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Effects of a Warm-Core Eddy on Fish Distributions in the Tasman Sea Off East Australia

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ABSTRACT: Distributions of fishes were determined in and near a warm-core eddy off the east coast of Australia from 28 November to 13 December, 1978. Samples were collected with a midwater trawl (n = 39) in the upper 500 m of the water column during day and night. 88 % of the 14602 fish caught belonged to the family Myctophidae. Few fish (< 4 % of total) were caught during day. At night the structure of the fish community within the eddy was recognizably distinct from that in surrounding water masses. Most fish distributions correlated well with thermal structure. Common species were categorized as eddy species (n = 5), outside eddy/cold-water species (n = 5), warm-water species (n = 1), cold-water species (n = 8) and widespread species (n = 7) based on nocturnal distributions. Eddy species were largely restricted to warm water within the eddy, whilst warm-water species were also abundant near surface outside the eddy. Outside eddy/cold-water species were caught almost exclusively outside the eddy or at the eddy edge. 2 of these species were concentrated in the cold water outside the eddy. For most cold-water species, the extent of the upward vertical migration at night did not appear to penetrate into the warmer surface layers. Widespread species included 4 of the 5 most abundant species caught (60 % of total catch) and occurred inside and outside the eddy and at the eddy edge. Individuals of 4 species caught inside and outside the eddy differed in size, and individuals of 2 species differed in diet. Distributional patterns are discussed in relation to competition, predation and thermal ecology of the species.

INTRODUCTION

Warm-core anticyclonic eddies or rings provide good experimental sites for studying oceanic processes since eddies are relatively closed structures, have extensive hydrographic variability over a small geographic space and form uniquely tractable bodies of water that can be revisited in time series (Wiebe, 1976). In the Tasman Sea, warm-core eddies form a major part of the circulation and water mass structure off the southeast coast of Australia (Hamon, 1965; Andrews and Scully-Power, 1976; Nilsson et al., 1977). These eddies apparently form when a meander of the southward flowing East Australian Current breaks off into a closed ring structure (Nilsson and Cresswell, 1981) and are largely analogous to eddies produced by other major western boundary currents such as the Gulf Stream (Parker, 1971; Fuglister, 1972) and the Kuroshio Current (Tomosada, 1978).

Tasman Sea eddies typically have diameters of 200–300 km (Andrews and Scully-Power, 1976). The eddies are lens-shaped with isotherms sloping downward from the eddy edge towards the centre. Wintertime cooling produces a deep vertically mixed layer that can extend to 360 m or more (Tranter et al., 1980 a; Brandt et al., 1981). Surface currents of 2.0 m s^{-1} have been measured in eddies and satellite tracking of drogued buoys has shown that eddies can move at least 1.5×10^{-2} m s^{-1} (13 km d^{-1}) and may exist for 18 months or more (Nilsson and Cresswell, 1981).

Nutrient cycling and phytoplankton productivity also differ between warm-core eddies and surrounding water masses (Scott, 1978; Tranter et al., 1980 a; Jeffrey and Hallegraeff, 1980). The responses of higher trophic levels are not known although many studies in other areas have shown that micronekton distributions often correspond with water mass structure (Hutchins, 1947; Ekman, 1953; Ebeling, 1962; Backus et al., 1969; McGowan, 1971; Foxton, 1972; Jahn and Backus, 1976; Robertson et al., 1979; Fasham and Foxton, 1979; Magnuson et al., in press). In particular, cold-core eddies shed by the Gulf Stream seem to be responsible for much of the large scale patchiness in micronekton distributions in the Western North Atlantic (Wiebe et al., 1976; Wiebe and Boyd, 1978; Ornter et al., 1979).

In this study I sought to determine, in a preliminary

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manner, the effects of a warm-core eddy on fish by comparing biomass, species composition and size structure and diet of selected species among samples collected inside, outside and at the edge of a warm-core eddy. This work forms the first part of a long term program to examine the physics and biology of warm-core eddies and to assess the impact of eddies on oceanic processes in surrounding water masses.

MATERIALS AND METHODS

Study Area

A warm-core eddy, named 'Eddy F', was studied in the Tasman Sea off the southeast coast of Australia from 28 November to 13 December 1978. A detailed history of Eddy F prior to this time can be found in Tranter et al. (1980 b) and references cited therein. Briefly, Eddies E and F were formed by the subdivision of a larger eddy sometime between May and September, 1978. The parent Eddy D apparently originated from a meander of the East Australian Current in February, 1978. During September Eddy F was in a typical winter condition with a uniformly mixed layer (17.5°–17.7 °C) extending from the surface to 200 m, high nitrate levels (2.9–3.2 µmol N l^{-3}) and phytoplankton concentrations lower than that of surrounding waters. By November, a warm summer cap (18.0°–18.2 °C) of 60–65 m had formed over the top of the eddy core, nutrient levels had decreased (0.3–0.8 µmol N l^{-3}) and near surface phytoplankton concentrations were higher inside the eddy than outside. By December phytoplankton was concentrated at the base of the shallow mixed layer, particularly near the eddy centre and perimeter (Tranter et al., 1980 b).

Hydrography

The trawl sampling scheme was based on thermal structure rather than geographic coordinates and thus necessitated routine mapping of the position and configuration of the eddy. Vertical temperature profiles (to 450 m) were measured using expendable bathythermographs (Fig. 1) and temperature at 3 m was recorded continuously. Salinity to 250 m was measured using water samples collected with Nansen bottles.

Fish Collections

Fish were collected with a 308 meshes × 800 mm Engel midwater trawl (n = 31) having a 10 mm stretch mesh liner in the cod end (Table 1). Trawls were towed horizontally at depth for 30 min at a speed of 1.5 m s^{-1}. A Simrad FB Trawl Eye was mounted to the headrope of the trawl and provided a continuous record of trawl depth, temperature and vertical opening of the net. The Engel trawl opened vertically about 12 m and sampled an estimated 600 m^2 at the mouth. Eight additional midwater samples were taken with a Frank and Bryce bottom trawl after the Engel net was ripped. This bottom trawl had a 32 m footrope, stretch mesh size ranging from 229 mm at the mouth to 38 mm at the cod end and a 10 mm stretch mesh liner in the cod end. When fished in midwater the Frank and Bryce trawl opened 4 m high. Since biomass catch per unit effort differed significantly at night between the two nets (Table 1), results from the Frank and Bryce trawl are used only as an indicator of species presence in an area.

These non-closing nets probably fished during setting and recovery. No attempt was made to subtract species suspected of being caught higher in the water column although the possibility of contamination is considered in the interpretations of individual species' distributions. Time spent fishing through a 100 m depth range is estimated to be 8–17 % of total fishing time at depth.

Trawl samples were taken inside the eddy, at the eddy edge and outside the eddy Position with respect to the eddy was determined by temperature at a depth of 250 m (T_{250}). Boland (1973) and Nilsson (1977) have shown that the fastest surface currents occur at the eddy edge at T_{250} = 15.0 °C. Therefore, I defined the eddy edge as stations with T_{250} = 14°–16 °C. A T_{250} less than 14 °C was considered outside the eddy. A T_{250} more than 16 °C was considered inside the eddy (Fig. 1, Table 1). At least 2 trawls were taken near 50 m, 150 m and 250 m inside and outside the eddy during day and night and near 150 m and 250 m at the eddy edge at night. Additionally, 1 deep tow (475 m) was taken at night near the eddy centre. Time of sampling was chosen at random. Mean trawl temperatures ranged from 10.5°–19.9 °C.

