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Distribution of Myctophidae (Pisces, Myctophiformes) during the four seasons in the mid North Atlantic

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Abstract

The distribution, temperature, and size ranges of 60 species of myctophids in the North Atlantic between 55°N and 24°N along approximately 30°W are recorded for the four seasons. The general zoogeography and migration is discussed. Faunal groups of species, faunal borders, and transition zones near 50°N, 41°N, and 29°N for myctophids are distinguished and discussed.

Résumé

Ont été enregistrées, pendant les quatre saisons, la distribution, les températures et les limites de la taille pour 60 espèces de Myctophidés dans l'Atlantique Nord entre 55°N et 24°N, approximativement à 30°O. Sont discutés des aspects tels que la distribution générale et les migrations. Sont distingués des groupements d'espèces, des limites faunistiques, et des zones de transition pour les Myctophidés au voisinage de 50°N, 41°N et 29°N; tous ces aspects sont discutés.

Introduction

This paper deals with the Myctophidae collected by the Amsterdam Mid North Atlantic Plankton Expeditions 1980, 1981, 1982, and 1983. The material was collected along approximately 30°W between 55°N and 24°N and along 25°N between 20°W and 30°W in the upper 1000 m with the combined Rectangular Midwater Trawl (RMT 1 + 8), in the periods April 11–May 2, 1980; September 13–October 16, 1981; February 9–21, 1982, and May 29–June 18, 1983. The cruise of 1980 is considered a spring cruise, that of 1983 a summer, of 1981 an autumn, and of 1982 a winter cruise. The hauls were usually made during each season at nearly the same localities. Some additional open net hauls from the upper 170 m and discrete samples down to 2000 m were used. For locality data, hydrographic measurements, and description of the gear, see Van der Spoel (1981, 1985) and Van der Spoel & Meerding (1983).

Myctophidae, known as rather strictly bound to marine provinces and water masses (Backus et al., 1965; Backus & Craddock, 1977), were studied to obtain indications of biogeographic boundaries in the area investigated. Although the sampling programme was not suitable to study diurnal vertical migration, for some species indications of such a migration could be reported. In total 477 myctophid specimens, from a total of 14135, could not be identified and are left out of consideration here. Mainly Bolin (1955), Gibbs et al. (1971), Napfaktitis (1968, 1975), Nafpaktitis & Paxton (1968), Nafpaktitis et al. (1977), and Hulley (1984) were used for identification.

Remarks on some of the species

Species are listed below with comments, in alphabetic order; for data on the material and localities see Table I and Figs. 1–2.

Benthosema glaciale. In spring this boreo-arctic species penetrates as far south as 35°N. From

Table I. Material collected (* = twilight samples excluded; Sp. = spring, Su. = summer, A. = autumn, W. = winter).

Species	Season	Temp. (°C) range day time*	Temp. (°C) max.	Size range (cm)	Depth day range*	Depth night range*	*N.* of specimens
NORTH of 50°N							
Protomyctophum arcticum	Sp.	5.00 – 6.90	10.9	1.33 – 4.09	40 – 995	215 – 400	181
(Lütken, 1892)	Su.	5.35 – 10.05	10.1	1.60 – 4.39	200 – 400	–	344
	A.	4.15 – 9.50	11.9	1.60 – 5.29	300 – 1000	–	159
Benthosema glaciale	Sp.	4.45 – 14.20	17.2	1.50 – 6.61	265 – 1010	0 – 400	1488
(Reinhardt, 1837)	Su.	4.45 – 12.90	15.5	1.10 – 7.04	200 – 995	0 – 105, 1000 – 1750	1243
	A.	4.15 – 11.95	15.9	1.15 – 6.79	300 – 1020	0 – 100	2868
Myctophum punctatum	Sp.	6.70 – 10.40	15.5	1.01 – 9.01	440 – 1005	40 – 100	17
Rafinesque, 1810	Su.	5.95 – 10.05	18.0	1.02 – 6.08	200 – 398, 500 – 995	0 – 105	196
	A.	6.90	17.5	1.99 – 5.95	500 – 1020	0 – 100	57
Notoscopelus kroeyeri	Sp.	4.45 – 5.95	10.9	5.30 – 13.64	265 – 1010	40 – 100, 210 – 310	12
(Malm, 1861)	Su.	9.45 – 11.90	21.4	1.47 – 6.54	300 – 5403	0 – 150	246
	A.	4.75 – 9.50	9.8	3.75 – 6.50	300 – 400	0 – 100	19
BETWEEN 50° AND 41°N							
Notoscopelus bolini	Sp.	9.85 – 10.50	10.5	2.20 – 2.55	440 – 1000	–	12
Nafpaktitis, 1975	Su.	–	20.3	2.23 – 6.72	–	0 – 105	36
	A.	7.25 – 10.00	15.2	6.00 – 6.45	405 – 500	55 – 100	7
Lampanyctus crocodilus	Sp.	5.00 – 9.85	13.5	4.66 – 9.06	480 – 1005	50 – 200	9
(Risso, 1810)	Su.	–	16.8	2.20 – 3.21	–	0 – 210	56
	A.	9.70 – 10.25	15.2	3.10 – 12.50	460 – 1010	45 – 100, 425 – 855	13
Lampanyctus macdonaldi	Sp.	5.00	5.0	12.88	290 – 995	–	1
(Goode & Bean, 1896)	Su.	–	16.9	2.33 – 6.60	–	45 – 150	18
	A.	–	15.9	4.05 – 7.80	–	0 – 190	2
BETWEEN 41° and 29°N							
Lampadena chavesi	Sp.	–	18.2	2.43 – 5.77	–	90 – 205	5
Collett, 1905	Su.	9.65	19.2	2.15 – 6.66	7.52 – 1005	55 – 200	7
	A.	9.80 – 11.75	19.4	2.10 – 2.90	490 – 1175	50 – 230, 270 – 395	8
	W.	–	15.3	1.40 – 3.69	–	195 – 302	9
Lampanyctus festivus	Sp.	10.25	18.2	3.51 – 8.11	500 – 1000	45 – 300	5
Tåning, 1928	Su.	–	20.3	3.05 – 8.02	–	0 – 50, 98 – 200	6
	A.	–	19.8	2.60 – 7.95	–	45 – 300	88
	W.	–	19.2	1.32 – 5.23	–	40 – 305	41
BETWEEN 50° and 29°N							
Lampanyctus pusillus	Sp.	4.45 – 10.50	19.5	1.49 – 3.98	480 – 1010	40 – 205	293
(Johnson, 1890)	Su.	8.60 – 11.90	20.3	1.19 – 3.99	400 – 1000	0 – 210	691
	A.	6.90 – 12.25	21.9	1.40 – 3.80	385 – 1020	0 – 230	240
	W.	–	15.3	2.02 – 3.93	–	0 – 150	22
Diaphus rafinesquei	Sp.	10.50 – 14.20	17.9	1.88 – 8.52	280 – 1000	40 – 1000	203
(Cocco, 1838)	Su.	9.95 – 11.90	19.0	1.99 – 8.05	300 – 503	0 – 528	101
	A.	6.90 – 12.85	15.2	1.61 – 8.59	310 – 1020	55 – 100, 195 – 1050	128
	W.	10.30 – 14.75	15.6	1.61 – 8.30	400 – 980	195 – 1010	39
Diaphus holti	Sp.	7.75	16.0	2.42 – 5.00	205 – 300	50 – 320	57
Tåning, 1918	Su.	13.70	14.9	3.28 – 4.65	200 – 300	205 – 305	23
	A.	4.75 – 14.10	19.8	1.06 – 4.90	300 – 570	0 – 230	25
	W.	–	18.6	1.80 – 4.18	–	0 – 190	4
Diaphus metopoclampus	Sp.	10.20 – 13.50	15.0	1.16 – 6.88	360 – 1000	265 – 1130	19
(Cocco, 1829)	Su.	11.90 – 11.90	14.4	2.04 – 7.06	400 – 503	280 – 400	25
	A.	10.00 – 12.25	12.5	3.05 – 4.85	385 – 565	–	10
Hygophum hygomi	Sp.	10.35 – 13.70	19.5	1.45 – 4.36	280 – 1000	40 – 205	24
(Lütken, 1892)	Su.	10.00	21.7	1.55 – 4.26	494 – 1000	0 – 105	17
	A.	9.15	9.2	3.80 – 4.50	570 – 1000	–	2
	W.	–	15.3	1.53 – 1.76	–	0 – 10	5

Table I. Continuation.

