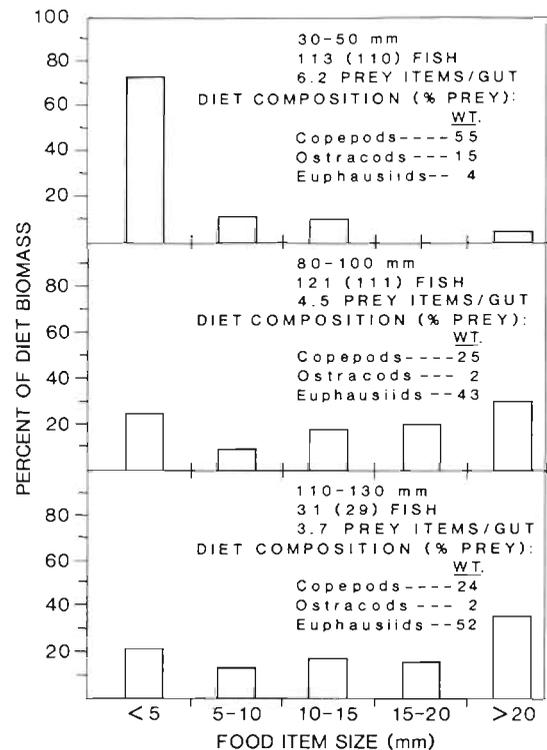


Fig. 6. *Gonostoma elongatum*. Biomass composition of diets of 3 size classes. Numbers in parentheses are numbers of fish examined which contained identifiable food

increase in the importance of euphausiids with increasing size of *Gonostoma elongatum*. Thus, larger prey become increasingly more important in the nutrition of this species with fish growth. This is demonstrated in Fig. 7, a size-frequency plot of prey eaten by 5 size classes of *G. elongatum*.

While *Gonostoma elongatum* fed on a broad spectrum of prey, there is evidence for both size and tax-

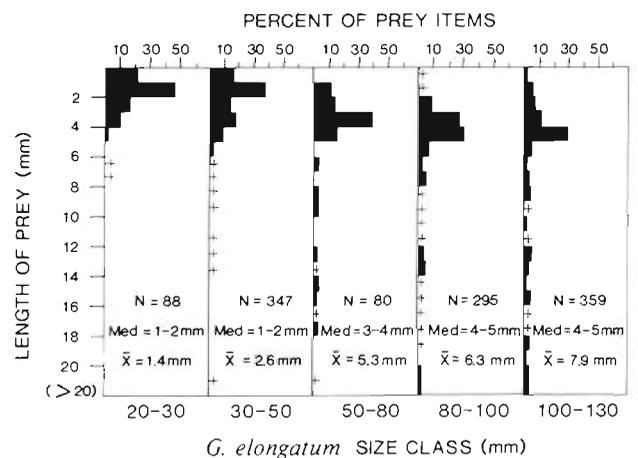


Fig. 7. *Gonostoma elongatum*. Size-frequency distribution of food items in 5 size classes. + = < 1 %

Table 2. *Gonostoma elongatum*. Diet composition of 3 size classes. N: number of fishes examined