Fish from each trawl were weighed en masse and preserved in 10 % seawater formalin. Occasionally, subsamples were frozen for stomach analyses. All fish were identified to species if possible and counted. Total length was measured to the nearest mm for the more common species. Systematics follow Greenwood et al. (1966), Baird (1971) and Bigelow et al. (1964). Species of the family Myctophidae were identified using a key to the Australian myctophids developed at the Australian Museum, Sydney (Paxton, unpubl.), Nafpaktitis et al. (1977) and Nafpaktitis (1978). Stomach contents of *Scopelopsis multipunctatus* (n = 69) and *Ceratoscopelus warmingii* (n = 20) were counted and identified.

Table 1. Trawl stations and fish catch (biomass and number of myctopid species per trawl). Beginning times and positions given

Position		Time	Date Dec.	Lat. S	Long. W	Depth (m)	T (°C)	T_{250} (°C)	No. Myc. species	Biomass (g)
Inside	Day	1020	9	36°34′	151°27′	48	18.2	17.3	0	20
		1920	1	36°24′	151°24′	50	18.1	16.6	0	25
		1350	9	36°33′	151°27′	52	18.2	17.6	0	10
		1500	9	36°35′	151°26′	148	17.7	17.6	0	20
		1240	9	36°30′	151°26′	160	17.8	17.7	0	20
		0945	12	36°31′	151°05′	244	16.3	16.2	2	20[a]
		1125	9	36°31′	151°27′	260	17.7	17.7	1	30
		1615	9	36°32′	151°27′	260	17.5	17.5	4	250
	Night	2350	1	36°29′	151°24′	32	18.3	17.4	14	3010
		2050	8	36°35′	151°26′	45	18.1	17.3	12	610
		0120	9	36°35′	151°27′	50	18.0	17.4	16	2270
		2150	8	36°33′	151°27′	155	17.5	17.3	16	1043
		0015	9	36°30′	151°28′	158	17.4	17.4	18	1820
		2305	8	36°31′	151°27′	255	17.3	17.3	23	1150
		0240	9	36°35′	151°27′	255	17.3	17.3	20	1417
		2215	1	36°26′	151°24′	475	10.5	17.0	22	1010
Edge	Day	1125	1	36°24′	151°01′	50	18.2	14.7	0	25
		1055	12	36°33′	151°03′	245	15.4	15.3	2	30[a]
	Night	2115	11	35°36′	151°26′	48	19.5	14.2	10	10[a]
		2215	11	35°34′	151°26′	152	16.6	14.2	13	140[a]
		2340	3	36°16′	151°56′	165	17.0	15.9	15	510
		0105	10	36°33′	150°56′	245	15.8	15.7	29	1388
		2330	11	35°37′	151°27′	248	15.4	15.3	6	50[a]
		0100	12	35°44′	151°24′	250	15.3	15.3	11	40[a]
		2345	9	36°30′	150°57′	260	15.6	15.7	26	1090
Outside	Day	1055	10	36°40′	150°30′	50	19.2	11.8	0	30
		1755	10	36°58′	150°40′	52	19.9	12.6	0	20
		1355	12	36°44′	150°58′	148	14.9	13.0	0	5[a]
		1330	10	36°46′	150°33′	149	14.2	11.8	0	50
		1505	12	36°40′	151°00′	150	16.0	13.7	1	20[a]
		0955	10	36°37′	150°30′	152	14.1	12.0	0	20
		1210	10	36°42′	150°30′	245	11.9	11.8	0	25
		1450	10	36°50′	150°35′	252	11.8	11.8	0	20
	Night	0315	3	36°04′	152°42′	52	17.5	11.3	11	13450
		0150	3	36°04′	152°41′	55	17.5	11.5	9	4400
		0005	3	36°04′	152°51′	150	13.4	12.2	21	1675
		0420	3	36°04′	152°45′	152	12.8	11.3	19	1650
		2130	2	36°04′	152°46′	255	13.1	13.2	24	1150
		2250	2	36°04′	152°50′	255	12.4	12.5	23	2002

[a] Frank and Bryce trawl

RESULTS

Eddy Structure

The thermal structure of Eddy F at a depth of 250 m is given in Fig. 1. The eddy was centred at Lat. 36°30′S, Long. 151°42′E. Eddy diameter (position of the 15 °C isotherm) was about 120 km at 250 m and decreased to 35 km at 400 m. Temperature at 250 m changed up to 8 C° over a distance of 90 km. Whether Eddy F was a closed ring during this study is not known because temperature data were not taken at the southern section of the eddy. Tranter et al. (1980 c), however, showed that the southern edge of Eddy F was closed 2 weeks before this study in late November.

Eddy F apparently moved north-northwesterly during the study (Fig. 1). The 15 °C isotherm at 250 m shifted approximately 55 km northward at an estimated mean rate of 6 km d^{-1}. This shift could have resulted from either an active movement of the eddy, or a deepening or tilting of the mixed layer. The latter may have been caused by the passage of a violent storm through the sampling area between 4–7 December.

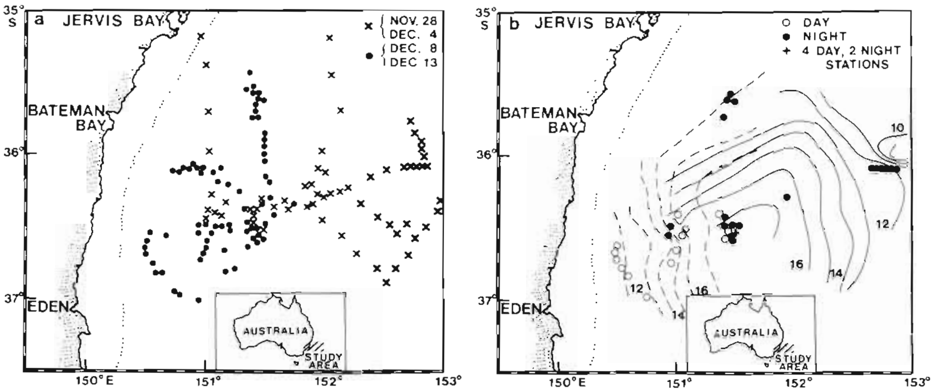

Fig. 1. XBT stations (a); trawl stations (b); temperature at a depth of 250 m from 28 November to 4 December (solid lines) and 8 to 13 December (dashed lines)

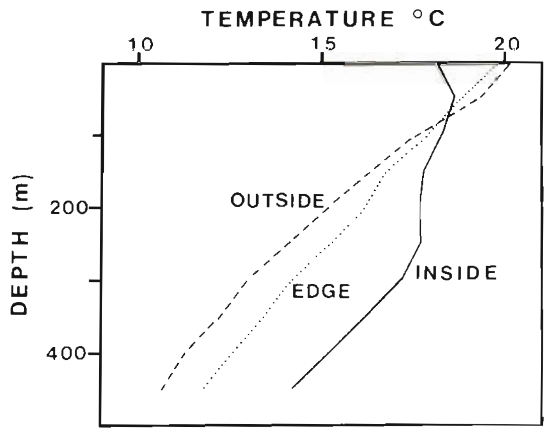

Fig. 2. Thermal profiles inside the eddy (Lat. 36°30'S, Long. 151°26'W), at the eddy edge (Lat. 35°42'S, Long. 151°26'W), and outside the eddy (Lat. 35°25'S, Long. 151°22'W)

