

Food and feeding activity of micronektonic fish, Gonostomatidae, from meso- and upper bathypelagic layers in the northeastern Atlantic

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北東 大西洋에서의 中深層 및 上部漸深層産
앨통이과 魚類 마이크로넥톤의 攝餌樣式

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Abstract

Diet and feeding patterns of 10 species of gonostomatid fish in the Rockall Trough and Porcupine Seabight, northeastern Atlantic, were investigated as a part of studies analyzing the meso- and upper bathypelagic micronektonic fish communities in these two areas. Copepods were the major food organisms, composing more than 72% in both areas, and ostracods the second most abundant prey organisms (>13%). The results of stomach content analyses reveals that most of gonostomatids, including two important species, *Cyclothone braueri* and *C. microdon*, feed continuously regardless of light cycle and a little at a time. The gonostomatids appear to be planktivores that consume small-sized prey; relative size of most preys was about one-tenth of fish length. These feeding patterns could be an adaptive characteristic of fish living in great deep water where the food items are scarcely present. In general there are no considerable inter- and intraspecific differences, not to mention regional differences, in the feeding of the gonostomatids at both stations except the large specimen of *Gonostoma elongatum* fed fish. Thus several coexisting species of the gonostomatid fish utilize the same resources, showing competitive relationships.

요약: 북동대서양 Rockall Trough (수심 약 3,000 m) 과 Porcupine Seabight (수심 약 4,000m) 의 중심층 및 상부 점심층에서 채집된 어류 micronekton 중, 우점생물인 Gonostomatidae 과 10개 종에 대해 먹이 및 식성을 조사했다. 양해역 모두에서 2 종류의 micronekton인 *Cyclothone braueri* 와 *C. microdon* 이 우점종이었으므로, 이 2 종류에 대해서는 상세히 기술했다. 이들 생물은 일정한 섭이시간대가 없이 비주기적으로 섭이했고, 한번에 조금씩 섭이하는 경향을 보였으며, 주요 먹이생물은 요각류(약 72% 이상) 및 패충류(약 13% 이상)로서 대부분이 어체장의 10% 미만인 소형생물이었다. 이러한 경향은 먹이생물이 풍부치 못한 환경인 심층에서의 서식에 매우 적합한 적응 현상이라고 생각된다. 시식층과 먹이생물을 둘러싼 중간 관계가 역시 논의 되었다.

INTRODUCTION

Gonostomatid fish are the most important components of the meso- and upper bathypelagic micronektonic fish communities in the Rockall Trough and Porcupine Seabight, northeastern Atlantic.

Although there have been many studies on

taxonomy and distribution of micronektonic fish in the northeastern Atlantic, a few studies have been conducted on the food and food habits of these fish (Gjosæter, 1973; Merrett and Roe, 1974; Kawaguchi and Mauchline, 1981; Roe and Badcock, 1984), and thus little is known of their role and importance in the pelagic food web. Some authors have examin-

ed feeding habits of mesopelagic fishes during the same diel period at a single depth (Merrett and Roe, 1974) and at four depths of 100, 250, 450 and 600 m (Roe and Badcock, 1984). These studies, however, have been achieved in one area and only into the the mesopelagic layer.

This paper presents results of stomach analysis of ten gonostomatid species in the Rockall Trough and Porcupine Seabight, as a part of a series of papers analyzing the meso- and upper bathypelagic micronektonic fish communities.

MATERIALS AND METHODS

The materials were collected in the Rockall Trough (St. 10105, sounding approximately 3,000 m) and Porcupine Seabight (St. 10115, sounding about 4,000 m) during RRS Discovery Cruise 105 (August/September, 1979) as shown in Figure 1. An acoustically controlled opening and closing net system, in which RMT1 (mesh 0.33 mm for zooplankton) and RMT8 (mesh 4.5 mm for micronekton) were combined in the same framework (Roe and Shale, 1979; Roe et al., 1980). The top of the 900 m water column was sampled throughout the day and night in contiguous 100 m strata for an hour, while below 900 m samples were collected uncyclically in the contiguous 200 m