Prey taxa	30–50 mm (N = 114)	80–100 mm (N = 121)	110–130 mm (N = 31)
COPEPODA			
<i>Aegisthus</i> spp.	2	–	–
<i>Candacia bipinnata</i>	5	–	–
<i>Candacia curta</i>	3	–	–
<i>Candacia longimana</i>	5	7	–
<i>Candacia pachydactyla</i>	2	–	–
<i>Candacia varicans</i>	5	3	–
<i>Candacia</i> spp.	4	1	1
<i>Chirundina streetsi</i>	–	11	4
<i>Corycaeus clausi</i>	–	–	1
<i>Corycaeus lautus</i>	3	–	–
<i>Corycaeus speciosus</i>	1	–	–
<i>Corycaeus</i> spp.	–	4	–
<i>Euaetideus</i> sp.	–	1	–
<i>Eucalanus sewelli</i>	3	1	–
<i>Eucalanus</i> sp.	1	–	–
<i>Euchaeta marina</i>	1	1	–
<i>Euchaeta media</i>	4	7	1
<i>Euchaeta spinosa</i>	–	1	–
<i>Euchaeta</i> spp.	6	5	–
<i>Euchirella amoena</i>	–	1	–
<i>Euchirella messinensis</i>	–	1	–
<i>Euchirella pulchra</i>	1	1	–
<i>Euchirella splendens</i>	1	–	–
<i>Gaetanus</i> spp.	2	–	1
<i>Heterorhabdus</i> spp.	1	2	–
<i>Heterostylites</i> sp.	–	1	–
<i>Lubbockia</i> spp.	1	1	–
<i>Lucicutia flavicornis</i>	–	1	–
<i>Nannocalanus minor</i>	8	–	–
<i>Oncaea</i> spp.	57	26	3
<i>Paracandacia simplex</i>	2	–	–
<i>Phaenna spinifera</i>	1	–	–
<i>Pleuromamma abdominalis</i>	101	65	5
<i>Pleuromamma gracilis</i>	8	–	–
<i>Pleuromamma piseki</i>	11	–	–
<i>Pleuromamma xiphias</i>	58	136	29
<i>Pleuromamma</i> spp.	36	2	–
<i>Pseudochirella obesa</i>	–	1	–
<i>Rhincalanus cornutus</i>	1	1	–
<i>Sapphirina metallina</i>	1	–	–
<i>Sapphirina opalina</i>	1	–	–
<i>Sapphirina</i> sp.	1	–	–
<i>Scolecithricella dentata</i>	2	–	–
<i>Scolecithrix bradyi</i>	1	–	–
<i>Scolecithrix danae</i>	10	–	–
<i>Scottocalanus helenae</i>	–	1	–
<i>Scottocalanus securifrons</i>	4	11	2
<i>Scottocalanus thomasi</i>	–	1	–
<i>Scottocalanus</i> spp.	3	10	1
<i>Temora stylifera</i>	8	–	–
<i>Undeuchaeta major</i>	–	3	1
<i>Undeuchaeta plumosa</i>	4	6	1
Unident. copepods	19	6	5
OSTRACODA			
<i>Conchoecia atlantica</i>	–	2	–
<i>Conchoecia curta</i>	66	–	–
<i>Conchoecia echinata</i>	4	1	–
<i>Conchoecia imbricata</i>	–	6	1

Table 2 (continued)

Prey taxa	30-50 mm (N = 114)	80-100 mm (N = 121)	110-130 mm (N = 31)
OSTRACODA			
<i>Conchoecia magna</i>	-	1	-
<i>Conchoecia oblonga</i>	10	6	-
<i>Conchoecia parthenoda</i>	1	-	-
<i>Conchoecia procera</i>	5	2	-
<i>Conchoecia rotundata</i>	-	1	-
<i>Conchoecia skogsbergi</i>	2	-	-
<i>Conchoecia spinifera</i>	1	1	-
Unident. ostracods	169	75	14
AMPHIPODA			
<i>Amphithyrus sculpturatus</i>	2	-	1
<i>Amphithyrus</i> sp.	-	1	-
<i>Anchylomera blossomii</i>	-	-	1
<i>Hyperioides sibaginis</i>	-	2	-
<i>Hyperionyx macrodactyla</i>	-	1	1
<i>Paraphronima</i> sp.	-	1	-
<i>Phronimopsis spinifera</i>	2	-	-
<i>Phrosina semilunata</i>	-	1	-
<i>Primno</i> spp.	2	1	2
Unident. Hyperidae	16	21	3
Unident. Platyscelidae	-	1	-
Unident. Scinidae	4	4	-
Unident. Amphipoda	-	2	-
EUPHAUSIACEA			
<i>Nematoscelis microps/atlantica</i>	5	32	12
<i>Stylocheiron abbreviatum</i>	-	7	2
<i>Stylocheiron affine</i>	1	6	1
<i>Stylocheiron carinatum</i>	2	-	-
<i>Stylocheiron longicorne</i>	-	2	-
<i>Stylocheiron suhmi</i>	3	-	-
<i>Stylocheiron</i> spp.	3	7	1
<i>Thysanopoda monochantha</i>	-	2	1
Euphausiid larvae	7	-	-
Unident. euphausiids	9	18	5
DECAPODA			
<i>Sergestes sargassi</i>	-	-	1
<i>Sergestes vigilax</i>	-	1	-
<i>Sergestes</i> spp.	-	7	2
Decapod larvae	-	1	-
Unident. decapods	-	1	-
SIPHONOPHORA			
<i>Eudoxoides mitra</i>	-	-	1
Calycephoran fragments	1	3	2
POLYCHAETA			
Alciopidae	-	3	-
Unident. polychaetes	2	-	-
CHAETOGNATHA			
<i>Sagitta</i> spp.	3	1	3
MOLLUSCA			
Unident. cephalopods	1	2	1
Pteropods	1	1	-
PISCES			
Leptocephalus larvae	1	-	-
Unident. fishes	-	10	2

Table 3. *Gonostoma elongatum*. Comparison of percentages of each prey size distribution in diet with that in the plankton at 150 to 200 m at night (see 'Methods')

A. Total zooplankton	Prey size class		
	<5 mm	5–10 mm	> 10 mm
<i>G. elongatum</i> :			
30–50 mm SL	96	3	<1
80–100 mm SL	80	9	11
110–130 mm SL	66	17	17
Zooplankton	99	1	<1
B. Copepods	Copepods		
	<2 mm	2–4 mm	> 4 mm
<i>G. elongatum</i> :			
30–50 mm SL	40	46	14
50–100 mm SL	11	40	49
110–130 mm SL	9	17	74
Zooplankton	96	2	2

onomic selectivity in food. Table 3 demonstrates that, in general, *G. elongatum* fed selectively on mid- to large-sized zooplankton with the trend becoming increasingly obvious in larger fish. Selection for mid- and large-sized copepods is especially apparent.