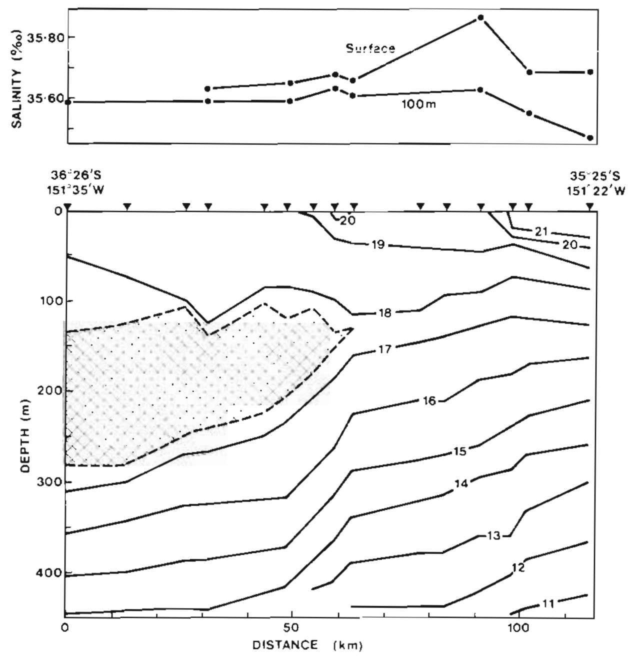

Fig. 3. Thermal structure across the northern section of the eddy (lower panel) during 11 to 12 December Station locations (▾) are given. Shaded region represents isothermal (17.4°–17.7 °C) eddy core. Salinity at the surface and at 100 m is given in the upper panel

Tranter et al. (1980 b) compared the T-S relationship inside and outside the eddy in the upper 200 m. Temperatures and salinities in Eddy F were clustered at 17°–19 °C and 35.55–35.65 ‰ S, respectively. Temperatures and salinities outside the eddy had a much broader range (12°–22 °C, 35.00–35.70 ‰ S). Near surface temperatures outside the eddy were about 2 C° higher than those inside the eddy (Fig. 2). Below 100 m temperatures outside the eddy were consistently cooler than those inside. Vertical thermal gradients in both regions generally ranged from 1.5°–2.5 °C per 100 m.

A thermal cross-section of the eddy is given in Fig. 3. Vertically, the eddy core was lens-shaped with isotherms deepening from the eddy edge towards the centre. The eddy core (17.4°–17.7 °C, 35.59 ‰ S) extended from 50 m to 290 m in the eddy centre and thinned towards the eddy edge. The core was overlaid by a warm (18°–19 °C) surface layer about 50–100 m thick that was probably caused by surface warming and the establishment of the seasonal thermocline (Tranter et al., 1980 a). A 2 °C thermal front and salinity peak were present at the eddy edge on the northern and western boundaries (Fig. 3) Maximum anticyclonic surface currents were 1.2 m s^{-1} at the eddy edge (B. Scott, pers. comm.)

Species Composition

A total of 14602 fish, representing 46 families, over 70 genera and 109 recognized species were caught (Table 2). Myctophids were by far the most abundant group both inside and outside the eddy and rep-

Table 2. Species list and catch for night (day) samples. Except for myctophids, only species representing more than 0.5 % of total catch are listed

Taxa	Number caught	% of total	% occurrence in trawls
BATHYLAGIDAE			
Bathylagus argyrogaster Norman, 1930	79 (1)	0.55	52 (6)
PHOTICHTHYIDAE			
Vinciguerria sp.	145 (4)	1.02	76 (11)
STERNOPTYCHIDAE			
Argyropelecus hemigymnus Cocco, 1829	73	0.50	57
MELANOSTOMIATIDAE			
Echiostoma barbatum Lowe, 1843	126 (1)	0.87	71 (6)
MYCTOPHIDAE			
Electrona risso (Cocco, 1929)	90 (15)	0.72	24 (28)
Hygophum hygomii (Lütken, 1892)	896	6.14	100
Hygophum reinhardtii (Lütken, 1892)	54	0.37	52
Hygophum proximum Becker, 1965	20	0.14	29
Benthosema suborbitale (Gilbert, 1913)	150	1.03	76
Myctophum phengodes (Lütken, 1892)	33	0.23	57
Myctophum brachygnathum (Bleeker, 1856)	1	0.01	5
Myctophum orientale (Gilbert, 1913)	3	0.02	10
Symbolophorus barnardi (Tånning, 1932)	60	0.41	81
Lobianchia dofleini (Zugmayer, 1911)	339	2.32	62
Lobianchia gemellarii (Cocco, 1838)	117	0.80	29
Diaphus anderseni Tåning, 1932	0 (1)	0.01	0 (6)
Diaphus brachycephalus Tåning, 1928	8	0.05	24
Diaphus mollis Tåning, 1928	140	0.96	62
Diaphus parri Tåning, 1932	23 (1)	0.16	38 (6)
Diaphus meadi Nafpaktitis, 1978	1453 (196)	11.29	86 (17)
Diaphus luetkeni (Brauer, 1904)	1	0.01	5
Diaphus termophilus Tåning, 1928	711	4.87	43
Diaphus metopoclampus (Cocco, 1929)	7	0.05	19
Diaphus danae Tåning, 1932	162	1.11	43
Diaphus fragilis Tåning, 1928	92	0.63	52
Diaphus perspicillatus (Ogilby, 1898)	12	0.08	33
Diaphus effulgens (Goode and Bean, 1896)	5	0.03	14
Diaphus bertelseni Nafpaktitis, 1966	2 (2)	0.03	10 (6)
Diaphus sp. nov.	22	0.15	38
Lampichthys procerus (Brauer, 1904)	28	0.19	38
Lampanyctodes hectoris (Günther, 1876)	79	0.54	24
Lampanyctus australis Tåning, 1932	48	0.33	38
Lampanyctus alatus Goode and Bean, 1896	292	2.00	76
Lampanyctus pusillus (Johnson, 1890)	245	1.68	71
Lampanyctus intricarius Tåning, 1928	15	0.10	48
Lampanyctus lepidolychnus Becker, 1967	5	0.03	14
Lampanyctus festivus Tåning, 1928	36	0.25	52
Lampanyctus ater Tåning, 1928	41	0.28	33
Bolinichthys longipes (Brauer, 1906)	14	0.10	29
Bolinichthys nikolayi Bekker, 1977	4	0.03	5
Ceratoscopelus warmingii (Lütken, 1892)	1194	8.18	100
Notoscopelus resplendens (Richardson, 1844)	953	6.53	95
Scopelopsis multipunctatus Brauer, 1906	5286	36.20	81
PERCICHTHYIDAE			
Howella sherborni (Norman, 1930)	337 (1)	2.31	57 (6)
CARANGIDAE			
Trachurus mccullochi Nichols, 1920	115 (101)	1.48	48 (39)
TRICHIURIDAE			
Lepidopus caudatus (Euphrasen, 1778)	89 (10)	0.68	52 (33)
TOTAL	13605 (333)	95.47	–