Species	Season	Temp. (°C) range day time*	Temp. (°C) max.	Size range (cm)	Depth day range*	Depth night range*	*N.* of specimens
Notolychnus valdiviae	Sp.	10.35 – 13.90	21.4	0.99 – 2.31	280 – 1000	40 – 220	147
(Brauer, 1904)	Su.	10.00 – 13.70	21.7	0.99 – 2.30	300 – 1000	0 – 205, 300 – 400	161
	A.	6.90 – 11.75	21.1	1.30 – 2.50	385 – 1020	30 – 105	21
	W.	–	19.2	1.38 – 2.25	–	40 – 115	22
Gonichthys coccoi	Sp.	10.25 – 13.30	19.1	1.85 – 4.72	420 – 1000	45 – 205	12
(Cocco, 1829)	Su.	9.90 – 11.90	20.3	1.91 – 4.60	400 – 1503	0 – 205	10
	A.	10.25 – 12.25	18.7	2.00 – 4.40	460 – 870	110 – 195	12
	W.	–	18.6	2.00 – 2.78	–	80 – 190	5
Lampanyctus ater	Sp.	9.85 – 10.40	16.5	1.15 – 10.90	440 – 1000	45 – 100	71
Tåning, 1928	Su.	9.45 – 10.00	20.7	1.74 – 9.55	300 – 398, 494 – 1000	45 – 400	55
	A.	6.90 – 10.25	19.8	3.40 – 10.80	460 – 1020	45 – 300, 425 – 855	36
	W.	–	18.6	0.89 – 3.10	–	80 – 305	11
Lampanyctus intricarius	Sp.	–	16.5	5.15 – 5.95	–	85 – 220	4
Tåning, 1928	Su.	10.00	18.1	2.45 – 5.04	494 – 1000	50 – 98	5
	A.	4.15 – 6.90	17.5	3.10 – 7.59	400 – 1020	0 – 230	8
	W.	10.30	10.3	2.13 – 2.82	505 – 980	–	4
SOUTH OF 50° NORTH							
Symbolophorus veranyi	Sp.	10.25 – 10.50	14.0	2.19 – 9.81	500 – 1000	50 – 100, 265 – 430	7
(Moreau, 1888)	Su.	–	20.3	2.28 – 10.85	–	0 – 100	51
	A.	–	19.3	2.40 – 8.90	–	40 – 105	10
Lobianchia dofleini	Sp.	7.75 – 14.20	21.5	0.97 – 4.16	205 – 1000	0 – 320	400
(Zugmayer, 1911)	Su.	4.90 – 16.70	21.7	1.05 – 3.92	295 – 1000	0 – 205	448
	A.	9.50 – 14.10	19.8	1.45 – 3.95	205 – 870	0 – 230	225
	W.	14.75	19.2	1.54 – 3.55	110 – 430	40 – 115	28
Bolinichthys indicus	Sp.	9.80 – 11.00	21.4	1.30 – 4.04	440 – 1090	40 – 205	174
Nafpaktitis & Nafpaktitis,	Su.	9.65 – 10.00	20.7	1.45 – 4.55	494 – 1005	45 – 305	137
1969	A.	9.15 – 11.75	21.1	1.15 – 3.90	490 – 1005	30 – 230	83
	W.	–	19.2	1.27 – 3.84	–	40 – 305	54
Lobianchia gemellarii	Sp.	9.80 – 15.10	21.5	1.20 – 8.20	280 – 1510	40 – 205, 265 – 505	96
(Cocco, 1838)	Su.	8.60 – 16.70	21.7	1.36 – 8.22	390 – 518	0 – 305	50
	A.	6.90 – 19.15	23.0	1.80 – 6.90	310 – 1020	30 – 100, 195 – 410	33
	W.	13.85	18.6	1.22 – 3.84	400 – 490	40 – 190	29
Electrona rissoi	Sp.	12.35	16.5	0.86 – 4.81	280 – 410	80 – 305	6
(Cocco, 1829)	Su.	–	14.9	0.95 – 2.42	–	–	22
	A.	–	16.3	1.41	–	200 – 325	1
	W.	–	15.3	1.18 – 1.73	–	195 – 305	3
SOUTH OF 41° NORTH							
Notoscopelus resplendens	Sp.	8.25	19.1	2.11 – 6.15	770 – 1250	40 – 300	10
(Richardson, 1845)	Su.	–	20.7	2.41 – 3.17	–	50 – 105	25
	A.	–	19.3	2.30 – 4.60	–	40 – 105	3
Diogenichthys laternatus	Sp.	10.25	19.5	1.45 – 2.27	500 – 1000	0 – 110	16
atlanticus (Tåning, 1928)	Su.	10.00	21.7	1.02 – 2.28	494 – 1000	0 – 210	166
	A.	–	19.4	1.30 – 1.90	–	40 – 300	15
	W.	10.30	15.3	1.20 – 2.13	505 – 980	40 – 100	6
Diaphus mollis	Sp.	9.80 – 14.20	21.4	1.11 – 4.92	285 – 1090	40 – 205	78
Tåning, 1928	Su.	13.70 – 16.70	21.7	1.12 – 5.22	390 – 532	0 – 305	21
	A.	11.75 – 12.85	21.1	1.10 – 4.40	390 – 745	30 – 300	23
	W.	–	18.6	2.97 – 4.91	–	40 – 190	6

Table I. Continuation.

Species	Season	Temp. (°C) range day time*	Temp. (°C) max.	Size range (cm)	Depth day range*	Depth night range*	*N.* of specimens
Lampanyctus photonotus	Sp.	8.25 – 10.90	21.4	2.32 – 5.96	475 – 1250	40 – 250	68
Parr, 1928	Su.	10.00	20.7	1.46 – 6.61	494 – 1000	0 – 205	174
	A.	9.85	23.3	1.80 – 6.05	490 – 1005	30 – 230	36
	W.	–	15.6	1.70 – 4.50	–	–	20
Ceratoscopelus warmingii	Sp.	8.25 – 10.50	21.5	1.09 – 6.96	475 – 1250	40 – 300	178
(Lütken, 1892)	Su.	–	21.7	1.07 – 6.64	–	0 – 205	104
	A.	9.80 – 9.85	23.0	1.55 – 6.00	490 – 1010	0 – 230	222
	W.	14.75	19.2	1.66 – 3.35	110 – 430	40 – 115	22
Benthosema suborbitale	Sp.	9.80 – 13.30	21.5	1.18 – 2.91	420 – 1090	40 – 110	100
(Gilbert, 1913)	Su.	–	21.7	1.19 – 4.54	–	0 – 105, 395 – 528	127
	A.	–	21.1	1.30 – 2.70	–	30 – 105	19
Ceratoscopelus maderensis	Sp.	–	17.2	4.15 – 7.44	–	40 – 110	27
(Lowe, 1839)	Su.	–	21.4	1.46 – 5.78	–	50 – 98	34
	A.	9.80 – 11.75	21.1	1.30 – 3.00	385 – 1010	30 – 105	41
	W.	–	19.2	1.75 – 3.12	–	40 – 115	10
Lampanyctus lineatus	Sp.	10.40	10.4	10.23	440 – 910	–	1
Tåning, 1928	Su.	9.65	21.7	1.72 – 6.66	752 – 1005	0 – 210	27
	A.	–	16.3	4.45 – 5.20	–	95 – 380, 425 – 855	3
	W.	10.30	10.3	1.72 – 10.22	505 – 980	490 – 1010	8
Lampadena urophaos	Sp.	8.25 – 10.50	19.9	1.91 – 5.57	490 – 1250	100 – 200, 510 – 1000	11
Paxton, 1963	Su.	5.95	20.3	2.13 – 7.55	500 – 990	95 – 210	9
	A.	–	19.3	9.10	–	40 – 105	1
	W.	–	18.6	2.02 – 2.13	–	80 – 305	2
Lepidophanes gaussi	Sp.	9.80 – 11.00	21.5	1.69 – 4.51	490 – 1090	40 – 205	35
(Brauer, 1906)	Su.	9.65	21.7	1.85 – 4.48	752 – 1005	0 – 50, 98 – 200	35
	A.	11.75	23.1	1.50 – 3.00	385 – 570	40 – 105, 270 – 395	13
	W.	–	14.7	2.52 – 5.84	–	–	3
Lowenia rara	Sp.	–	18.2	2.64 – 3.32	–	90 – 205	6
(Lütken, 1892)	Su.	–	20.3	2.89	–	–	1
	A.	–	18.7	2.15	–	110 – 195	1
Lampanyctus cuprarius	Sp.	9.80 – 10.50	17.1	3.52 – 7.22	490 – 1090	100 – 405, 510 – 1000	17
Tåning, 1928	Su.	4.45	20.3	2.34 – 7.24	490 – 995	50 – 105, 200 – 305	16
	A.	–	19.8	4.60 – 7.30	–	45 – 325	19
SOUTH OF 29° NORTH							
Hygophum taaningi	Sp.	9.80 – 10.50	21.2	1.31 – 4.59	475 – 1090	40 – 205	17
Becker, 1965	Su.	–	21.4	1.65 – 3.32	–	–	5
	A.	9.15 – 9.85	23.0	1.60 – 4.34	490 – 1005	30 – 105	27
	W.	–	14.8	2.64 – 3.66	–	515 – 995	3
INCIDENTALLY COLLECTED							
Diaphus brachycephalus	Sp.	–	17.0	1.11 – 3.49	–	–	2
Tåning, 1928	Su.	19.30	20.3	3.90 – 4.12	105 – 200	–	2
Diaphus bertelseni							
Nafpaktitis, 1966	W.	–	8.6	7.70	–	505 – 1000	1
Diaphus effulgens	Sp.	–	9.0	9.84	–	–	1
(Goode & Bean, 1896)	Su.	11.90	20.3	3.50 – 8.99	400 – 503	98 – 200	5
	A.	9.15 – 11.75	16.3	2.75 – 7.10	490 – 1000	95 – 395	4
	W.	–	18.6	3.52 – 11.80	–	80 – 190, 515 – 995	6
Diaphus fragilis							
Tåning, 1928	A.	9.80	21.1	6.20 – 8.00	490 – 1005	30 – 92	2

Table I. Continuation.