Taxonomic selectivity is demonstrated in Table 4 which shows that diet composition of 110–130 mm SL *Gonostoma elongatum* was strikingly different from prey composition in the plankton in both the day and night zones of occurrence of this species. Copepods of the genus *Pleuromamma* and conchoecid ostracods, for example, were proportionately far more abundant in guts than in the plankton. Also, non-crustacean invertebrates (e.g. chaetognaths, tunicates, coelenterates, polychaetes and molluscs) constituted an insignificant fraction of the *G. elongatum* diet whereas in the day/night zones of occurrence these organisms form 21 to

65 % of the plankton in the size range of food ingested by *G. elongatum*.

Seasonal variability in diet composition was examined through comparisons of data from 110–130 mm SL *Gonostoma elongatum* taken in different months during 1984 and 1985 (Table 5). Using the criterion for adequate sample size (i.e. > 20 fish sample⁻¹), comparisons are probably valid for 5 of the 6 data subsets in that only the March 1985 collection had fewer than 20 fish. While the percentages of the principal diet components varied considerably, no consistent seasonal trend was obvious. Conspicuous variability in specific food types was observed from cruise to cruise, but the combined percentages of the 3 major kinds of prey, copepods, ostracods and euphausiids, were consistently over 85 % of the food items. With the exception of March data, *Pleuromamma* consistently exceeded 20 % of the number of prey ingested. *Nematoscelis* euphausiids were important in the diet throughout the sampling period as well, and January 1986 excepted, accounted for over 10 % of the food items.

Diel periodicity in feeding was examined by comparing the total number of food items in guts for the time periods listed in 'Methods' (Fig. 8). For the 3 size groups of *Gonostoma elongatum* analysed, guts were fullest at night (21:00 to 5:00 h) with the largest average values being approximately twice those for daytime (7:00 to 18:00 h). Student *t*-tests showed this difference to be significant ($p < 0.05$).

DISCUSSION

Hydrographic setting

The Loop Current is that portion of the Gulf Stream System connecting the Yucatan Current and the Florida Current in the eastern Gulf (Maul 1977). It generally

Table 4. *Gonostoma elongatum*. Comparison of percentages of each prey type consumed by the 110–130 mm size class with plankton composition at depths of occurrence of this size class

Food type	Diet of <i>G. elongatum</i> 110–130 mm No. fish = 178 No. food items = 508	Zooplankton composition	
		150–200 m (night)	600–700 m (day)
Copepods 1–6 mm	46	75	95
<i>Pleuromamma</i> spp. 1–6 mm	27	6	1
Conchoecid ostracods 0.5–3 mm	33	6	1
Non-crustacean invertebrates 5–20 mm	3	65	21

Table 5. *Gonostoma elongatum*. Intercruise comparison of major diet components of the 110–130 mm size class. Values in body of table are percentages of food items in all guts of that cruise

Diet component	Date:	Jan 1986	Mar 1985	May 1986	Jul 1985	Sep 1984	Nov 1985
	No. food items:	50	27	86	114	148	116
	No. guts examined/ no. guts with food:	23/20	14/12	27/22	31/29	62/56	52/47
<i>Pleuromamma</i> spp.		26	15	30	31	21	22
Total copepods		48	30	43	52	43	41
Conchoecid ostracods		24	26	9	15	12	6
<i>Stylocheiron</i> spp.		10	4	7	4	10	9
<i>Nematoscelis</i> spp.		6	19	17	11	14	21
Total euphausiids		18	30	33	21	30	38
Total of major components (copepods, ostracods & euphausiids)		90	86	85	88	85	85