resented 88 % of total catch. Other taxa representing over 0.5 % of total catch were Percichthyidae (*Howella sherborni*, 2.3 %), Carangidae (*Trachurus mccullochi*, 1.5 %), Photochthyidae (*Vinciguerria* sp. 1%), Melanostomiatidae (*Echiostoma barbatum*, 0.9 %), Trichiuridae (*Lepidopus caudatus*, 0.7 %), Bathylagidae (*Bathylagus argyrogaster*, 0.6 %) and Sternoptychidae (*Argyropelecus hemigymnus*, 0.5 %). 15 species were represented by only 1 individual and over one-third (47) had fewer than 5 individuals. 26 species occurred in only 1 trawl and 11 occurred in only 2 trawls. Of the species contributing greater than 0.1 % of total catch (i.e. 15 individuals) all were more common at night than during the day, except *T. mccullochi* which occurred in about equal numbers in day and night samples.

Thirty nine species of myctophids were caught (Table 2). Seven species represented 85.7 % of the myctophid catch. *Scopelopsis multipunctatus* was the most abundant myctophid (41.1 %) and the most abundant species caught (36.2 % of total fish catch). Other common myctophids were *Diaphus meadi* (12.8 % of myctophids), *Ceratoscopelus warmingii* (9.3 %), *Notoscopelus resplendens* (7.4 %), *Hygophum hygomii* (7.0 %), *Diaphus termophilus* (5.5 %) and *Lobianchia dofleini* (2.6 %). 98 % of myctophids were caught at night. *C. warmingii* and *H. hygomii* were taken in every (21) night sample.

Fish Biomass

Fish biomass per Engel sample (Table 1) ranged from 0.51–13.45 kg at night and was significantly larger than the 0.01–0.25 kg per sample caught during day (Table 1). Catches from the Frank and Bryce trawl at night ranged from 0.01–0.14 kg and were smaller than catches from the Engel net when corrected for differences in trawl sampling volume. The 2 largest catches were made at a depth of 50 m outside the eddy and consisted primarily of *S. multipunctatus*. Large catches of 2.27 and 3.00 kg were also taken at 2 of the 3 50 m tows inside the eddy. All other night trawls caught 2 kg of fish or less and no differences were found among depths, temperatures and positions. Catches during the day were small and similar for all samples.

Distribution of Taxa

Taxa diversity as estimated by number of families per trawl did not differ significantly with position. More families however, occurred at depths of 250 m or more (mean = 18.0, range 10–21, n = 7) and temperatures less then 16 °C (mean = 17.7, range 13–21, n = 7) than in shallower (mean = 10.1, range 4–14, n = 10) water at night. Fewer families were caught during the day (mean = 5.1, range 1–9, n = 14) than at night (mean = 13.4, range 4–21, n = 17) for all temperatures and depths.

More species of myctophids were caught at night than during the day (Table 1). At position/depth strata (replicate trawls combined) number of species per trawl ranged from 12–26 at night and 0–4 during the day. Within positions more species were caught in deeper water at night. Species counts were largest at 250 m at the eddy edge and smallest in warm water at 50 m outside the eddy and at the eddy edge.

Species Distributions

Species representing more than 0.5 % of total catch were grouped into general distributional patterns based on position with respect to eddy and temperature (Table 3). A Mann-Whitney U test was used to compare night catches between inside and outside the eddy (250 m stations and shallower) and between warm (≥ 17.0 °C) and cold (≤ 16.0) water at all depths. For position comparisons, if a species was absent from a particular depth in both positions, the depth interval was excluded from the analyses. The following categories were recognized: (1) eddy species; (2) outside eddy/cold-water species; (3) cold-water species; (4) warm-water species; (5) widespread species.

Five common species (*Benthosema suborbitale* [19–34 mm total length]), *Howella sherborni* (35–93 mm), *Bathylagus argyrogaster*, *Diaphus fragilis* (57–106 mm), and *Lobianchia gemellarii* (27–52]) were caught primarily inside the eddy (Table 3). Only scattered individuals were found outside the eddy or at the eddy edge. *L. gemellarii* was not caught at the 50 m stations. Length frequency distributions of the myctophids *B. suborbitale*, *L. gemellarii* and *D. fragilis* are given in Fig. 4.

Lepidopus caudatus (80–422 mm) and *Trachurus mccullochi* (13–58 mm) were caught primarily outside the eddy at all depths and temperatures and secondarily at 250 m at the eddy edge (Table 3). During day, *T. mccullochi* also occurred entirely outside the eddy (82 % of total catch) and at 250 m at the eddy edge (18 %). Capture temperatures ranged from 11.8°–19.9 °C for *T. mccullochi* during the day and 12.8°–17.5 °C for both species at night. *T. mccullochi* is basically epipelagic and most deep catches were probably from surface contamination. *T. mccullochi* and *L. caudatus* were juveniles and no significant size differences were found among depths and temperatures.

Diaphus danae (14–38 mm) and *Lampanyctodes hec-*

Table 3. Ranges of numbers caught in trawl samples at night. Mean depth and temperature (1–3 samples) for each stratum are given. One zero represents absence of species in all samples

	Position								
	Outside			Edge		Inside			
Depth (m):	54	151	255	165	252	42	156	255	475
Temperature (°C):	17.5	13.1	12.8	17.0	15.7	18.1	17.4	17.3	10.5
Cold-water species									
Diaphus termophilus	0	5–104	91–154	0	59–222	0	0	3–13	60
Electrona risso	0	17–52	0–14	0	4–4	0	0	0	0
Lobiancha dofleini	0	29–96	57–101	1	9–20	0–8	0–2	2–3	0
Lampanyctus australis[a]	0	0–13	4–23	0	2–3	0–4	0	0	10
Chauliodus sloani[a]	0	0–5	6–9	0	6–7	0–1	0–1	0	10
Lampanyctus pusillus	0	9–32	39–52	2	3–4	0–18	0–8	4–4	53
Argyropelecus hemigymnus	0–1	2–9	13–24	0	4–5	0–1	0	4–5	4
Diaphus mollis	0	5–5	23–33	1	19–20	0	2–4	7–17	2
Warm-water species									
Ceratoscopelus warmingii	112–237	16–28	15–17	14	27–38	18–150	64–73	94–99	41
Eddy species									
Benthosema suborbitale	0	0–3	0–6	1	4–5	8–34	2–15	8–8	8
Howella sherborni	0	0	2–13	4	1–4	0–208	14–21	22–43	4
Bathylagus argyrogaster	0–2	0–4	0	0	2–2	0–34	3–4	2–3	5
Diaphus fragilis	0–1	0–2	0	1	2–13	0–2	23–31	7–9	0
Lobianchia gemellarii	0	2–3	0	0	0	0	35–45	15–17	0
Outside eddy/cold-water species									
Lepidopus caudatus	2–30	15–23	5–6	0	1–3	0	0	1–1	2
Trachurus mccullochi	4–13	8–15	12–22	0	14–20	0	0–1	0	0
Scopelopsis multipunctatus (>70 mm)	731–2381	53–95	53–94	18	8–21	0–5	0	0–3	11
Lampanyctodes hectoris	0	1–8	17–34	0	0	0	0	0	0
Diaphus danae	0–1	34–35	19–49	0	0–1	0	0	0	0
Widespread species									
Scopelopsis multipunctatus (< 70 mm)	7–34	125–657	21–34	13	4–9	84–416	38–58	36–36	15
Diaphus meadi	0–1	53–165	28–32	8	55–206	6–13	154–365	117–189	28
Notoscopelus resplendens	25–37	3–24	20–44	6	28–68	63–383	13–26	18–21	31
Hygophum hygomii	16–18	28–34	15–55	29	19–46	2–184	25–61	62–90	14
Lampanyctus alatus	0	2–9	19–25	8	6–7	0–97	19–20	18–25	25
Vinciguerria sp.	0	3–13	8–8	1	11–13	0–40	3–8	3–7	10
Echiostoma barbatum	1–2	1–2	3–5	0	0–5	3–41	0–7	1–12	5