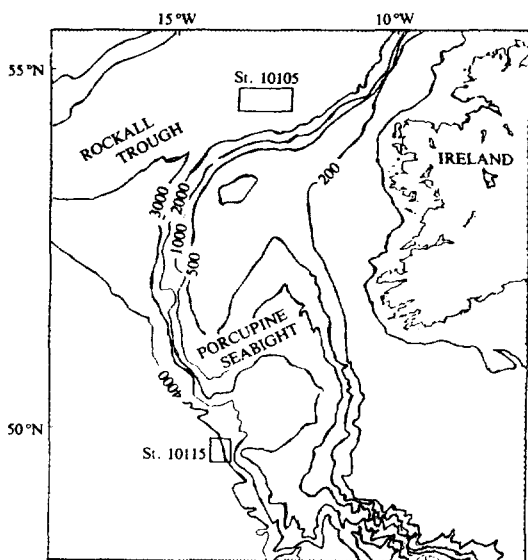


Fig. 1. Station positions in the Rockall Trough and Porcupine Seabight.

strata for two hours. The maximum depth of fishing at St. 10105 and St. 10115 were 1,900 m and 1,500 m, respectively. Observations on the gonostomatid fish were based only on RMT8M samples. Zooplankton caught by RMT1M was not used for examining of food selectivity of fish due to too wide depth ranges of fishing at each sampling stratum.

Study of feeding was focused mainly on the two most abundant species, *Cyclothone braueri* and *C. microdon*. Over 20 specimens per haul were examined at random, or as many as possible samples when less than 20 were caught. The stomachs of 480 specimens were dissected from the formalin-preserved specimens. The amount of food (state of fullness) was assessed visually as follows: stage 0, empty; stage 1, partly full ($< \frac{1}{2}$ full); stage 2, relatively full ($\leq \frac{1}{2}$ full); stage 3, full. Stages of digestion of the stomach contents were distinguished depending upon the conditions of prey; stage A, little digested; stage B, $\geq \frac{1}{2}$ identifiable; stage C $< \frac{1}{2}$ identifiable;

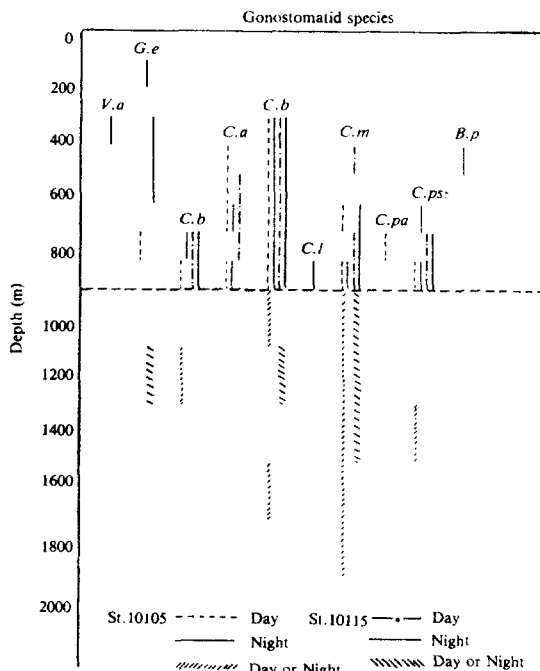


Fig. 2. Gonostomatidae. Depths of species occurrence in the Rockall Trough (st. 10105) and Porcupine Seabight (st. 10115). *V.a.*; *Vinciguerria attenuata*, *G.e.*; *Gonostoma elongatum*, *G.b.*; *G. bathyphilum*, *C.a.*; *Cyclothone alba*, *C.b.*; *C. braueri*, *C.l.*; *C. livida*, *C.m.*; *C. microdon*, *C.pa.*; *C. pallida*, *C.ps.*; *C. pseidopallida*, *B.p.*; *Bonapartia pedaliota*.

Table 1. Gonostomatidae. Percentage composition of the stages of stomach fullness and digestion for each species in all the haul from the Rockall Trough (RT, 10-1900m) and Porcupine Seabight (PS, 10-1500m), northern north-east Atlantic. Stage 0 to 3 and stage A to D, see text for explanation.