Species	Season	Temp. (°C) range day time*	Temp. (°C) max.	Size range (cm)	Depth day range*	Depth night range*	*N.* of specimens
Diaphus lucidus	Sp.	–	19.4	2.03 – 6.59	–	90 – 300	3
(Goode & Bean, 1896)	Su.	–	9.3	5.48	–	–	1
	A.	–	16.3	7.30 – 8.40	–	210 – 395	2
Diaphus splendidus							
(Brauer, 1904)	Su.	–	20.3	7.83	–	–	1
Diaphus subtilus	Sp.	10.35	10.4	7.44	475 – 1000	–	1
Nafpaktitis, 1968	Su.	–	13.2	5.81	–	370 – 520	1
	A.	11.15	11.2	4.40	310 – 390	–	1
Diaphus vanhoeffeni							
Brauer, 1906	A.	–	19.8	4.51	–	45 – 107	1
Hygophum benoiti	Sp.	13.50	13.5	2.46 – 3.39	360 – 470	50 – 100, 520 – 1130	3
(Cocco, 1838)	Su.	–	18.3	4.02	–	0 – 55	1
	A.	9.85 – 10.25	19.3	1.50 – 2.68	460 – 870	0 – 105, 200 – 325, 425 – 855	12
	W.	10.30	10.3	1.51	490 – 1005	–	1
Hygophum reinhardti	Sp.	10.35 – 10.50	19.9	1.30 – 2.22	475 – 1000	100 – 205	9
(Lütken, 1892)	Su.	–	20.1	1.82 – 3.83	–	0 – 50, 98 – 200	5
	A.	9.85 – 11.75	23.0	1.60 – 2.30	490 – 1005	30 – 92	8
	W.	–	18.6	2.70 – 3.36	–	80 – 190	2
Lampanyctus alatus	Su.	4.45	20.7	2.89 – 8.36	490 – 995	–	5
Goode & Bean, 1896	A.	–	18.7	5.00	–	110 – 195	1
Lampadena speculigera	Sp.	6.70	6.7	6.73	480 – 1005	–	1
Goode & Bean, 1896	Su.	–	15.0	2.29 – 3.25	–	50 – 98, 280 – 440	4
	A.	9.35 – 9.80	11.3	3.70 – 7.00	505 – 1010	–	3
Lepidophanes guentheri	Sp.	–	18.2	5.69 – 6.64	–	110 – 205	2
(Goode & Bean, 1896)	Su.	–	21.7	1.77 – 5.85	–	0 – 100	6
	A.	9.80	16.8	3.20	505 – 1010	110 – 200	1
	W.	–	15.3	5.58	–	40 – 100	1
Lampanyctus nobilis	Su.	–	21.7	1.22 – 1.93	–	0 – 50	5
Tåning, 1928	W.	–	19.2	1.60 – 5.74	–	40 – 190	53
Lampanyctus tenuiformis							
Brauer, 1906	Su.	–	16.3	7.61	–	–	1
Lampanyctus macropterus							
Brauer, 1904	Su.	–	16.9	2.92	–	45 – 100	1
Bolinichthys supralateralis							
(Parr, 1968)	W.	–	15.3	1.95	–	–	1
Loweina interrupta	Sp.	–	15.5	2.97	–	45 – 95	1
(Tåning, 1928)	Su.	9.45	15.4	2.41 – 7.01	300 – 398	52 – 105	10
	A.	10.25	10.3	2.57	460 – 870	–	1
Myctophum selenops							
Tåning, 1928	Sp.	–	18.2	1.71 – 1.72	–	110 – 205	2
Notoscopelus caudispinosus	Sp.	–	19.5	2.50 – 6.10	–	40 – 205	4
(Johnson, 1863)	Su.	–	19.0	2.60 – 2.75	–	0 – 50	2
Notoscopelus elongatus							
(Costa, 1844)	Su.	–	19.9	2.45 – 13.21	–	–	42
Symbolophorus rufinus							
(Tåning, 1928)	A.	–	14.7	2.63	–	–	1
Taaningichthys bathyphilus	Su.	–	9.3	3.24	–	–	1
(Tåning, 1928)	A.	9.70	9.7	4.60	500 – 995	–	1
Taaningichthys minimus	Su.	–	16.8	3.94	–	200 – 305	1
(Tåning, 1928)	A.	9.80	9.8	1.80	505 – 1010	–	1

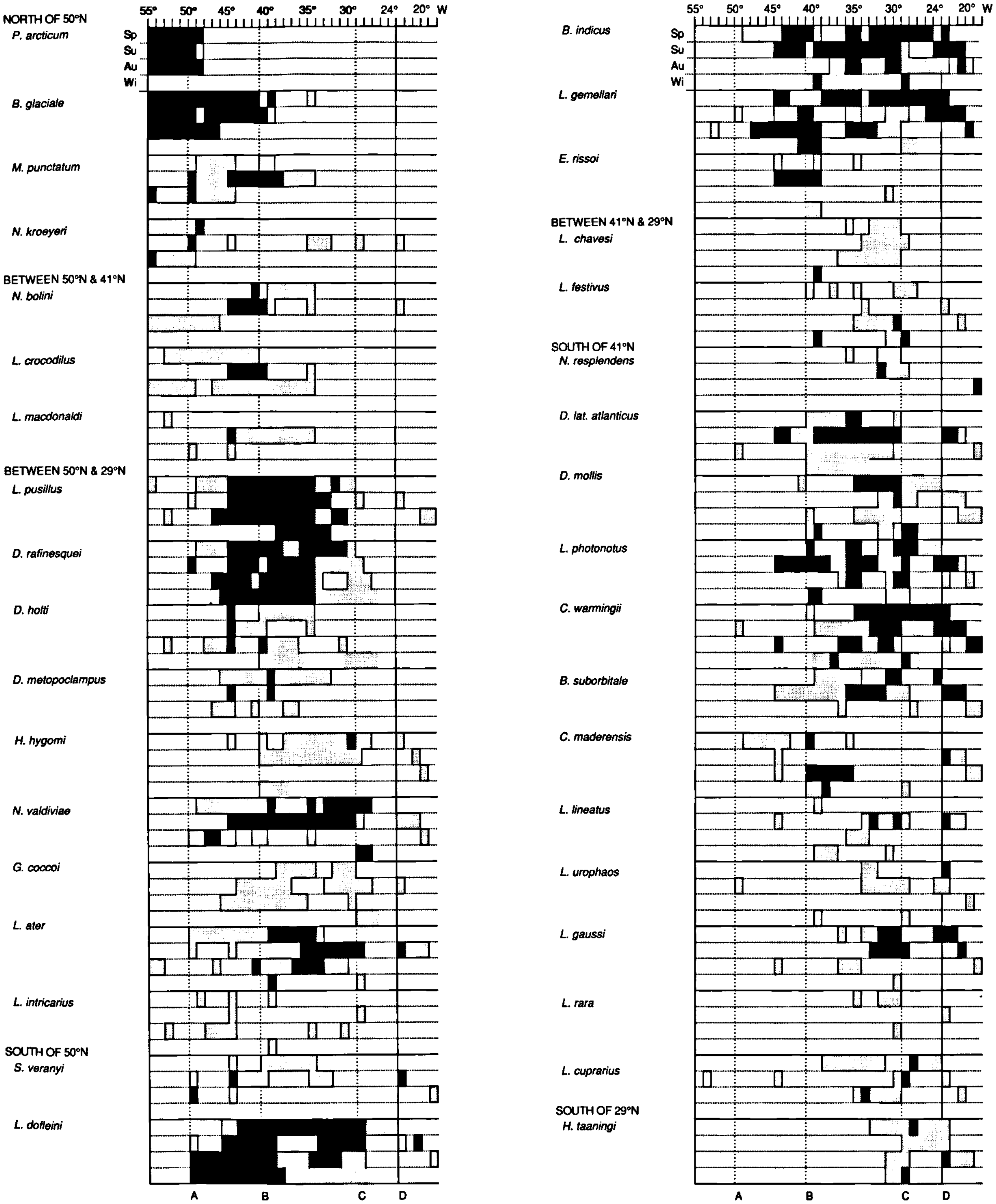

Fig. 1. North-south ranges of myctophids between 24°N and 55°N along approx. 30°W left of line D, and between 20°W and 30°W along approx. 25°N right of line D. For each species the ranges for spring (Sp), summer (Su) autumn (A) and winter (W) are given below each other. The lines A, B, and C mark the latitudes considered to separate the groups distinguished in Table I. Dark is abundant, dotted is rare occurrence.