[a] only 0.3 % of total catch

toris (34–45 mm) were restricted almost entirely to the cooler water (12.4°–13.4 °C) at 150 m and 250 m outside the eddy. Length frequency distributions are given in Fig. 4.

Eight species – *Diaphus termophilus, Electrona risso* (17–39 mm), *Lobianchia dofleini* (14–48 mm), *Lampanyctus australis* (19–118 mm), *Chauliodus sloani* (64–220 mm), *Lampanyctus pusillus* (13–46 mm), *Argyropelecus hemigymnus*, and *Diaphus mollis* (20–45 mm) – were caught mainly at temperatures less than 16 °C at night (Table 3). Cold-water species were most abundant at 150 m and 250 m outside the eddy, at 250 m at the eddy edge and occasionally at 475 m (10.5 °C) inside the eddy. Depth of the mixed layer seemed to determine the shallowest occurrence for most of these species, particularly *D. termophilus, E. risso, L. australis* and *C. sloani*. Cold-water species (e.g. *D. dofleini, D. danae* and *L. pusillus*) had thermal distributions quite distinct from warm-water species (e.g. *L. gemellarii* and *D. fragilis*) caught in the eddy (Fig. 5). No significant differences were found in size distribution of *L. dofleini, L. pusillus, E. risso* and *L. australis* among depths, temperatures or positions (Fig. 4). Mean size of *D. termophilus* at 250 m was larger at cooler temperatures (Fig. 6). Larger individuals (50–75 mm) were caught mainly at temperatures less than 14 °C; only small fish were caught in warmer water. Catches of small *D. termophilus* in the cooler water may have occurred as the trawl sampled warmer upper layers during setting and retrieval.

Diaphus mollis caught outside the eddy were larger than those caught inside the eddy ($p < 0.5$, Median test) for all samples combined or between equivalent depths (Fig. 7). Fish at the edge of the eddy were

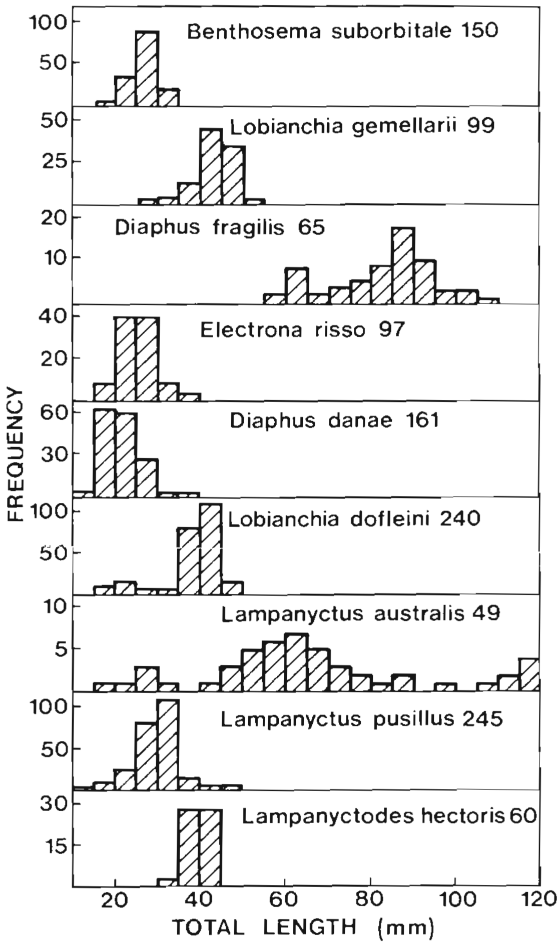

Fig. 4. Frequency distributions of total length of nine species of myctophids. Total number measured follows species name

intermediate in size. These size differences were small and were more likely due to growth rather than age class differences. Within any position, *D. mollis* were more common in deeper water.

Ceratoscopelus warmingii (44–109 mm) was the third most abundant species and was caught in all trawl hauls. This species was most common in warm water (Table 3). Largest catches were made inside the eddy and at the warm 50 m sample outside the eddy Catches at lower temperatures at 150 m and 250 m outside the eddy represent 7–25 % of the catches at 50 m and may be due to trawl contamination. *C. warmingii* inside the eddy were larger than those outside the eddy ($p < 0.5$, Median Test) for all samples combined or between equivalent depths (Fig. 7). Edge samples were intermediate in size.

A preliminary examination of stomach contents of *Ceratoscopelus warmingii* showed that individuals caught outside the eddy contained a large number of salps (mainly *Thalia democratica*), whereas no salps were found in stomachs of fish caught inside the eddy

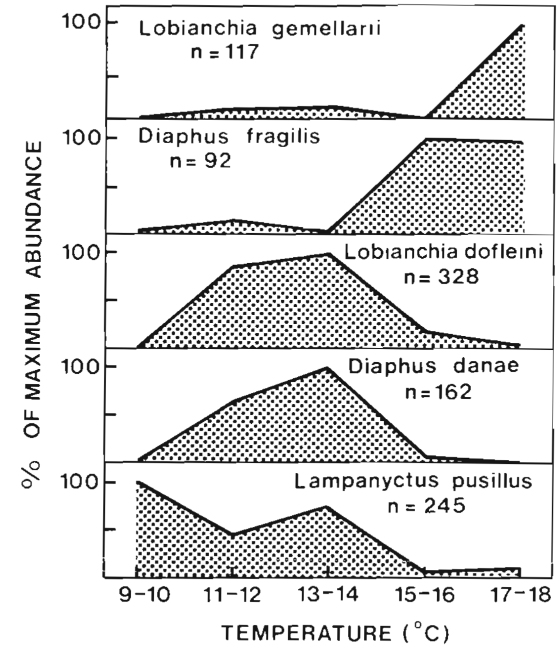

Fig. 5. Abundance of selected species of myctophids at different temperatures. Total number of individuals (n) caught is given. Catches are standardized to per cent of maximum abundance based on mean catch at each 2 °C for night Engel samples only