Species	Area	Day								Night										
		No. of fish	Fullness				Digestion				No. of fish	Fullness				Digestion				
			0	1	2	3	A	B	C	D		0	1	2	3	A	B	C	D	
<i>Vinciguerria attenuata</i>	RT	0									0									
	PS	0									1	100								100
<i>Gonostoma elongatum</i>	RT	1	100					100			1	100								
	PS	3	66.7	33.3						3	33.3	66.7					50.0			50.0
<i>G. bathyphilum</i>	RT	1	100							2	50.0	50.0								100
	PS	8	50.0	50.0						15	40.0	60.0								100
<i>Cyclothone alba</i>	RT	7	57.1	42.9				33.3		3	33.3	66.7								50.0
	PS	3	66.7	33.3						0										50.0
<i>C. braueri</i>	RT	105	78.1	21.9				30.4	8.7	60.9	102	83.3	15.7	1.0			11.8	5.9		83.3
	PS	121	73.6	25.6	0.8			40.6	3.1	56.3	115	80.0	20.0			4.4	43.5	17.4		34.7
<i>C. livida</i>	RT	0									6	33.3	66.7				25.0			75.0
	PS	0									0									
<i>C. microdon</i>	RT	80	62.5	36.3	1.2			30.0	13.3	56.7	98	67.4	30.6	2.0			18.8	31.2		50.0
	PS	145	61.4	38.6				26.8	37.5	35.7	42	50.0	50.0				42.9	23.8		33.3
<i>C. pallida</i>	RT	2	50.0	50.0						100	0									
	PS	0									0									
<i>C. pseudopallida</i>	RT	1	100					100			3	66.7	33.3							100
	PS	2	50.0	50.0						100	4	75.0	25.0							100
<i>Bonapartia pedaliota</i>	RT	1	100								0									
	PS	0									0									
Total	RT	198	69.7	29.8	0.5			31.7	10.0	58.3	215	73.5	25.1	1.4			15.8	21.0		63.2
	PS	282	66.3	33.3	0.4			29.5	23.2	47.3	180	68.3	31.7			1.8	35.1	15.8		47.3

stage D, almost unidentifiable.

The contents were identified and the number of organisms was estimated. Because of the unidentifiable fraction, however, accurate assessment of numbers was impossible on many occasions. For example, copepod remains were frequently fragmentary and consequently the number of prey in each stomach may be underestimated. For convenience, night included dusk haul (St. 10105, 900-1,100 m).

RESULTS

General pattern

The species of gonostomids were identified and depths of appearance of each species in both areas are shown in Figure 2. The results

of the stages of fullness and digestion of the stomach contents by day and night are given in Table 1. At the Rockall Trough station 70% of 198 gonostomatid specimens examined had empty stomachs by day and about 74% at night. At the Porcupine Seabight station 66% of 282 specimens dissected was empty by day and 68% at night. Most of the fed stomachs were less than half full. More than 47% of fed stomach contents contained almost unidentifiable food of digestion stage D, and 16-35% were in stage B in both areas.

Table 2 shows the frequency of occurrence of prey in fed stomachs of all the gonostomatid fish examined throughout all the combined survey depths. Copepods were the most frequently encountered prey, forming more than 72% of stomach contents in both

Table 2. Gonostomatidae. Comparison (%) of stomach contents Obtained from 2 stations to show inter-regional variation in diet.

Prey group	Rockall Trough			Porcupine Seabight		
	Day n = 30	Night n = 31	D + N n = 61	Day n = 50	Night n = 40	D + N n = 90
Copepoda	66.7	77.4	72.1	84.0	82.5	83.3
Ostracoda	26.7	22.6	24.6	16.0	10.0	13.3
Chaetognatha	6.6	—	3.3	—	—	—
Pteropoda	—	—	—	—	5.0	2.3
Fish	—	—	—	—	2.5	1.1

Table 4. *Cyclothone microdon*. Analyses of stomach contents of fish examined at each depth by day and night. Percentage composition of stomach contents shows the proportion of occurrence to fish with food.

Depth (m) Day/Night	Area	400-500		600-700		700-800		800-900		900-1100		1100-1300		1300-1500		1500-1700		1700-1900		Total No.			
		D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	All	
No. examined	RT			2				16	4		37		30		27		30		32		80	98	178
	PS	1				4	3	5	35	33	40		36	30		30					145	42	187
No. with food(%)	RT			100				31	50		41		33		19		33		41		38	34	35
	PS	100				25	33	80	54	49	30		39	30							39	50	41
SL (mm)	RT			32				33	29		30		34		38		42		44		41	34	37
	PS	34				32	40	36	32	33	36		34		37						35	33	34
Stomach contents																							
% < 1/2 full	PS			100				100	100		100		80		100		90		100		97	94	95
	PS	100				100	100	100	100	100		100		100							100	100	100
% > 1/2 identifiable																							
	RT			0				60	0		20		20		20		30		23		30	19	24
	PS	0				100	0	25	63	44	17		7		0						27	43	31
Prey group																							
Copepoda	RT					1			3	2		9		3		1	1		2		6	16	22
	PS							2	16	13		2		6							24	15	39
Ostracoda	RT								1			3		1		1	3		2		6	5	11
	PS																				8	1	9
Chaetognatha	RT						1	1	2			3		2					2		2		2
	PS																						
Identifiable species																							
<i>Bathycalanus princeps</i>													1									1	1
<i>Metridia</i>																			1			1	1
<i>Pleuromamma</i> sp.					1		2	16	12		3	3									19	18	37
<i>P. robusta</i>									1												1		1
<i>Heterorhabdus</i>									1												1		1
<i>Candacia</i>												4									1		4
<i>Eucalanus</i>													1								1		1
<i>Undeuchaeta plumosa</i>									1												1		1
<i>Oncaea</i>														1							1		1
<i>Conchoecia borealis</i>										2							1		1		4		4
<i>C. discovery</i>																1					1		1
<i>C. daphnoides</i>									1										1		2		2
<i>C. magna</i>											1										1		1
<i>C. rhynchena</i>									1												1		1
<i>C. stigmatica</i>																	2				2		2