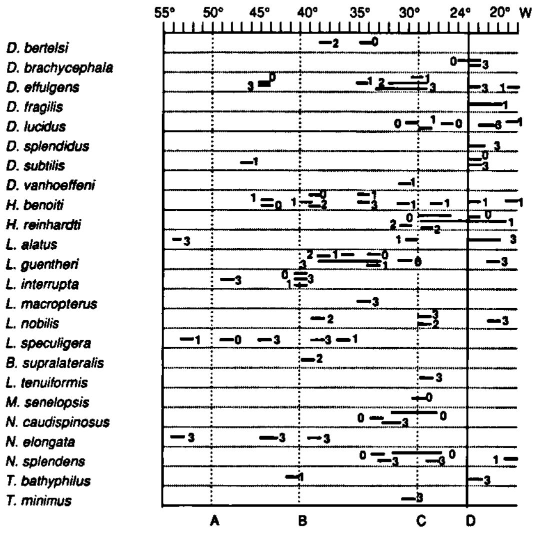

Fig. 2. North-south ranges of incidentally collected myctophids, grouped as in Fig. 1 but the seasons are given together, marked with 0 = spring, 1 = autumn, 2 = winter, and 3 = summer.

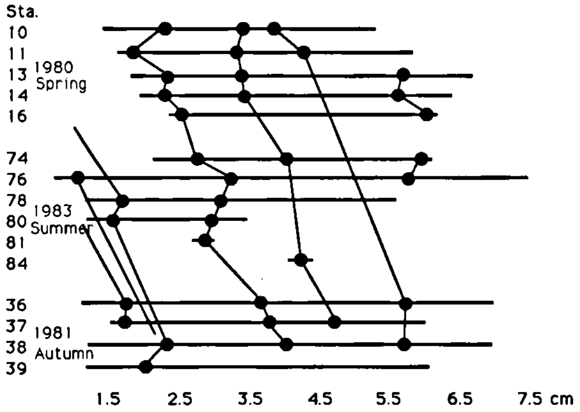

Fig. 3. Size-class maxima per station for spring (1980), summer (1983), and autumn (1981) showing the relation between local and time differences in size of *Benthosema glaciale.*

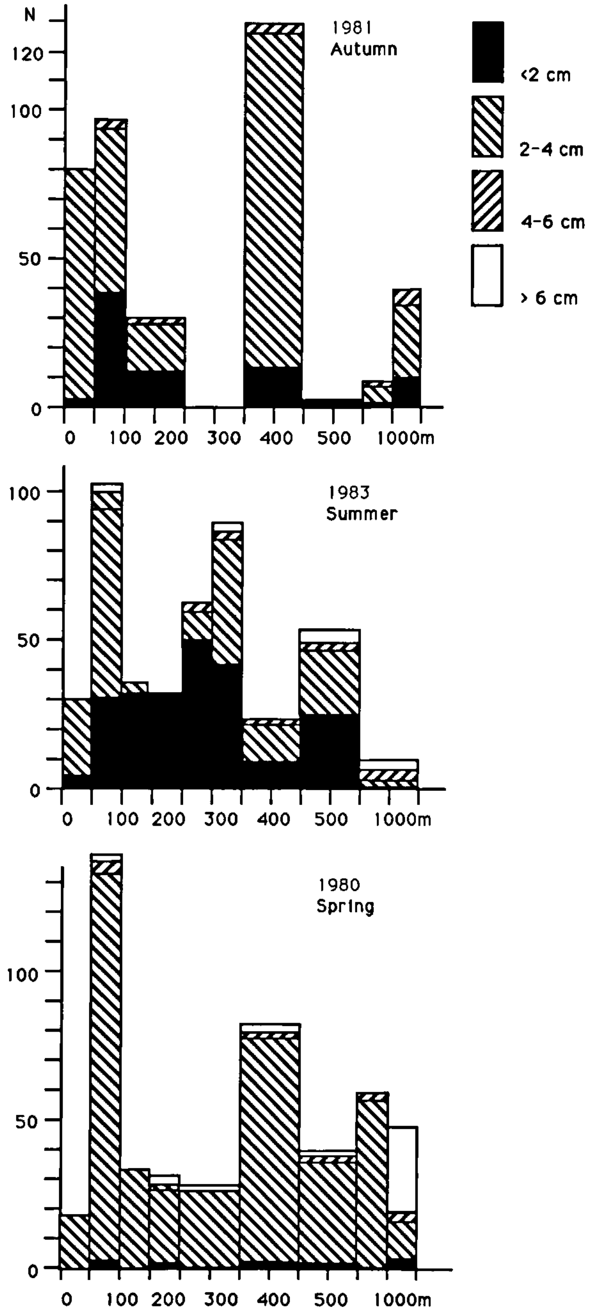

Fig. 4. Depth distribution of four size-groups of *Benthosema glaciale* in spring (1980), summer (1983), and autumn (1981); number of specimens along horizontal, depth along vertical axis.

southwards to 35°N the average size of the specimens increases, though even at 55°N no small size-class representatives are collected. In summer the population withdraws to 41°N and an extra size-class, probably due to earlier reproduction (Halliday, 1970), is found in the population between 50°N and 41°N (Fig. 3). The largest specimens of this size-class are found in the southern stations (78, 80), so that a transport from a northern breeding ground (Fig. 3) is supposed. In autumn the population occurs only north of 47°N. The penetration to 35°N occurs in spring, followed by a regression towards the north later in the year.

Table II. Size ranges (cm) for *Benthosema glaciale* in the upper 100 m; stations arranged from north to south.

Spring (1980)		Summer (1983)		Autumn (1981)	
Sta.	size range	Sta.	size range	Sta.	size range
11	2.0–2.7	74	2.2–6.0	36	1.2–3.9
13	1.9–6.6			37	1.6–5.4
14	2.0–6.0	78	1.2–4.8	39	1.3–2.3
16	2.6–3.1	80	1.2–3.2		
17	2.4–3.6				
20	2.4–2.8				

A clear trend in vertical size distribution is found. The highest concentration of smaller specimens (< 20 mm), expressed as averages of percentual occurrence per depth level at each station, occurs between 50 m and 300 m (Fig. 4) in summer as well as in autumn. The largest specimens (> 60 mm) are mostly deeper living. In analogy with the migration of pteropods and medusae (Pafort – Van Iersel, 1985) it can be supposed that the population of the present species, together with its juveniles, is transported southwards in the area between 55°N and 35°N in the submerging (sub)polar wates. If, however, the upper 100 m of the water column is studied separately (Table II) the northern stations yield larger specimens than the southern stations. An overall northward migration seems to prevail in the upper 100 m, which may also explain a summer withdrawal from the area between 47°N and 35°N. Diurnal vertical migration in *B. glaciale* is found in spring, summer, and autumn. In spring, the day and night levels overlap, but in the other seasons separation of these levels is evident (Fig. 5).

Benthosema suborbitale is an eurytropical species occurring south of 41°N, migrating northwards in summer (Fig. 1).

Bolinichthys indicus. No distinct size-classes could be separated, though specimens of 12–20 mm form a small size-class in spring. A group of specimens ranging from 20–40 mm shows three maxima, one below and two above the minimum size of maturity (31 mm). In summer, the majority reaches mature size and the group of small ones decreases in numbers. In autumn, a number of small specimens (13–26 mm) seems to originate from recent hatching. Reproduction throughout the year, with a maximum in early summer, may explain these size distributions.

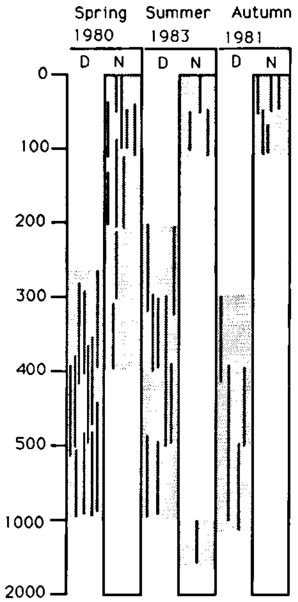

Fig. 5. Vertical migration of *Benthosema glaciale* in spring (1980), summer (1983), and autumn (1981) in the upper 2000 m; D = day, N = night.

Bolinichthys supralateralis. The single specimen in the present material is collected at 39°43′N 35°48.9′W, 100–200 m depth, on 15 February 1982. It constitutes a very northern record for this side of the North Atlantic Ocean.