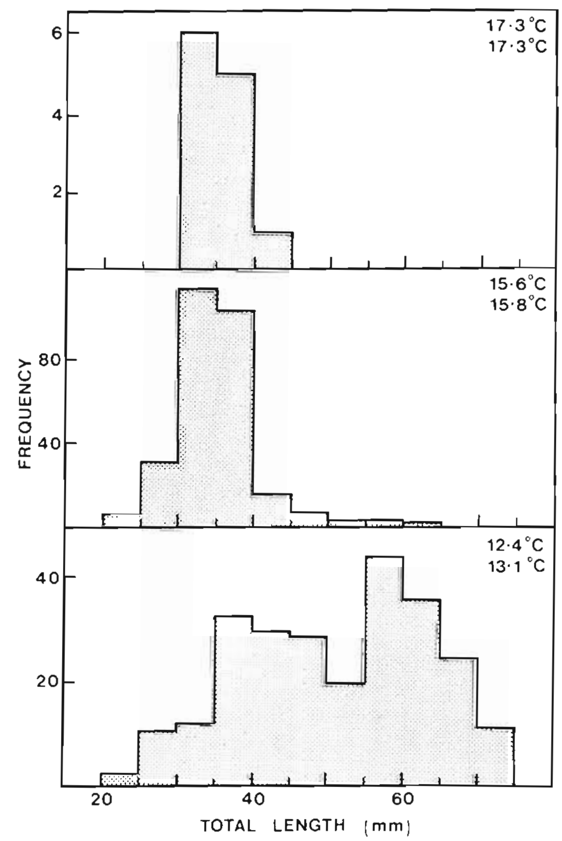

Fig. 6. *Diaphus termophilus* Frequency distributions of total length at different temperatures at 250 m Each frame represents the combined catch from two trawl samples

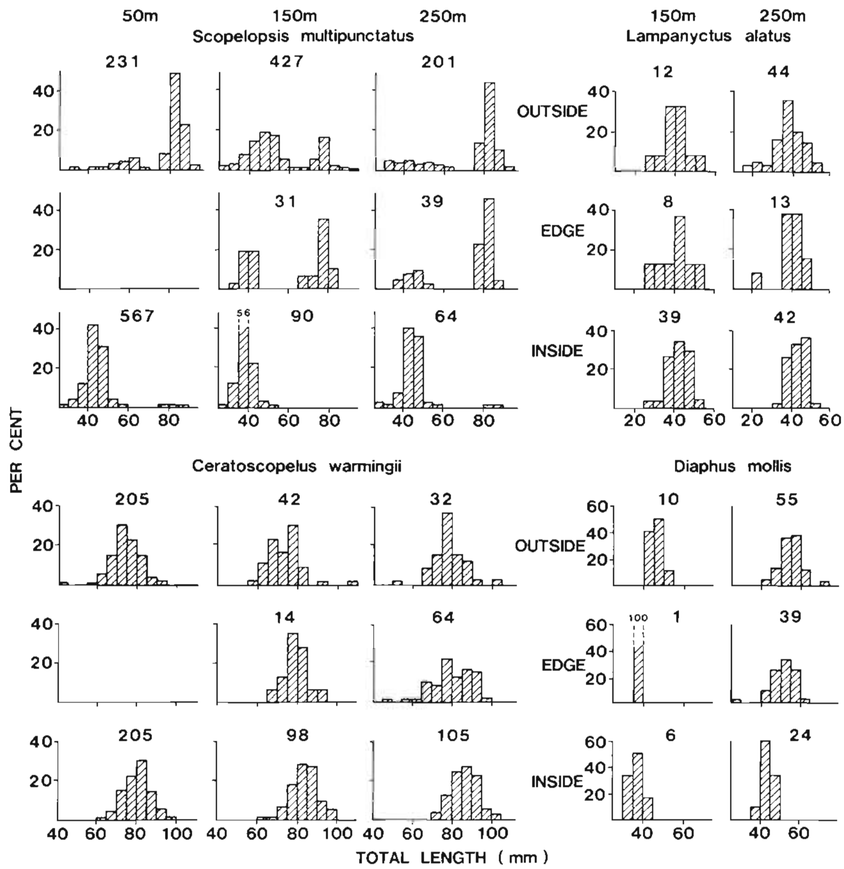

Fig. 7. Comparison of frequency distributions of total length of four species of myctophids among depths and positions (replicate samples combined). Data represent per cent of total measured, which is given

(Table 4). Fish from both regions ate copepods, amphipods, euphausids, and occasionally larval molluscs, ostracods, polychaetes and siphonophores.

Seven common species – *Scopelopsis multipunctatus* (25–95 mm), *Diaphus meadi* (20–56 mm), *Notoscopelus resplendens* (21–115 mm), *Hygophum hygomii* (23–75 mm), *Lampanctus alatus* (16–58 mm), *Vinciguerria* sp. and *Echiostoma barbatum* – occurred inside the eddy, at the eddy edge and outside the eddy (Table 3). These widespread fishes include 4 of the 5 most abundant myctophids.

Diaphus meadi, Notoscopelus resplendens, Hygophum hygomii, Vinciguerria sp. and *Echiostoma barbatum* did not differ in size distribution among temperatures, depths or positions. *Lampanctus alatus* were larger inside the eddy than outside the eddy for all samples combined and for the 250 m depths (Fig. 7). Edge samples were intermediate in size. Size differences were small.

The myctophid *Scopelopsis multipunctatus* was the most abundant species and accounted for over one third of all fish. This species occurred inside, outside and at the edge of the eddy but a distinct difference was noted in the distribution of size classes. *S. multipunctatus* caught outside the eddy were larger than those caught inside ($p < 0.5$, Median Test) for all samples combined and between equivalent depths (Fig. 7). Large *S. multipunctatus* (70–95 mm) were caught almost exclusively outside the eddy or at the eddy edge. Although this group has been statistically placed in the outside eddy/cold-water category (Table 3) it is believed that these fish were concentrated in the shallower warm-water outside the eddy. Catches at 150 m and 250 m in the cooler water outside the eddy represent only 2.2–13.0 % of the catches at 50 m and may have been caught during setting and retrieval of the trawl. Small *S. multipunctatus* (25–70 mm) had a widespread distribution (Table 3) with largest catches at 50 m inside the eddy and 150 m outside the eddy. Within this smaller size range, individuals were larger outside the eddy than inside the eddy (Fig. 7).

Stomach contents of large and small *Scopelopsis multipunctatus* were compared at different depths and temperatures (Table 4). All stomachs contained copepods, amphipods and euphausiids, and occasionally larval molluscs, ostracods, pollychaetes and

Table 4. Stomach contents of *Scopelopsis multipunctatus* and *Ceratoscopelus warmingii* caught inside and outside the eddy. Values represent mean (standard deviation) number of items per stomach