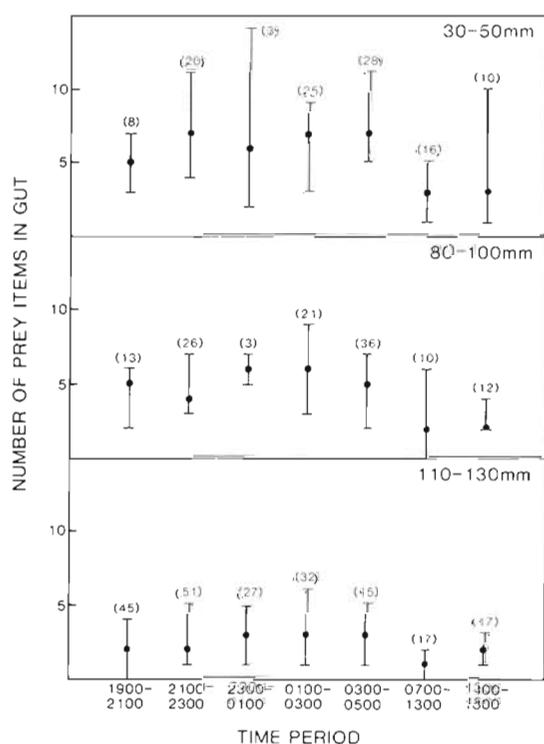


Fig. 8. *Gonostoma elongatum*. Diel feeding patterns in 3 size classes. Solid circle is median number of prey items in guts; vertical bar is range between 17th and 83rd percentiles, i.e. includes the central 3% of the values; number in parentheses are numbers of guts examined

penetrates furthest into the Gulf during the summer though there is a variable annual cycle of growth and decay (Maul 1977). The eastern boundary of the warm and saline Loop water generally moves down the west coast of Florida mixing with the cooler, fresher resident Gulf water to form the transitional water that occupied the study area for all of the cruises except March 1985.

Primary productivity in the eastern Gulf of Mexico is low (El-Sayed 1972) with transition waters generally being slightly more productive (Bogdanov et al. 1968, Hopkins 1982). Our unpublished integrated (0 to 200 m) seasonal chlorophyll *a* values averaged 29 mg m⁻² (range for 5 mo: 12 to 64 mg m⁻²). Low zooplankton standing stock from a previous study (Hopkins 1982) and our study (average: 1.8 g DW m⁻², range for 8 mo: 1.3 to 2.9 g DW m⁻²) also enabled us to characterize the study area as oligotrophic.

Biology

In the eastern Gulf of Mexico the entire population of *Gonostoma elongatum* vertically migrated about 400 m with larger fish living deeper. Other authors (Clarke 1974, Badcock & Merrett 1976) have suggested that some adults do not regularly undergo diel migrations but also indicated a positive size-depth relationship. *G. elongatum* was found in greater depths in those studies (down to 1500 m in the northeast Atlantic) than in the Gulf but was never found shallower than 25 m. Apparently *G. elongatum*, like many Gulf myctophids (Gartner et al. 1987), avoids the higher temperatures of the upper mixed layer in lower latitude ecosystems.

In the upper 1000 m of the Gulf of Mexico, the numerical abundance (0.199 fish m⁻²) and standing crop (75.6 mg DM m⁻²) of *Gonostoma elongatum* were higher than from many other Gulf mesopelagic fish. Hopkins & Baird (1985a) reported sternoptychids ranging from 0.021 to 0.053 fish m⁻². In another paper (Hopkins & Baird 1985b), one species of abundant lanternfish, *Lampanyctus alatus*, averaged 0.14 fish m⁻² (10 mg DW m⁻²). While some of the 7 most abundant myctophids in the Gulf (Gartner et al. 1987) may equal or exceed the numbers of *G. elongatum*, its contribution to overall biomass (0 to 1000 m) was nearly equal

to all 7 species combined (based on data from Hopkins & Lancraft 1984). *Cyclothone* species often occur in numbers many times that of other midwater fish (1 to 2 fish m^{-2}) but because of their diminutive size and high water content (D. G. Stickney & J. J. Torres unpubl.) they even contribute less than *G. elongatum* to overall dry weight biomass (Hopkins & Lancraft 1984). Considering its size and abundance, *G. elongatum* is the most important stomiiform species and potentially the most important midwater fish in the Gulf of Mexico.

Subtropical waters are typified by small seasonal changes (Blackburn 1981, Hayward 1986) and the study area was no exception (Bogdanov et al. 1968, this study). Small changes in *Gonostoma elongatum* abundance, with maxima slightly more than twice minima, were observed. Other investigators (Maynard et al. 1975, Blackburn 1981), observing approximately 2-fold temporal variations in standing stock of some tropical-subtropical micronektonic groups, could not find any predictable seasonal cycle. In the central North Pacific, Hayward (1986) found a 2- to 3-fold variability in primary and secondary production that he attributed to meso-scale patchiness which, in turn, exceeded seasonal variation. If seasonal changes actually occur in the Gulf, their amplitudes are probably small enough to be masked by meso-scale patchiness generated by the unpredictable and ephemeral nature of the Loop Current (Leipper 1970, Maul 1977).