Ceratoscopelus maderensis. In spring and summer only large specimens (> 40 mm) are found in the area influenced by the branches of the North Atlantic Drift (Fig. 6). Small specimens (< 40 mm) are collected in summer, autumn, and winter along the whole transect south of 45°N. This is reverse of what is found for *C. warmingii*; the two species seem to be vicariating when the large individuals are considered. This is also in agreement with the statement that *C. maderensis* breeds in the northern part of the Gulf Stream (Gibbs et al., 1971) as a temperate species (Backus & Craddock, 1977), in contrast to the tropical-subtropical *C. warmingii.*

Ceratoscopelus warmingii. There are two size-classes throughout the year except in winter. The size-class maxima are in spring 20 and 42 mm, in summer 22 and 43 mm, in autumn 20 and 42 mm,

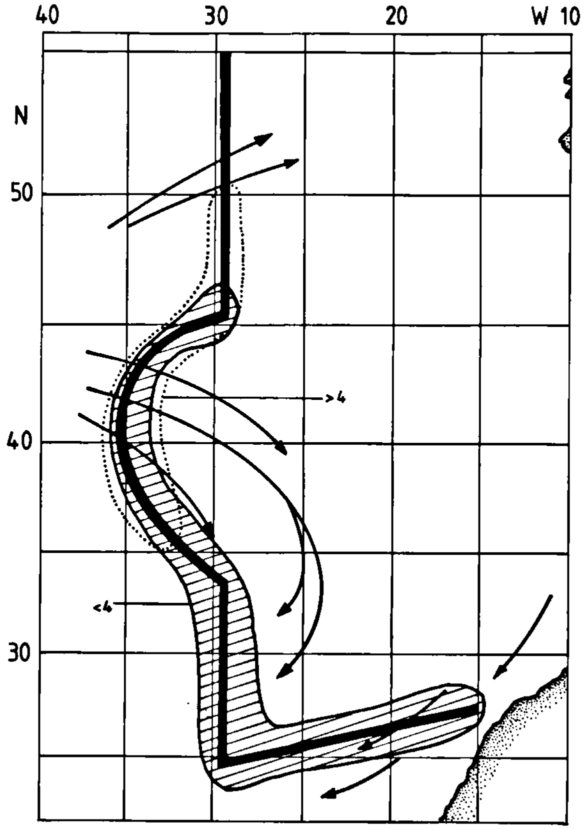

Fig. 6. Geographic pattern of *Ceratoscopelus maderensis*: large specimens (> 4 cm) in dotted frame and small specimens (< 4 cm) hatched, showing the larger ones in the North Atlantic Drift area.

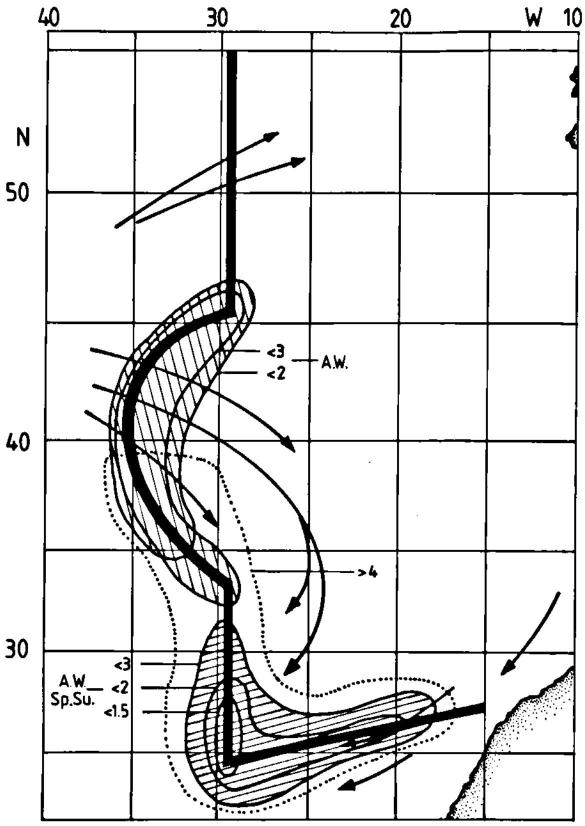

Fig. 7. Geographic pattern of *Ceratoscopelus warmingii*: large specimens (> 4 cm) in dotted frame, smaller size groups (< 2 and < 3 cm) hatched, collected in autumn and winter (A. W.) and in all seasons (A. W. Sp. Su.).

and in winter 24 mm. In winter the larger size-class disappears from the area investigated. The minimum sizes are for spring 11 mm, for summer 11 mm, for autumn 16 mm, and for winter 17 mm. The larger size-class is most abundant in spring and decreases subsequently. In summer and spring small specimens are found only in the area influenced by the Canary Current. In autumn and winter small ones are also found more to the north in waters influenced by the North Atlantic Drift. The specimens of the larger size-class are restricted mainly to the area south of 40°N in all seasons (Fig. 7). In winter, *C. warmingii* is probably restricted to European waters over the continental slope to disperse in spring to oceanic waters south of 40°N.

For *C. warmingii* evident differences are found in the diurnal vertical distribution in the different seasons (Fig. 8). The upper night level is found above 50 m in summer and autumn and below 50 m in spring and winter. The (upper) day levels in spring and autumn are identical, reaching the 500–1000 m layers. In summer the species is not collected at daytime as it occurs probably too deep; in winter the day level is found between 100 and 300 m.

Diaphus lucidus is only collected south of 30°N though it may occur more northward (Hulley, 1984).

Diaphus metopoclampus is not found in the winter samples. In spring there are two size groups (12–25 mm and 53–70 mm). In summer these groups are still present (20–36 mm and 58–71 mm). In autumn one specimen of 20 mm and a group of 31–50 mm is found.

Diaphus mollis. In spring large (> 30 mm), and in autumn small (< 30 mm) specimens are

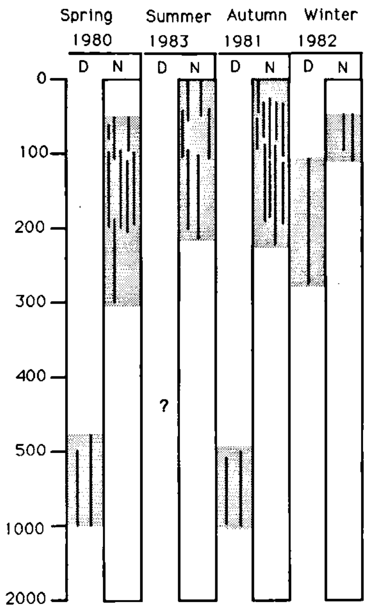

Fig. 8. Vertical migration of *Ceratoscopelus warmingii* in spring (1980), summer (1983), autumn (1981), and winter (1982).

dominating. No small specimens were collected winter.

Diaphus rafinesquei is mature at a standard length of 50 mm. It breeds in the eastern Atlantic and transport by currents brings the specimens in the western Atlantic (Nafpaktitis, 1968).

Size-classes are found around maxima of 21 mm, 34 mm, 57 mm, and 70 mm in spring, 20 mm, 38 mm, and 60 mm in summer, 47 mm and 66 mm in autumn, and 20 mm, 55 mm, and 65 mm in winter. The maximum length of specimens in the present collection is 86 mm. In autumn nearly no small specimens are found. In winter a new size-class occurs and this group can also contribute to the higher numbers of small specimens in spring and summer. The small specimens in spring were concentrated around the stations 16, 17, and 18 in the North Atlantic Drift. Size-classes are indicated by 'A' to 'J' in Fig. 9; it is supposed that the size-classes up to 'D' consist of juveniles and those from 'E' to 'J' of adults, in which the group 'J' can be considered as probably representing large expatriated specimens. Due to inefficient preservation a study of otoliths was impossible.

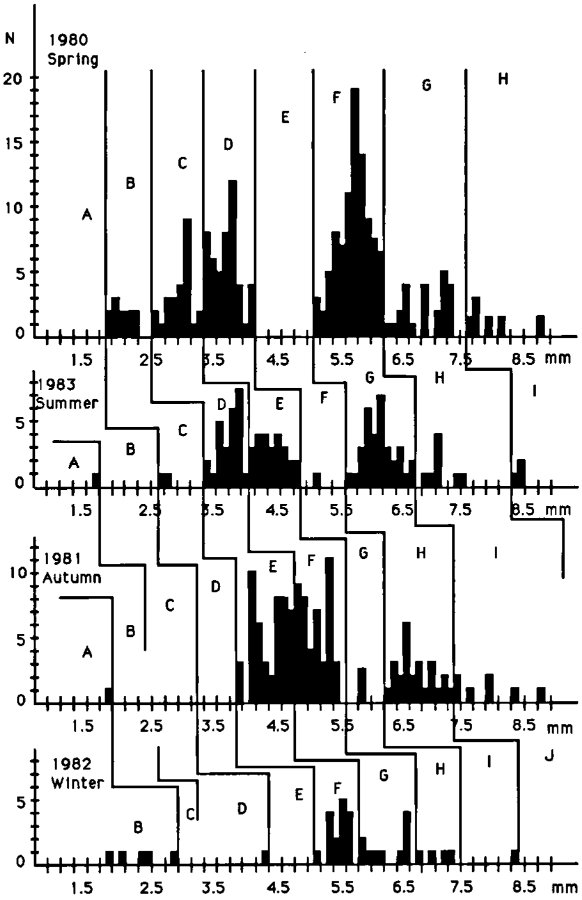

Fig. 9. Histogram of size (standard length) distribution for *Diaphus rafinesquei*: for spring (1980), summer (1983), autumn (1981), and winter (1982). Numbers of specimens along vertical, standard length along horizontal axis. The size-classes are indicated with A–J for each season so that class A in spring becomes B in summer and C in autumn, etc.