Species	Position	T (°C)	Depth (m)	n	Mean S.L.[a] (mm)	S.L. range (mm)	Diet: Salps[b]	Copepods	Amphipods	Euphausids	Larval molluscs	Other[c]
S. multipunctatus												
	Inside eddy	18.0–18.1	45	17	38.6	31–42	0	3.6	0.9	0.9	0.3	0.6
							–	(2.3)	(0.9)	(0.9)	(0.7)	(0.7)
		17.4–17.5	156	12	39.5	34–45	0	4.6	0.7	0.5	0.2	0.5
							–	(2.8)	(0.9)	(0.5)	(0.4)	(1.0)
	Outside eddy	17.5	54	10	46.0	39–53	25.4	8.0	1.2	1.0	0.4	0.2
							(11.0)	(3.5)	(1.3)	(0.9)	(0.5)	(0.4)
			54	10	70.8	68–73	96.8	6.7	1.3	1.2	0.1	0.3
							(40.7)	(4.7)	(0.9)	(1.0)	(0.3)	(0.5)
		12.8–13.4	151	10	44.2	41–49	29.3	9.9	1.5	0.7	0.5	0.2
							(13.4)	(4.6)	(1.2)	(0.5)	(0.7)	(0.4)
			151	10	71.7	69–81	76.0	7.5	1.1	1.1	0.2	0.1
							(62.0)	(5.7)	(1.0)	(1.3)	(0.6)	0.3
C. warmingii												
	Inside eddy	18.0	50	5	71.2	67–76	0	2.0	0.8	0.4	0	0
							–	(1.9)	(0.8)	(0.9)	–	–
		17.5	155	5	75.4	70–80	0	0.8	1.0	0.8	0	0.6
							–	(0.8)	(0.7)	(0.8)	–	(0.9)
	Outside eddy	17.5	54	10	72.9	67–78	53.8	2.2	2.0	0.1	0.4	0.1
							(29.1)	(1.6)	(1.0)	(0.3)	(0.7)	(0.3)

[a] Standard length
[b] Mainly *Thalia democratica*
[c] Includes ostracods, polychaetes and siphonophores

siphonophores. The dominant prey of large and small *S. multipunctatus* caught at cold and warm water outside the eddy was salps (mainly *Thalia democratica*). Salps were not found in the stomachs of fish caught inside the eddy.

Some of the less common species also showed distributional trends. *Argyropelecus aculeatus* were caught primarily at 250 m (42 individuals out of 45), and were present in all regions. The myctophid *Lampichthys procerus* was uncommon (only 28 individuals), although it occurred in 6 out of 7 cold water (< 16 °C) samples and 26 individuals were taken in cold water (2–11 ind. tow^{-1}). Similarly, 38 out of 41 *Lampancytus ater* were caught at temperatures less than 16 °C and this species occurred in 6 out of 7 cold water samples (2–13 ind. tow^{-1}). *Myctophum phengodes* was restricted to temperatures greater than 15 °C, occurring in 10 out of 12 such tows (1–10 ind. tow^{-1}). Catches of other species were too small for analyses.

Community Structure

The community structure at each position (inside eddy, eddy edge and outside eddy) was defined as those species contributing 1 % or more by number to the total catch at that position (Table 5).

Community structure within the eddy was recognizably distinct from that outside the eddy. Five species (*Scopelopsis multipunctatus, Diaphus meadi, Ceratoscopelus warmingii, Hygophum hygomii* and *Notoscopelus resplendens*) were common in all regions. No other overlap in dominant species was observed between inside and outside the eddy. Seven species were common only outside the eddy or at the eddy edge. Eight species were common only inside the eddy or at the eddy edge. The edge community was largely intermediate in character with 3 species shared with the inside community only, 3 species shared with the outside community only, and 4 species important only at the edge. Fewer edge samples were taken than in other regions.

DISCUSSION

Individual Species Distribution and Zoogeography

Many zoogeographic studies have linked the distribution of mesopelagic fishes (primarily myctophids) and other fauna to specific water masses (Ebeling, 1962; Backus et al., 1969, 1970, 1977; Nafpaktitis and Nafpaktitis, 1969; McGowan, 1974; Backus and Craddock, 1977; Nafpaktitis, 1978). Most work has relied on samples scattered over wide geographic ranges. The

Table 5. Species composition (> 1.0 % of total number of individuals at each position) of communities outside, inside and at the edge of the eddy. Values represent percent contribution of each species to each position

Species	Per cent of total		
	Outside eddy	Eddy edge	Inside eddy
Scopelopsis multipunctatus	60.0	5.6	18.1
Ceratoscopelus warmingii	6.0	6.1	12.7
Diaphus meadi	3.9	20.6	17.1
Hygophum hygomii	2.3	7.2	11.7
Notoscopelus resplendens	2.1	7.8	12.7
Diaphus danae	1.9		
Lampanyctus pusillus	1.9		
Electrona risso	1.1		
Lepidopus caudatus	1.1		
Diaphus termophilus	5.0	21.6	
Lobianchia dofleini	4.0	2.3	
Trachurus mccullochi	1.0	2.6	
Diaphus mollis		3.1	
Lampanyctus ater		1.3	
Argyropelecus aculeatus		1.2	
Chauliodus sloani		1.0	
Lampanyctus alatus		1.6	3.7
Diaphus fragilis		1.2	1.4
Vinciguerria sp.		1.9	1.3
Howella sherborni			6.2
Lobianchia gemellarii			2.2
Echistoma barbatum			2.0
Benthosema suborbitale			1.9
Bathylagus argyrogaster			1.3
Total number of individuals	7145	1304	4994

present study differs because samples were taken in different hydrographic conditions over a small geographic space. The data show that fish distributions corresponded to water masses and the community structure of dominant fishes within a warm-core eddy at night was recognizably distinct from that outside the eddy. The eddy edge was largely a transition zone. A small increase in myctophid diversity was evident at 250 m at the eddy edge but other ecotone 'edge effects' such as increased diversity or biomass (Odum, 1971; Terborgh, 1971) were not evident.

The associations of particular species with the water masses near Eddy F were similar to those shown from larger scale zoogeographic studies. For example, Backus et al. (1977) classify *Benthosema suborbitale* and *Lobianchia gemellarii* as tropical-subtropical species and *Diaphus fragilis* as a tropical species in the Atlantic Ocean. These species are also considered tropical or subtropical in the Pacific and Indian Oceans (Rass, 1960; Nafpaktitis and Nafpaktitis, 1969; Wisner, 1976; Nafpaktitis, 1978). These eddy species were caught mainly in warm water and probably originated from tropical-subtropical water to the north (Nilsson and Cresswell, in press). The warm-water *Ceratoscopelus warmingii* also has a tropical-subtropical distribution in the Atlantic (Backus et al., 1977).

Similarly, cold water species have more temperature zoogeographic distributions. Backus et al. (1977) classify *Lampanyctus pusillus* and *Lobianchia dofleini* as temperate-semisubtropical species in the Atlantic Ocean. *Electrona risso* and *L. australis* are included in Becker's (1964) temperate-cold water complex and *L. australis* occurs primarily between Lat. 31 °S and Lat. 44 °S in the Indian Ocean (Nafpaktitis and Nafpaktitis, 1969).

Widespread species have distributions in the Atlantic Ocean (Backus et al., 1977) ranging from tropical (*Lampanyctus alatus*) to tropical-subtropical, (*Notoscopelus resplendens*) to temperate-semisubtropical (*Hygophum hygomii*). *N. resplendens* has a tropical-subtropical distribution in all oceans (Nafpaktitis, 1975). The widespread *Scopelopsis multipunctatus* taken both in and near Eddy F has a circumglobal distribution restricted to the southern oceans (Wisner, 1976). This species is generally regarded as a warm-water species. Wisner (1976) records *S. multipunctatus* only between 15° and 25 °S in the Pacific Ocean and Nafpaktitis and Nafpaktitis (1969) record it from 23° to 29 °S in the Indian Ocean. *S. multipunctatus* was not found among the essentially temperate assemblages by Robertson et al. (1979).