Reproductively mature fish and numerous juveniles were present during all periods indicating year-round breeding. Continual spawning has also been suggested for tropical myctophids (Oven 1985, Lisovenko & Prut'ko 1986). However, because the largest fish were always ripe females, and since no large females were observed with only small eggs or spent ovaries, and because ripe female abundance dropped abruptly after the median age at spawning, it is suggested that female *Gonostoma elongatum* spawn without regard for season and only once a lifetime.

Several medium-sized tropical-subtropical myctophids are also thought to die after spawning (Gjosæter & Kawaguchi 1980). Semelparity also has been suggested for sternoptychids *Maurolicus muelleri* (Clarke 1982, Kawaguchi & Mauchline 1987) and *Argyropelecus hemigymnus* (Kawaguchi & Mauchline 1987) as well as several bathypelagic fish (Childress et al. 1980). However, Fisher (1983) and we in our study encountered fish with ovaries containing bimodal egg sizes, so a second spawning is possible. Badcock & Merrett (1976) identified spent ovaries in eastern North Atlantic *Gonostoma elongatum* and suggested a second spawning for individuals larger than 238 mm SL. However, since this size exceeds our maximum size it is doubtful that a second spawning commonly occurs in the Gulf.

The microstructure of otoliths and their use in estimating age encompasses a vast body of literature, reviewed by Campana & Neilson (1985). These authors, concerned as to the exact periodicity of the formation of increments, suggested a unifying hypothesis consistent with the numerous and often contradictory age and growth studies they reviewed. An endogenously controlled circadian rhythm (24 h), entrained by photoperiod and potentially modified by environmental factors was postulated as the controlling factor of increment formation (Campana & Neilson 1985). Pannella (1980) found that fish exhibiting pronounced diel activities (e.g. vertical migration and distinct feeding periods) tend to have more distinct daily increments than non-migratory and non-cyclical feeding fish. Since *Gonostoma elongatum* is a strong daily migrator and displays a daily feeding chronology it is probable that the increments counted are daily in nature.

There was a close correspondence between the number of increments counted in recently metamorphosed individuals (60 at 23 mm SL) and an abrupt change in otolith growth (57 increments) that can be interpreted as a metamorphic check (Gjosæter 1987). Our counts suggest a 2 mo interval before metamorphosis in *Gonostoma elongatum*, a value which agrees well with that observed in other mesopelagic species (Methot 1981, Miya & Nemoto 1986, Gjosæter 1987), and serves as an indicator of the accuracy of the technique. Because of these observations we feel that primary rings are formed daily (i.e. 60 rings in 2 mo) in *G. elongatum* otoliths.

Our growth rate for *Gonostoma elongatum* is unique in that it is the first stomiiform growth rate estimated by using daily growth increments. *G. elongatum* was found to live less than 2 yr growing linearly at a rate of 0.34 mm d^{-1} to a maximum size of 225 mm SL. Linear growth has been reported in other stomiiforms (Childress et al. 1980, Miya & Nemoto 1987) as well as deep-living myctophids (Childress et al. 1980). Other authors (J. Gjosæter 1984, J. Gjosæter et al. 1984, H. Gjosæter 1987), using daily increment counts, estimated tropical myctophid growth rates ranging between 0.16 and 0.36 mm d^{-1} with lifespans of less than 1 yr. Clarke (1974), using length-frequency data, estimated a growth rate of 70 to 100 mm yr^{-1} (0.19 to 0.27 mm d^{-1}) for *Chauliodus sloani*, another large subtropical stomiiform (maximum size = 250 mm SL). Annual lifespans for small tropical-subtropical myctophids have been suggested by Clarke (1973) and Karnella & Gibbs (1977) while larger myctophids are believed to require more than a year to reach maximum size (Clarke 1973), which is similar to *G. elongatum*.

Diet analysis reveals: (1) *Gonostoma elongatum* is predominantly a predator on crustaceans, (2) diet shifts

to larger prey with growth, (3) both positive and negative food selection occurs, and (4) most feeding occurs in the epipelagic zone at night. The present results on diet composition confirm our earlier findings on *G. elongatum* (Hopkins & Baird 1975, 1977) and are in general agreement with those of Clarke (1978) and Gorelova (1981). Also, our data concur with Gorelova's (1981) in demonstrating a change in diet with increasing fish size. Our results show a proportional shift from copepods and ostracods in the diet of fishes < 50 mm SL, to euphausiids in older fish. Gorelova's (1981) results show a sequence wherein copepods and amphipods are dominant prey of juveniles < 50 mm SL, euphausiids at intermediate fish sizes and fish in the diets of the largest individuals (> 120 mm SL). Fish were infrequently encountered in our analyses in that only 24 occurred among a total of 1967 food items. However, only 15 *G. elongatum* > 130 mm SL were available to us, this being the size class most likely to prey on other fishes. Our data show strong positive prey selection by *G. elongatum* for ostracods and particularly for the copepod genus *Pleuromamma* and are in agreement with Gorelova's (1981) findings of an obvious strong negative selection for non-crustacean invertebrate prey. Also we found a cyclic feeding pattern as did Gorelova (1981), though Gorelova's results show stomachs were fullest at 19:00 to 23:00 h whereas we found maximum fullness later at night, at 23:00 to 5:00 h. Clarke (1978) was unable to discern diel periodicity in *G. elongatum* feeding off Hawaii, though this may have been a function of small sample size and the wide size range of his material.