The size-classes plotted in Fig. 10 along the cruise transect show their relative position with regard to the North Atlantic Drift. The southern branch of the North Atlantic Drift is populated by small and large specimens; further remote from this water mass only larger ones are found. The temperature/salinity (T/S) ratios of the actual, positive sampling localities were plotted in Fig. 11 with the T/S ratio for the North Atlantic Drift in the upper 50 m of the water column for 1981 and 1983, the only two years for which accurate T and S data are available (Van der Spoel, 1985). From this figure it is evident that there is a relation of small specimens

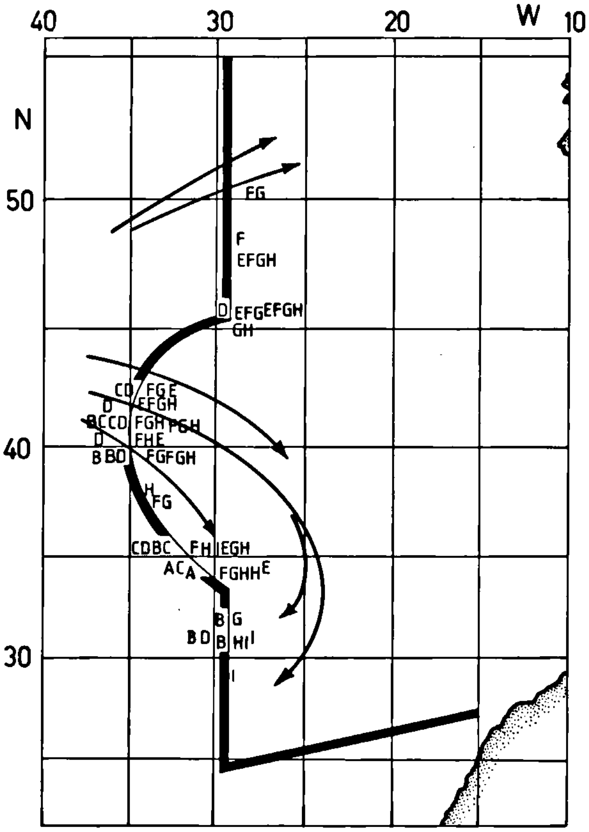

Fig. 10. Geographic distribution of the size-classes A–J from Fig. 9 along the cruise transect.

with the North Atlantic Drift expressed in T/S values. In summer, when there are many small specimens (< 4 mm), these are found in water masses in T/S close to the North Atlantic Drift. In autumn the few small ones are already further away from the current than in summer, and in summer and autumn the full-grown are found in water masses which differ in T/S ratios more from the North Atlantic Drift than the water masses in which the small specimens are found (Fig. 11).

It is concluded on the basis of geographic evidence and water mass characters that the smaller size-classes are transported by the North Atlantic Drift and that the aging animals migrate from this area north and southwards, so that the largest specimens are found at greater distances from the current. This does not exclude of course that a group of adults remains in the current; these may produce the next year's offspring.

Vertical migration shows slight differences in the four seasons. In summer the night and daytime depths are both shallower than in spring. In autumn the spring situation is found again, but in winter both daytime and night depths are greater than in spring (Fig. 12).

The record of *Diaphus subtilis* at 47°46.5′N 30°25.8′W on 5 October 1981 at 310–390 m is the northernmost record of this species, of which hitherto isolated records up to 40°N were known for this area (Hulley, 1984).

Hygophum benoiti. All specimens are found in Sargasso Sea water or in waters influenced by the North Atlantic Drift.

Lampanyctus ater is most abundant between 28°N and 42°N. In spring small specimens (11–40 mm) are the most abundant. In winter only small specimens are found (8–30 mm) and in autumn no small ones are found at all.

Lampanyctus crocodilus. All small specimens are found in the vicinity of the North Atlantic Drift. No small specimens are found in spring. The larger specimens found in spring and autumn probably migrate northwards to the latitudes of 49°N to 53°N (cf. Fig. 1).

Lampanyctus photonotus shows in all seasons, except for spring, a dominance of small specimens (< 30 mm). In spring the size-class with a maximum of 40 mm dominates. In summer this maximum is found around 50 mm; in autumn and winter this group of specimens has disappeared. Geographic separation of size-classes is not found.

Lampanyctus pusillus shows two size-classes in spring: a small size-class and a more abundant large size-class. In summer the small size-class becomes more abundant, probably due to early spring reproduction (Hulley, 1984). In winter the catch is small and no small specimens are present.

Lepidophanes gaussi. Though material is limited in spring and autumn, a clear maximum of small specimens (< 20 mm) is collected.

Lobianchia dofleini. This widespread species shows four size-classes in spring (10–18, 19–26, 27–29, and 30–35 mm).

Lobianchia gemellari. The previous species was collected more frequently than the present subtropical species; in all seasons juveniles are found. The

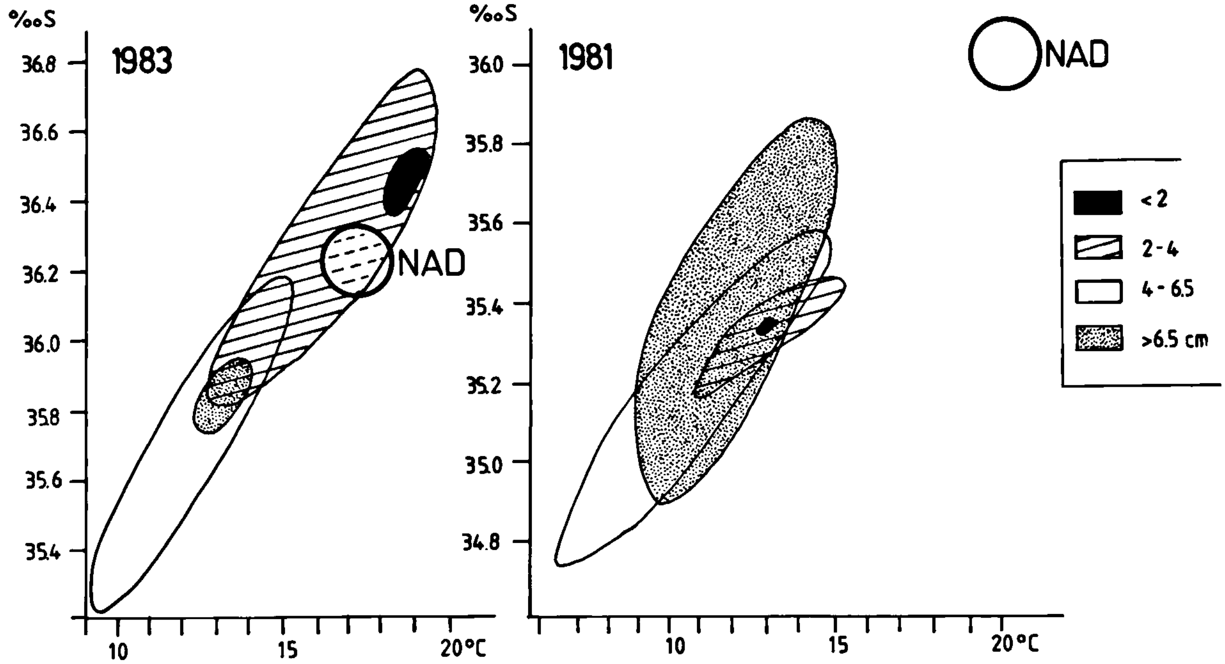

Fig. 11. The temperature/salinity (TS) relations of the positive hauls for *Diaphus rafinesquei* in summer (1983) and autumn (1981), showing the position of the different size-classes (<2, 2–4, 4–6, and > 6 cm) in relation to the T/S values of the North Atlantic Drift (NAD).

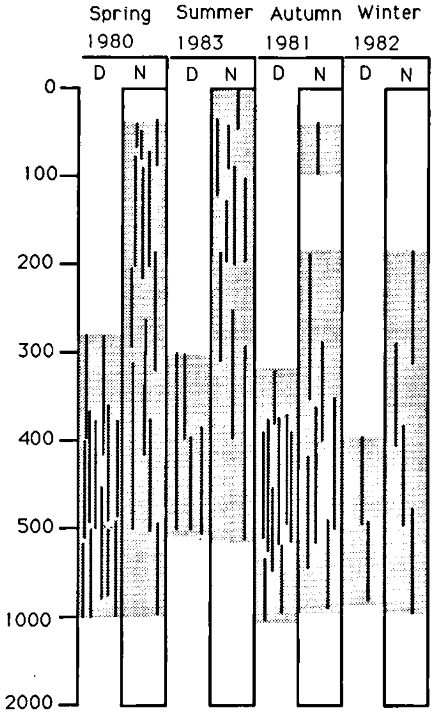

Fig. 12. Vertical migration of *Diaphus rafinesquei* during spring (1980), summer (1983), autumn (1981), and winter (1982).

large specimens (> 80 mm) are no expatriates as they are collected in the normal range of the species (cf. Hulley, 1984).

Myctophum punctatum. The large specimens (> 50 mm) are found only at the northernmost positions (spring 49°N, summer 51°N, autumn 55°N). Reproduction seems to start in the north in spring (specimens of ±20 mm) and to shift towards the south with the seasons, as in summer smaller juveniles (±20 mm) are found at more southern localities than larger juveniles (±30 mm). The north-south range (Fig. 1) also shows an extension to the south in summer.

Notolychnus valdiviae. The mean size increases from 16.5 mm in spring, 17.4 mm in summer, 19.0 mm in autumn, to 18.1 mm in winter.