Two exceptions to the zoogeographic literature exist. The cold water species *Diaphus mollis* and *D. termophilus* are considered to be tropical-subtropical and tropical species, respectively (Wisner, 1976; Backus et al., 1977). This may point out a possible source of variability of general species classification based on large scale geographic distributions without consideration of the local (i.e. at the trawl) hydrographic conditions. Indeed, this study found cold water (temperate-semisubtropical) and warm water (tropical) species within a geographic space of about 100 km. For example, the closely related species *Lobianchia dofleini* and *L. gemellarii* are considered to be a temperate-subtropical species and a tropical-subtropical species respectively in the Atlantic (Backus et al., 1977). Nafpaktitis (1978) reported that, in the Indian Ocean, the northernmost limit of *L. dofleini* coincides with the southernmost limit of *L. gemellarii*. In the present study both species were abundant, however, *L. dofleini* was caught primarily in colder waters (98 % of total at < 16 °C) and *L. gemellarii* occurred in warm water (96 % of total at > 17 °C). These data indicate that the 2 species may be separated by temperature (Fig. 5).

It is not known how fish are distributed during day because of small catches. During day most of the common fishes (*Lobianchia dofleini, L. gemellarii, Ceratoscopelus warmingii, Lampanyctus alatus, L. pusillus, Hygophum hygomii, Notoscopelus resplen-*

dens, *Diaphus fragilis* and *Benthosema suborbitale*) migrate to depths of 400–1000 m in other areas (Badcock, 1970; Clarke, 1973; Badcock and Merrett, 1976; Karnella and Gibbs, 1977), which is deeper than my day tows. Trawl avoidance is unlikely to be a major cause of reduced day catches for these small fishes because of the large sampling area of the Engel midwater trawl.

Sampling Limitations

My conclusions are limited by the sampling strategy. The limitations are:

(1) Small sample size is, perhaps, the most serious shortcoming of the sampling program. Patchy distributions, stray catches and variations in trawl performance can lead to erroneous conclusions when only 1–3 samples are taken per stratum. However, the consistent distributional patterns both within and among species argue that the sampling was generally representative.

(2) Midwater trawling gear biases the type and size of species captured (Harrison, 1967). The Engel midwater trawl probably missed the small species and size classes because of escapement through the large meshes near the mouth and the 10 mm mesh cod lining.

(3) The open trawl increased variability since samples were contaminated by fishes caught at shallower depths during setting and retrieval. Catches of *Ceratoscopelus warmingii* and *Scopelopsis multipunctatus* at depths greater than 50 m outside the eddy were of the same magnitude as might be expected from near surface contamination.

(4) The sampling program was limited to a 2 week period and biological structure of eddies can change seasonally (Tranter et al., 1980 a) or with eddy age (Wiebe et al., 1976).

(5) Positions with respect to the eddy were defined by temperature at 250 m, which may not exactly correspond to those water masses directly affected by eddy dynamics.

(6) Vertical migrations of fishes throughout the night may have affected results since trawl samples were not standardized at time intervals shorter than 10 h.

Physical and Biological Factors

The mechanism creating and maintaining the contrasts in the fish communities cannot be determined with my data. The eddy community was probably originally established during eddy formation when a group of organisms was trapped within the eddy and transported with it. This process is similar to that proposed for the euphausid community associated with cold-core rings of the Gulf Stream (Wiebe et al., 1976).

This biological system has probably changed during the eddy's 7–10 months' existence. Whether the eddy remains ecologically distinct from surrounding water masses is not known. Scattered catches of some species throughout all regions suggest that the eddy is not 100 % effective as a barrier (see discussion by Brandt and Wadley, in press). Fish migrations into and out of the eddy would dilute any original differences in species assemblages. Perhaps the eddy has not been in existence long enough for species to mix completely although a mean speed of only 3.5 mm s^{-1} (300 m d^{-1}) would be sufficient to traverse an eddy radius for a 200 d old eddy. Emigrating species would tend to be lost to surrounding water masses.

Fish could also be advected into the eddy when water from the East Australian Current is entrained along the eddy perimeter (Tranter et al., 1980 a; Brandt et al., 1981; Nilsson and Cresswell, 1981). These intrusions were unlikely during the few months before this study because the East Australian Current was over 600 km north of Eddy F (Tranter et al., 1980 a). The degree to which migrations and advection are important is probably species and size dependent.

Habitat selection by fishes could maintain or even reinforce the differences in species assemblages. Differences in habitat preferences among species would isolate the eddy community from the surrounding water masses because of the sharp environmental gradients at the eddy edge. Both physical-chemical (temperature, salinity, turbidity, water velocity, oxygen, nutrients) and biological (phytoplankton productivity, prey availability, predator intensity, competitors) factors could be important. For example, distributions of some of the species in this study corresponded closely to temperature, and behavioural thermoregulation of fish has been well documented (Ferguson, 1958; Hela and Laevastu, 1970; Brett, 1971; Fry, 1971; Neill and Magnuson, 1974; Wylie et al., 1976; Coutant, 1977; Magnuson and Beitinger, 1978). Vertically migrating species would also experience a different (higher) total heat budget inside than outside the eddy (Griffiths and Brandt, unpubl.).

Biological interactions could be important. The abundances of potential prey, predators and competitors may differ inside and outside the eddy and responses of fishes to these factors could help maintain the differences in species assemblages between the two regions. For example, Tranter et al., (1980 a) have documented a time lag of 1–2 months between the development of a phytoplankton bloom inside Eddy F and in surrounding water masses. In September 1978 phytoplankton levels were much higher outside Eddy

F than inside; by November the situation had reversed. These differences in phytoplankton productivity could in turn affect prey availability. Indeed, individuals of *Scopelopsis multipunctatus* and *Ceratoscopus warmingii* did differ in diet inside and outside the eddy. Perhaps the apparent growth differences between individuals of the same species occurring inside and outside the eddy may have been caused by differences in both thermal environment and diet.

Extending this argument further, if species inhabit and forage in different thermal zones or water masses, potential predator-prey and competitive interactions could also be minimized (MacLean and Magnuson, 1977). Since most myctophid species are morphologically (functionally) similar, one might expect such fine-scale resource partitioning among and within species (Schoener, 1974; MacLean and Magnuson, 1977; Magnuson et al., 1979; Brandt, 1980; Brandt et al, 1980). For example the closely related species *Lobianchia gemellarii* and *L. dofleini* appeared to be segregated by temperature and there is evidence that size classes of *Diaphus termophilus* were occupying different thermal zones. These potential secondary effects of eddies need to be examined further

My data suggest that warm-core eddies play an important, yet relatively unknown role in the biological processes of western boundary regions. In the Tasman Sea these eddies may exist for at least 18 months (Nilsson and Cresswell, in press) and at times are more productive than surrounding water masses. Whether fishes within the eddy are thriving or are expatriates (Zurbrigg and Scott, 1972) is not known. Since about two thirds of the eddies re-coalesce with the East Australian Current (Nilsson and Cresswell, 1981) the eddy community may be reintroduced into the main current system. A time-series study of one or more eddies is needed to assess the impact of eddies on the pelagic community as a whole.

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