As quantitative data were available for both *Gonostoma elongatum* (Fig. 4) and plankton (see 'Methods') we estimated predation impact of this abundant fish on one of its principal food items, *Pleuromamma* spp. These data come from the summer RV 'Columbus Ise-lin' cruises ('Methods'; Table 1). To do this we calculated the abundance (number m^{-2}) of various size classes of *G. elongatum* and *Pleuromamma* in the upper 1000 m. We then calculated the 'daily ration' of *Pleuromamma* for each size class of *G. elongatum* (Table 6). 'Daily ration' of *Pleuromamma* is here defined as the average number of these copepods in

the guts of fishes taken between 23:00 and 5:00 h when guts were fullest. *Pleuromamma* was selected not only because it is a major component of the diet but also because it can be quantitatively accounted for throughout the digestive tract. The metasomal spot characteristic of this genus is easily recognized and is refractory to digestion as is much of the exoskeleton and diagnostic mandibles of *Pleuromamma*. Ours is probably a minimal estimate of daily ration because some fishes may have been captured before they had fed, some of the prey eaten earlier in the evening may have been egested, and some prey could have been eaten and egested at depth during the day. Regarding the latter, our data do indicate guts were least full during the day which suggests most feeding occurs at night. Further, 'daily ration' computed by this method and with the Elliot & Persson (1978; see also Clarke 1978) gastric evacuation method gave comparable results for *Lamppanyctus alatus*, a myctophid with a similar feeding cycle (Hopkins & Baird 1985b) to *G. elongatum*.

Table 6 shows that *Gonostoma elongatum* removes 0.025 *Pleuromamma* $m^{-2} d^{-1}$ in the 1 to 6 mm size range. Predation impact is unequal over the size range of *Pleuromamma* in that greatest pressure falls on > 3 mm copepods, that is, on adult *P. abdominalis* and on copepodite Stage 5 and adult *P. xiphias*. For example, it would require 10^5 d for *G. elongatum* to remove the existing standing stock of 1 to 2 mm *Pleuromamma* (mostly adult *P. gracilis* and *P. piseki*) assuming no replacement, but only 208 d for removal of > 4 mm *Pleuromamma* (adult *P. xiphias*). If it is assumed that most feeding occurs after both predator and prey have reached their night-time depths (the fact that stomachs are fullest after 23:00 h suggests this is the case) then the data in Table 7 predict that vertical distribution of predation impact is uneven. Heaviest pressure occurs in the 150 to 200 m zone, especially on > 3 mm *Pleuromamma*.

Since the probable daily removal rate by post-larval *Gonostoma elongatum* is less than 0.1 %, this species alone has relatively little impact on *Pleuromamma*. However, the eastern Gulf, as characteristic of low latitude oceanic ecosystems, has high micronekton diversity and weak species dominance (e.g. Hopkins &

Table 6. *Gonostoma elongatum*. Removal rate of *Pleuromamma* spp. in upper 1000 m

	<i>Pleuromamma</i> length (mm)				Total
	1-2	2-3	3-4	> 4	
No. m^{-2}	730	202	94	27	1053
No. eaten m^{-2}	0.008	0.015	0.105	0.130	0.258
% eaten d^{-1}	0.001	0.007	0.112	0.481	0.025
Days required to consume standing stock	10^5	1.4×10^4	893	208	

Table 7. *Gonostoma elongatum*. Estimated removal rate by depth of *Pleuromamma* spp. in upper 250 m at night. Numbers are no. eaten 100 m⁻² in each depth zone

Depth (m)	<i>Pleuromamma</i> length (mm)				Total
	1-2	2-3	3-4	> 4	
25-50	0.39	0.29	0.45	0.10	1.23
50-100	0.09	0.08	0.20	0.07	0.44
100-150	0.21	0.43	2.37	1.54	4.55
150-200	—	0.61	6.00	7.49	14.10
200-250	0.10	0.12	1.40	3.78	5.46

Lancraft 1984). Our data and those of others indicate that *Pleuromamma* is an important prey item for a number of relatively abundant species of fishes (Merrett & Roe 1974, Hopkins & Baird 1977, 1981, 1985b, Clarke 1980, Gorelova 1981, Kinzer & Schulz 1985), shrimps (Foxton & Roe 1974, Heffernan & Hopkins 1981, Flock & Hopkins 1987), and even squids (e.g. *Pterygioteuthis gemmata*, *P. giardi* and *Histioteuthis margaritifera*; K. Passarella pers. comm.). The relatively small predation impact calculated for *G. elongatum*, then, may be typical for other abundant micronekton species feeding on this genus.