Discussion

To determine the different faunas in the areas investigated, the species can be grouped according to: (1) the occurrence over the provinces proposed by

Table III. Sum of first and last occurrences of myctophids for each station. The winter cruise is not considered as too few samples were available. The geographic position of the maxima and the position of the faunal borders proposed by Backus & Craddock (1977) are added.

Spring (1980)		Summer (1983)		Autumn (1981)		Borders after Backus & Craddock
Sta.	Σ	Sta.	Σ	Sta.	Σ	
10	4	74	6	36	10	.
11	3	75	0	37	4	.
13	11 (48°)	76	12 (50°)	38	8 (49°)	51°N
14	10	77	0	39	8	.
16	3	78	18 (45°)	40	6	.
17	6	80	2	42	3	.
18	8	81	6	43	6	.
19	2	84	14 (35°)	45	12 (37°)	36°N
20	12 (35°)	85	11	47	4	.
21	3	87	5	48	2	.
22	3	987	5	49	7	.
23	1	88	0	50	9 (30°)	30°N
24	11 (29°)	89	25 (25°)	51	1	.
25	4	90	18	52	1	.
26	3			53	2	.
27	16			54	4	.
				55	21	.

Backus & Craddock (1977), (2) the north-south distribution along the transect, (3) the temperature preferences, and (4) the co-occurrences in the samples.

The study of first and last occurrences, a method only giving an indication for faunal borders, may also be mentioned. This mathematical method for estimating faunal borders proposed by Backus et al. (1965) is not followed as the model assumes homogeneous dispersal which is certainly not the case. The simple sum of first- and last-occurrences for all stations is given in Table III. There is a slight resemblance between the faunal borders proposed by Backus & Craddock (1977) and the first and last occurrences in the present material.

Difficulties with the methods mentioned above induced us to propose a mathematical approach (also published by Bleeker & Van der Spoel, 1988) to measure the collected material of each station departing from the following assumptions:

A species has no value for a sample when it does not contribute to the diversity of the sample and when it does not determine the character of the sample by a certain dominance. The importance of a species for a sample is thus greater when its diversity value (D) and its dominance value (C) are higher. The difference of these values from zero is the loading of the species (B) (for full discussion of the formulas see Bleeker & Van der Spoel, 1988) which is expressed in the formulas:

$$B = \sqrt{D^2 + C^2}$$

and

$$C = \frac{100 \times F \cdot N - \Sigma N}{F \times N_{max} - \Sigma N} \times \frac{F}{F_{max}}$$

and

$$D = \sqrt{(1 + A_{max} - A)^2 \times (1 + M - A) \times N}$$

in which A = the number of samples in which the species is found, A_{max} = the number of samples in which the most frequently occurring species is found, B = the species loading, C = value of a species' dominance for the sample, D = diversity value of a species for the sample, F = number of species

Table IV. ΣB for Myctophidae (ΣB), Phronimidae ($\Sigma B'$) and Periphyllidae ($\Sigma B''$) for the spring, summer, and autumn cruise. The geographic positions (°N) of the maxima are added.

Spring (1980)				Summer (1983)			Autumn (1981)		
Sta.	ΣB	$\Sigma B'$	$\Sigma B''$	Sta.	ΣB	$\Sigma B''$	Sta.	ΣB	$\Sigma B''$
10	691 (55°)	–	10	74	468	209	36	908	135
11	457	–	169	75	174	9	37	1691 (53°)	111
12	–	0	–	76	797 (50°)	234 (50°)	38	1231	148 (50°)
13	836	54	180	77	0	–	39	762	42
14	841 (45°)	80	229	78	1516 (45°)	174	40	632	–
16	319	120	231 (41°)	80	875	–	42	407	205 (41°)
17	641	383	75	81	645	230	43	345	204
18	661	429	194	84	661	429 (35°)	45	639	94
19	438	464 (38°)	366 (38°)	85	1005 (33°)	–	47	702 (35°)	313 (35°)
20	1236 (35°)	99	343	87	461	80	48	336	141
21	249	692 (33°)	295	987	510	0	49	592	43
22	811 (32°)	74	243	89	1040 (25°)	151 (25°)	50	688 (30°)	0
23	0	4	304 (31°)	90	431	–	51	15	286 (28°)
24	640 (29°)	330 (29°)	0				52	182	236
25	483	125	0				53	0	–
26	281	288 (25°)	0				54	337	–
27	437	123	0				55	621	–

found in the sample, F_{max} = total number of species in the most diverse sample, M = total number of samples, N = total number of specimens in the sample, N_{max} = total number of specimens in the most abundant sample.

The total of loadings of species (B) in a sample (ΣB) is an expression of the diversity and quality of the sample. In Table IV the ΣB is given for Myctophidae (ΣB), Phronimidae (Crustacea, Amphipoda) ($\Sigma B'$) and Periphyllidae (Medusae, Scyphozoa) ($\Sigma B''$). Table IV shows more transition zones for the spring period than the ones indicated by first and last occurrences (Table III); borders near 29°N, 35°N, and 45°N are evident in both tables, but the loading of the stations shows also transitions near 55°N and 32°N. Near 25°N, 29°N, 33°N, 38°N, and 31°N, 38°N, 41°N, respectively, Phronimidae and Periphyllidae show other transition zones than the Myctophidae. In the summer series the loading of the stations gives transitions for Myctophidae near 50°N, 45°N, 33°N, and 25°N, which is rather different from the results in Table III. The Periphyllidae show borders at 50°N, 35°N, and 25°N in summer. In autumn there is great difference between the results with the loadings per station and first and last occurrence, but the results of the species loading are much closer to the provinces by Backus & Craddock (1977). All data together show in spring a transitional zone between 29°N and 33°N, between 35°N and 41°N, and between 45°N and 48°N. In summer these zones are found at 25°N, between 33°N and 35°N, and at 50°N, together with a transitional zone near 45°N. In autumn the transitional zones are found at 28°N–30°N, 35°N–41°N, and 49°N–53°N. There is thus a clear shift in transitional areas.

A shift of the borders of the individual species is also obvious; the northern fauna elements migrate southwards in summer and autumn, the temperate elements penetrate northwards and southwards in summer and autumn, and the warm-water elements go northwards in summer. These shifts are also seen in Fig. 1 when the groups as given in Table I are compared. In Table I the species are divided into eight sections. The eighth section comprises species collected incidentally and is not considered any further. The other seven groups are based on the occurrence in relation to the 50°, 41° and 29°N borders (lines A, B, and C in Fig. 1). The latitudes 50°N and 29°N are chosen as they represent the

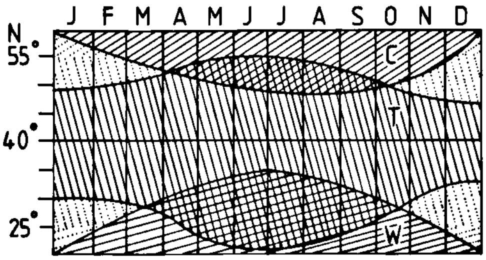

Fig. 13. Diagram of the seasonal shift of cold (C), temperate (T), and warm-water (W) taxa; successive months indicated with J to D.

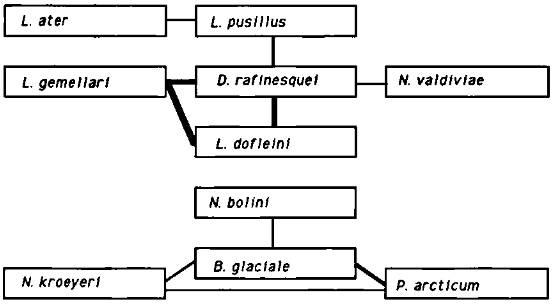

Fig. 14. Co-occurrence model for the autumn samples of the most frequent species based on simultaneous collecting in one net haul. The stronger the co-occurrence, the thicker are the connecting lines.

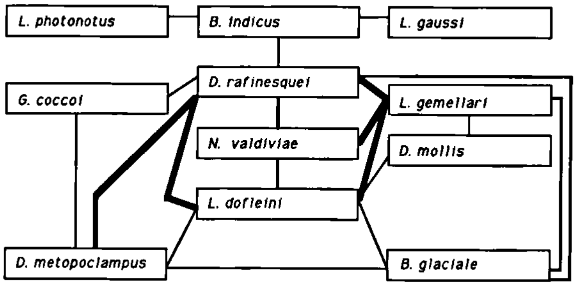

Fig. 15. Co-occurrence model for the spring samples of the most frequent species based on simultaneous collecting in one net haul. The stronger the co-occurrence, the thicker are the connecting lines.

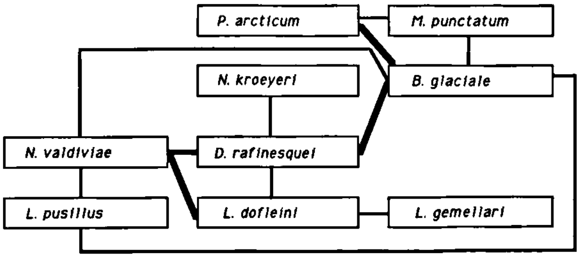

Fig. 16. Co-occurrence model for the summer samples of the most frequent species based on simultaneous collecting in one net haul. The stronger the co-occurrence, the thicker are the connecting lines.

faunal borders also given by Backus & Craddock (1977) and because they are close to the maxima of first and last occurrences. The border at 36°N of Backus & Craddock (1977) is not considered because it is a transition zone which also delimits extreme southward penetration of northern elements and northward penetration of southern elements (Figs. 1, 13). The provinces given by Backus & Craddock (1977) could therefore not be used; the faunal elements shift too much during the year to delimit the processes accurately. The border for myctophids at 41°N is a hydrographic phenomenon as well. Moreover, this border at 41°N is reflected in the zoogeography of other taxonomic groups.