Two individuals of chaetognaths were also found in the stomach from the great deep water specimen (1,700-1,900 m depth). The small-sized *C. microdon* (19 mm SL) has been eaten by large *Pleuromamma* (relative size, 15% of fish length) and large copepods, *Bathycalanus princeps* (5.5 mm, relative size, 15% of fish length) was found in the stomach of the individual of 37 mm SL. However, the relative sizes of intact preys were an average of 8% of fish length, ranging from 2% to 15%.

Remaining species

Species, other than the above two species, appeared infrequently. A summary of the stages of fullness and digestion of the stomach contents for all the combined survey depths for each species is given in Table 1.

One specimen of *Gonostoma elongatum* was caught by day and one by night in the Rockall Trough, and only one specimen (33 mm SL) caught during the daytime (700-800 m) had stage 1 of fullness containing one

Pleuromamma sp. In the Porcupine Seabight one fish, 176 mm SL, contained *Cyclothone braueri* (27 mm SL) in the stomach contents at night (500-600m). Relative length of *C. braueri* eaten was 15% of *G. elongatum*, while small organisms of two pteropods were found in this species of 191 mm SL at night (400-500 m).

Gonostoma bathyphilum was more abundant in the Porcupine Seabight than in the Rockall Trough. There were no identifiable preys (stage D of digestion) in stomach contents at two stations although more than one half of specimens examined had some contents in stomachs (stage 1 of fullness).

Although ten specimens and three of *Cyclothone alba* in the Rockall station and Porcupine station respectively were dissected, only five specimens had stage 1 of fullness. In the latter station any one prey was not identified but in the former station one *Pleuromamma* sp. was recognized by day (800-900 m) and one by night (600-700m); relative size 11% of the fish length.

Six specimens of *Cyclothone livida* were

caught from only one haul of 800-900 m where one *Pleuromamma* sp. and one ostracod were identified from just one fish stomach. The stomach contents of the other specimens could not be recognized in spite of four specimens having stage 2 of stomach fullness.

Ten specimens of *Cyclothone pseudopallida* were dissected in both areas but only one specimen by day (800-900 m), in the Rockall station, had one identifiable prey, *Pleuromamma* sp. (relative size 7% of fish length). On the other hand any prey from the stomachs of *Vinciguerria attenuata*, *Cyclothone pallida*, and *Bonapartia pedaliota* could not be identified.

DISCUSSION

Most of the early work on the feeding of mesopelagic micronektonic fish has been reviewed by Hopkins and Baird (1977) and more recently the food of mesopelagic fish has been studied in some detail (Clark, 1978, 1980, 1982; Gorelova and Tseitlin, 1979; Kawaguchi and Mauchline, 1981; Roe and Badcock, 1984).

Direct evidence of net feeding is not available here. A low level of net feeding may have been interpreted as natural predation, and the presence of fresh food in stomachs could have been considered to be active feeding at a time when the fish were naturally only digesting previously eaten prey (Roe and Badcock, 1984). In the present study most stomachs of the gonostomatids were not $>1/2$ full and even though they had some stomach contents the

number of eaten prey in one stomach was small in number. Furthermore, the mesh size of the RMT8M was 4.5 mm, and the available prey could escape from the net before being eaten.

Although the interpretation of cyclic feeding from the presence or absence of fish and/or digested prey is not easy, all the gonostomatid fish at the present areas feed at anytime irrespective of feeding chronology and a little at a time. For a long time the reasons for cyclic feeding have been considered that diel migration is closely associated with feeding. Feeding cycles in many migrants, which rise to depths shallower than 200 m at night, are apparent and varied feeding patterns in species which remained at greater depths are also found (Hopkins and Baird, 1977; Go, 1979). However, in the present study all the deep water gonostomatids have represented only one feeding pattern irrespective of light cycle.