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LITERATURE CITED

- Backus, R. H., Craddock, J. E. (1982). Mesopelagic fishes in Gulf Stream cold-core rings. *J. mar. Res.* 40 (Suppl.): 1-20
- Backus, R. H., Craddock, J. E., Haedrich, R. L., Shores, D. L. (1970). The distribution of mesopelagic fishes in the Equatorial and Western North Atlantic Ocean. *J. mar. Res.* 28: 179-201
- Badcock, J. (1984). Gonostomatidae. In: Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Neisen, J., Tortonese, E. (eds.) *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris, p. 284-301
- Badcock, J., Merrett, N. R. (1976). Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30° N, 23° W, with developmental notes on certain myctophids. *Prog. Oceanogr.* 7: 3-58
- Bennett, J. L. (1986). Vertical distribution, abundance and feeding of the copepod genus *Pleuromamma* in the eastern Gulf of Mexico. Masters's thesis, University of South Florida
- Blackburn, M. (1981). Low latitude gyral regions. In: Longhurst, A. R. (ed.) *Analysis of marine ecosystems*. Academic Press, London, p. 3-29
- Bogdanov, D. V., Sokolov, V. A., Kromov, N. S. (1968). Regions of high biological and commercial productivity in the Gulf of Mexico and Caribbean Sea. *Oceanology* 8: 371-381
- Campana, S. E., Neilson, J.D. (1985). Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42: 1014-1032
- Childress, J. J., Taylor, S. M., Cailliet, G. M., Price, M. H. (1980). Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. *Mar. Biol.* 61: 27-40
- Clarke, T. A. (1973). Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull. U. S.* 71: 401-434
- Clarke, T. A. (1974). Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *Fish. Bull. U. S.* 72: 337-351
- Clarke, T. A. (1978). Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fish. Bull. U. S.* 76: 495-513
- Clarke, T. A. (1980). Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fish. Bull. U. S.* 78: 619-640
- Clarke, T. A. (1982). Distribution, growth and reproduction of the lightfish *Maurollicus muelleri* (Sternoptychidae) off South-East Australia. CSIRO Marine Laboratories Report No. 145 p. 1-10
- Davies, I. E., Barham, E. G. (1969). The Tucker opening-closing micronekton net and its performance in a study of the deep scattering layer. *Mar. Biol.* 2: 127-131
- Elliott, J. M., Persson, L. (1978). The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977-980
- El-Sayed, S. Z. (1972). Primary production and standing crop of phytoplankton. In: Bushnell, V. C. (ed.) *Chemistry, primary productivity, and benthic algae of the Gulf of Mexico*. Serial Atlas, Folio 22. American Geophysical Society, New York
- Fisher, R. A. (1983). Protandric sex reversal in *Gonostoma elongatum* (Pisces; Gonostomatidae) from the eastern Gulf of Mexico. *Copeia* 1983: 554-557
- Flock, M. E., Hopkins, T. L. (1987). The vertical distribution and feeding ecology of sergestid shrimps in the eastern Gulf of Mexico. *ABSTRACT 31G-01 EOS* 68: 1731
- Foxton, P., Roe, H. S. J. (1974). Observations on the nocturnal feeding of some mesopelagic decapod crustacean. *Mar. Biol.* 28: 37-49
- Gartner, J. V. Jr, Hopkins, T. L., Baird, R. C., Milliken, D. M. (1987). The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. *Fish. Bull. U. S.* 85: 81-98
- Gjosaeter, H. (1987). Primary growth increments in otoliths of six tropical myctophid species. *Biol. Oceanogr.* 4: 359-382
- Gjosaeter, J. (1984). Mesopelagic fish: a large potential resource in the Arabian Sea. *Deep Sea Res.* 31: 1019-1035
- Gjosaeter, J., Dayaratne, P., Bergstad, O. A., Gjosaeter, H., Sousa, M. I., Beck, M. I. (1984). Ageing tropical fish by