In Fig. 13 the yearly shift of cold- temperate- and warm-water species is diagrammatically illustrated. This shift explains the different results of co-occurrence tests in the different seasons. In autumn cold-water species and temperate species form separate clusters (Fig. 14). *B. glaciale*, *P. arcticum*, *N. kroeyeri*, and *N. bolini* form a cold-water cluster separated from the warm-water cluster of *D. rafinesquei*, *L. gemellari*, *N. valdiviae*, and *L. dofleini* to which also *L. ater* and *L. pusillus* are linked. In spring there is strong mixing of both clusters probably also induced by new offspring (Fig. 15). A warm-water cluster is recognized in *D. rafinesquei*, *L. gemellari*, *N. valdiviae*, and *L. dofleini*, but strong co-occurrence of these with *B. glaciale* points to mixing of faunas. In summer no separation could be made on the basis of co-occurrence. The cold-water elements *P. arcticum*, *M. punctatum*, *B. glaciale*, and *N. kroeyeri* are frequently co-occurring with *D. rafinesquei* and *N. valdiviae* from the temperate cluster (Fig. 16).

The temperature ranges at which the species occur do not give an indication of different faunas, neither when day samples or night samples are considered separately, nor when the temperature at 200 m depth is considered. The temperatures at which

Table V. Temperature ranges of the N-S ranges distinguished in Table I.

North-south range	Rounded off temp. of daytime samples
north of 50°N	4°–14°C
between 50° and 41°N	5°–10°C
between 50° and 29°N	4°–15°C
south of 50°N	5°–19°C
between 41° and 29°N	10°–12°C
south of 41°N	5°–17°C
south of 29°N	9°–10°C

the species live at daytime still are the most indicative; in Table V the rounded off temperatures are given for the patterns distinguished in Table I.

Species living in the same latitudinal range may show strong differences in temperature preference as they live at different depths, whereas species from different latitudinal belts may show identical temperature ranges as they live at different depths. *L. pusillus* (Fig. 17, C) and *D. metopoclampus* (Fig. 17, E) are both subtropical species with comparable north-south ranges, but they differ in temperature preference as they live at different depths. The holo-eurytropical *L. photonotus* occurs at temperatures where also boreal and temperate species (Fig. 17, F, D, B, C) live, due to the different depth strata occupied. Subarctic species usually show daytime temperatures of 4°–7°C, but occasionally they may occur at 10°C (Fig. 17). Boreal species prefer temperatures of 7°–10°C. The widespread species like *L. dofleini* normally do not occur in colder waters and show temperature curves for the daytime samples between 8° and 17°C with maxima between 11° and 15°C (Fig. 17).

The geographic separation of provinces is thus difficult, especially when this should also cover the yearly fluctuations. Faunal elements based on literature references, however, can be recognized.

Boreoarctic faunal elements (cf. Hulley, 1984) or subarctic faunal elements (cf. Backus & Craddock, 1977) are *P. arcticum*, *B. glaciale*, and *N. kroeyeri*. They show high abundances north of 48°N (> 5 specimens, per haul and per hour) and only *B. glaciale* is frequently found up to 38°N. Except for *P. arcticum* these faunal elements are in spring and summer found also more southwards, but the centres of their stable ranges are north of 50°N.

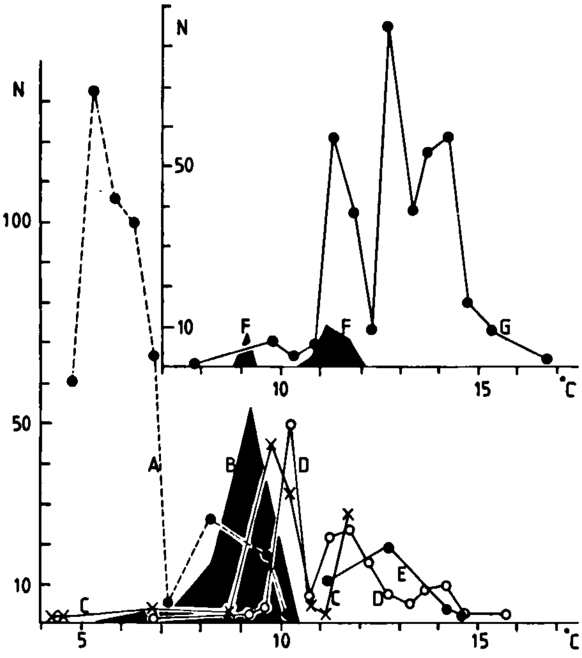

Fig. 17. Temperature preference at daytime depth for: *Protomyctophum arcticum* (A), *Myctophum punctatum* (B), *Lampanyctus pusillus* (C), *Diaphus rafinesquei* (D), *D. metopoclampus* (E), *Lampanyctis photonotus* (F), and *Lobianchia dofleini* (G); temperature along horizontal, numbers of specimens along vertical axis.

Boreal faunal elements are *M. punctatum* and *L. crocodilus* (cf. Hulley, 1984). *N. bolini*, though usually considered a temperate-subtropical element, shows the same pattern in the present material as the boreal faunal elements. The last mentioned three species co-occur frequently in low numbers with boreoarctic faunal elements, but the area of most abundant occurrence is around 41°N (in spring and summer). This group is found higher north in autumn. The co-occurrence of boreal and boreoarctic faunal elements is thus explained by the southward migration of the latter and the northward migration of the first.

L. macdonaldi resembles in distribution *L. crocodilus* and *N. bolini* but it is usually considered a bitemperate faunal element and not a boreal faunal element (cf. Hulley, 1984). In the present material these three species show the greatest abundance between 50°N and 41°N.

Temperate-subtropical and eurytherm subtropical faunal elements like *D. rafinesquei*, *D. metopoclampus*, *H. hygomi*, *L. ater*, *L. pusillus*, and *S. veranyi* could not be separated. They all occur between 29°N and 50°N, with a summer extension to the south and in autumn mainly a migration to the north. A distribution comparable to that of this group is, however, shown by the temperate faunal elements *D. holti* and *L. intricarius* as well; the slightly northward occurrence of these two is not different from the pattern of e.g. *L. pusillus* and *L. ater*. The widespread species *N. valdiviae* and the holo-eurytropical *G. coccoi* joins the pattern of the temperate-subtropical group.

Northern subtropical faunal elements are *L. chavesi* and *L. festivus*. They occur typically between 29°N and 41°N.

Holo-eurytropical and subtropical faunal elements occur in the present material along the whole transect up to 50°N, like *L. gemellari* and *B. indicus*. The pattern of these two species is shared by widespread species like *L. dofleini* and *E. rissoi*.

The thermophylous eurytropical faunal elements, like *H. taaningi*, occur south of 29°N only.

A group of species occurring along the transect mainly south of 41°N is given separately in Table I. This group is dominated by holo-eurytropical faunal elements (*L. photonotus*, *N. resplendens*, *D. mollis*, *C. warmingii*, *L. rara*). *B. suborbitale* and *L. lineatus* are sometimes considered thermophylous-eurytropical but in the present material they show (Fig. 1) much more the pattern of holo-eurytropical faunal elements. The Central water faunal elements *L. gaussi* and *L. cuprarius* join this pattern as well, living between 29°N and 38°N, though incidentally caught more to the north.

C. maderensis resembles the holo-eurytropical faunal elements in distribution but it vicariates clearly with *C. warmingii* so that it can be considered a temperate-subtropical faunal element.

Conclusions

It was not possible to distinguish provinces with clear borders for the Myctophidae collected in the four seasons. Transitional zones could only be traced between boreoarctic, boreal, subtropical and tropical areas as very broad zones between 48°N and 50°N, 41°N and 45°N, and 28°N and 37°N.

Along 30°W the boreoarctic faunal elements occur roughly north of 50°N. The boreal faunal elements occur mainly between 50°N and 41°N, and northern subtropical faunal elements live between about 29°N and 41°N. The temperate faunal elements are in our material frequently mixed with subtropical faunal elements at the latitudes of 29°N to 50°N. Holo-eurytropical and (southern) subtropical faunal elements are found along the whole transect south of 50°N, while south of 41°N mainly holo-eurytropical elements are found together with Central water species. South of 29°N the thermophylous eurytropical faunal elements are found.

A seasonal shift of species ranges is evident: the boreal or temperate taxa spread north and southwards in summer, the cold-water elements go southwards in the summer months, and the tropical elements migrate northwards. These shifts obscure faunal borders and the composition of the different faunas, so that in the present material only a small number of species could be clustered in a cold-water and a warm-water group.

The subdivision into sharply delimited faunas and the description of discrete faunal borders is only possible with artificial tools or unacceptable simplifications and cannot be deduced from the original data.

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