Near Hawaii the large gonostomatids like *Diplophos taenia* ate micronekton but appeared to feed in the same manner as the small individuals and species (Clark, 1982). In general there are no considerable inter- and intra-specific differences, not to mention regional differences, in the feeding of gonostomatids in both the Rockall Trough and Porcupine Seabight although the large specimens of *Gonostoma elongatum* feed on fish. Table 5 summarizes vertically distributional and trophical relationships between gonostomatid fish in all the hauls in the present study. Thus, although they feed at different depths, several coexisting species of fish

Table 5. Vertically distributional and trophical relationships between gonostomatid fish in all the haul from the Rockall Trough and Porcupine Seabight. Reading cross the table, the relationships between each species on dwelling layer (As-almost same layer, Ps-partial same layer, Ud-utterly different layer) and food (C-competition, E-enemy, V-victim) are seen. Empty column to food shows no data, and question mark, uncertain relationship to each other.

Species	V.a	G.e	G.b	C.a	C.b	C.l	C.m	C.pa	C.ps	B.p.
<i>Vinciguerria attenuata</i>	—	Ps,?	Ud	Ud	Ps,?	Ud	Ud	Ud	Ud	Ud
<i>Gonostoma elongatum</i>	Ps,?	—	Ps,?	Ps,C	As,C,E	Ps,C	As,C	Ps,?	As,C	Ps,?
<i>G. bathyphilum</i>	Ud	Ps,?	—	Ps,?	Ps,?	Ps,?	Ps,?	Ps,?	As,?	Ud
<i>Cyclothone alba</i>	Ud	Ps,C	Ps,?	—	Ps,C	Ps,C	Ps,C	Ps,?	Ps,C	Ps,?
<i>C. braueri</i>	Ps,?	As,C,V	Ps,?	Ps,C	—	Ps,C	As,C	Ps,?	As,C	Ps,?
<i>C. livida</i>	Ud	Ps,C	Ps,?	Ps,C	Ps,C	—	Ps,C	Ud	Ps,C	Ud
<i>C. microdon</i>	Ud	As,C	Ps,?	Ps,C	As,C	Ps,C	—	Ps,?	As,C	Ps,?
<i>C. pallida</i>	Ud	Ps,?	Ps,?	Ps,?	Ps,?	Ud	Ps,?	—	Ps,?	Ud
<i>C. pseudopallida</i>	Ud	As,C	As,?	Ps,C	As,C	Ps,C	As,C	Ps,?	—	Ud
<i>Bonapartia pedaliota</i>	Ud	Ps,?	Ud	Ps,?	Ps,?	Ud	Ps,?	Ud	Ud	—

are utilizing the same resources, revealing competitive relationship.

The diets of the planktivorous gonostomatids, except *G. elongatum*, were similar to each other. As *Vinciguerria* heavily grazed *Oncaea* sp. and *Pleuromamma gracilis* (Clark, 1980, 1982), certain zooplankton (e.g., *Pleuromamma* sp. and *Conchoecia* sp.) also appear to be a little heavily eaten by *C. braueri* and *C. microdon*, and there is interspecific overlap in diet, especially *Pleuromamma*. It indicates the possibility that this fish often feeds on patches or aggregation of prey types and *Pleuromamma* were probably more visible than other zooplankton in appropriate size range. In addition to the possibility, where digestion was advanced, individual copepods of the genus *Pleuromamma* could still be counted as their black thoracic spots were seemingly resistant to digestion. However, it is not distinct that this provided corroborative evidence on feeding selectivity. *V. nimbaria* stomachs tend to be either quite full or nearly empty throughout the day, suggesting encounters with patches of prey as well (Clark, 1978).

The prey size of micronektonic fish tends to be large with increasing fish length (Okiyama, 1971; Hopkins and Baird, 1973; Gorelova, 1975; Go, 1979). Most of gonostomatids appear to be essentially planktivores that consume small sized prey, and the large specimens usually contained several relatively small size prey as well; relative size of most items was ca. 10% of fish length with a few 15%. As many midwater species resident (Baird, 1971; Baird et al, 1975), such feeding patterns involving a diet of small prey items and uncyclical feeding may be an important adaptable characteristic in the poor food environment of the meso- and upper bathypelagic layer.

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