- growth rings in the otoliths. FAO Fish. Circ. No. 776, p. 1–54
- Gjosæter, J., Kawaguchi, K. (1980). A review of the world resources of mesopelagic fish. FAO Fish. Tech. Paper No. 193, p. 1–15
- Gorelova, T. A. (1981). Notes on feeding and gonad condition in three species of the genus *Gonostoma* (Gonostomatidae). J. Ichthyol. 25: 82–92
- Grey, M. (1964). Family Gonostomatidae. In: Olsen, Y. H. (ed.) Fishes of the western North Atlantic. Mem. Sears Fdn mar. Res. 1: 78–240
- Hayward, T. L. (1986). Variability in production and the role of disturbance in two pelagic ecosystems. In: Pierrot-Bults, A. C. (ed.) Pelagic biogeography. UNESCO Tech. Papers Mar. Sci. 49: 133–140
- Heffernan, J. J., Hopkins, T. L. (1981). Vertical distribution and feeding of the shrimp genera *Gennadas* and *Bentheogennema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. J. Crust. Biol. 1: 461–473
- Hopkins, T. L. (1982). The vertical distribution of zooplankton in the eastern Gulf of Mexico. Deep Sea Res. 29: 1069–1083
- Hopkins, T. L. (1987). The midwater food web in McMurdo Sound, Ross Sea, Antarctica. Mar. Biol. 96: 93–106
- Hopkins, T. L., Baird, R. C. (1975). Net feeding in mesopelagic fishes. Fish. Bull. U. S. 73: 908–914
- Hopkins, T. L., Baird, R. C. (1977). Aspects of the feeding ecology of oceanic midwater fishes. In: Andersen, N., Zahuranec, B. J. (eds.) Proc. Int. Symp. Prediction of sound scattering in the ocean. Plenum Press, New York, p. 325–360
- Hopkins, T. L., Baird, R. C. (1985a). Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. Bull. mar. Sci. 36: 160–277
- Hopkins, T. L., Baird, R. C. (1985b). Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. Biol. Oceanogr. 3: 285–313
- Hopkins, T. L., Lancaft, T. M. (1984). The composition and standing crop of mesopelagic micronekton at 27° N 86° W in the eastern Gulf of Mexico. Contr. mar. Sci. 27: 143–158
- Karnella, C., Gibbs, R. H., Jr (1977). The lanternfish *Lobianchia dollfleitini*: an example of the importance of life-history information in prediction of oceanic sound scattering. In: Andersen, N. R., Zahuranec, B. J. (eds.) Oceanic sound scattering prediction. Plenum Press, New York, p. 361–379
- Kawaguchi, K., Mauchline, J. (1987). Biology of sternoptychid fishes in the Rockall Trough, northeastern Atlantic Ocean. Biol. Oceanogr. 4: 99–120
- Kinzer, J., Schulz, K. (1985). Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. Mar. Biol. 85: 313–322
- Leipper, D. F. (1970). A sequence of current patterns in the Gulf of Mexico. J. geophys. Res. 75: 637–657
- Lisovenko, L. A., Prut'ko, V. G. (1986). Reproductive biology of *Diaphus suborbitalis* (Myctophidae) in the equatorial part of the Indian Ocean. I. Nature of oogenesis and type of spawning. J. Ichthyol. 26: 47–58
- Loeb, V. J. (1979). Larval fishes in the zooplankton community of the North Pacific Central Gyre. Mar. Biol. 53: 173–191
- Maul, G. A. (1977). The annual cycle of the Gulf Loop Current. Part I: Observations during a one-year time series. J. mar. Res. 35: 23–47
- Maynard, S. D., Riggs, F. D., Walters, J. F. (1975). Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. Fish. Bull. U.S. 73: 726–736
- Merrett, N. R., Roe, H. S. J. (1974). Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. 28: 115–126
- Method, R. D., Jr (1981). Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobranchius leucopsarus*. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 424–431
- Miya, M., Nemoto, T. (1986). Life history and vertical distribution of the mesopelagic fish *Cyclothone alba* (Family Gonostomatidae) in Sagami Bay, Central Japan. Deep Sea Res. 33: 1053–1068
- Miya, M., Nemoto, T. (1987). Some aspects of the biology of the micronektonic fish *Cyclothone pallida* and *C. acclimens* (Pisces: Gonostomatidae) in Sagami Bay, Central Japan. J. oceanogr. Soc. Jap. 42: 473–480
- Mukhacheva, V. A. (1972). Material on taxonomy, distribution and biology of the species of *Gonostoma* (Pisces, Gonostomatidae). Tr. In-ta. Okeanol. Akademiia Nauk, SSSR 93: 205–249
- Oven, L. S. (1985). Comparative analysis of reproductive biology of some lanternfishes (Myctophidae) from the tropical zone of the Atlantic Ocean. J. Ichthyol. 25: 50–60
- Pannella, G. (1980). Growth patterns in fish sagittae. In: Rhoads, D. C., Lutz, R. A. (eds.) Skeletal growth of aquatic organisms. Biological records of environmental change. Plenum Press, New York, p. 519–624