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DISTRIBUTION OF MYCTOPHID FISHES ACROSS THE EQUATORIAL CURRENT SYSTEM  
IN THE CENTRAL PACIFIC

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IN OCEANOGRAPHY

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## PREFACE

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## INTRODUCTION

Ranges of pelagic species often conform with major water masses as defined by temperature-salinity curves (Johnson and Brinton, 1963). Because T-S curves exclude the upper 100 m of the water column, variations of temperature and salinity in the upper layers do not affect the shape of the curves. Thus, major water masses, so defined, are large scale, sub-surface features. There may be considerable variation in the hydrography of the mixed layer above a given water mass which may affect organisms living within, or periodically inhabiting the surface layers, resulting in subpatterns of species' distributions which do not follow the horizontal limits of the water mass below.

Sampling along the equator in the Pacific, Grandperrin and Rivaton (1966) have demonstrated the existence of four distinct longitudinal faunal zones which are correlated with variations in the depth of the Cromwell Current and associated variations in carbon dioxide concentration, oxygen concentration, nutrient levels and productivity. All four zones lie along the equator within the Pacific Equatorial Water mass, yet each is characterized by a distinct faunal assemblage including endemic species. Major faunal changes, then, occur within the Pacific Equatorial Water mass coincident with longitudinal hydrographical changes in the surface layers. Thus, it may be expected that faunal breaks also occur latitudinally across the Pacific Equatorial Water mass where major and presumably biologically relevant changes in surface hydrographic conditions are observed.

Myctophids were chosen for this study for several reasons. They are primarily mesopelagic fishes, but typically migrate upward at night. Most species cross into the mixed layer where they are sus-

ceptible to capture by the sampling methods used in this study. Many species of this family inhabit equatorial waters and some are quite abundant. Recently, their taxonomy has become stabilized, thus allowing definitive investigations of their distribution.

This study attempts to determine the latitudinal zonation of myctophids occurring in the equatorial waters of the Pacific. The study is limited to shallow water samples collected at night. Distribution patterns of myctophids and several hydrographical features are examined and an attempt is made to determine which features are most closely related to the distribution of myctophid fishes.

#### MATERIALS AND METHODS

Data for this study were collected during cruise 43 of the U.S. Fish and Wildlife Service Vessel Townsend Cromwell from April 29 to June 11, 1969. Pelagic trawl collections were made along a transect at  $145^{\circ}$  west longitude at five locations, approximately at  $12\frac{1}{2}^{\circ}$  N,  $7\frac{1}{2}^{\circ}$  N,  $3\frac{1}{2}^{\circ}$  N,  $0^{\circ}$ , and  $3\frac{1}{2}^{\circ}$  S (Table 1). At each latitude five tows were made (except at  $3\frac{1}{2}^{\circ}$  S, where four tows were made) using an anchovy number two Cobb pelagic trawl (Higgins, 1970). All tows were taken at night and each lasted from about 2000 to 0200 hours. Depths of tows, determined from wire angle and amount of wire out, was 20 m and 50 m. (More precise depth determinations made on a later cruise indicate that tows made on cruise 43 were probably at 30 m and 75 m.) Towing depth was alternated nightly except at the equator where all tows were at 50 m. Depth was regulated by controlling ship's speed and amount of wire out.

When the total sample size exceeded four gallons, one gallon

TABLE 1

Positions, depths, and dates of Cobb pelagic trawl stations  
on Bureau of Commercial Fisheries cruise TC 43

<u>Station number</u>	<u>Position</u>	<u>Depth (M)</u>	<u>Date</u>
8	12 04' N 144 54' W	20	07-M
10	12 03' N 144 55' W	50	08-M
12	12 11' N 145 11' W	20	09-M
14	11 56' N 144 54' W	50	10-M
16	11 58' N 144 57' W	20	11-M
22	07 41' N 145 01' W	50	13-M
24	07 27' N 145 05' W	20	14-M
26	07 33' N 144 50' W	50	15-M
28	07 33' N 144 48' W	20	16-M
30	07 19' N 145 09' W	50	17-M
36	03 29' N 145 03' W	20	19-M
38	03 30' N 145 06' W	50	20-M
40	03 31' N 145 00' W	20	21-M
42	03 32' N 144 59' W	50	22-M
44	03 40' N 144 54' W	20	23-M
46	00 01' N 144 50' W	50	25-M
48	00 04' N 145 07' W	50	26-M
50	00 03' N 145 05' W	50	27-M
52	00 01' N 145 03' W	50	28-M
54	00 04' N 144 59' W	50	29-M
55	02 59' S 144 53' W	20	30-M
57	03 31' S 145 11' W	50	31-M
59	03 34' S 145 00' W	20	01-J
61	03 35' S 145 11' W	50	02-J

subsamples were taken prior to preserving. All myctophids in the preserved samples were counted and counts were adjusted when subsampling procedures were necessary. Species were identified, for the most part, with the aid of an unpublished manuscript loaned by Robert L. Wisner, Scripps Institute of Oceanography. Frequently, specimens were badly damaged and could not be positively identified. Such problems are further elaborated under discussions of the different species.

Contamination of the samples by specimens captured above the towing depth was a minor problem. Although the net was open at all times, ascent and descent took only a small percentage of the total towing time. Even for the 50 m tows, the trawl required approximately 10 minutes to reach towing depth and 15 minutes to ascend. Total time at depth was approximately 360 minutes for each tow.

Kuba (1970) has demonstrated that the Cobb trawl used during the present study provides better samples of the mesopelagic fish fauna than the commonly used Isaacs-Kidd midwater trawl. Comparing the relative sampling efficiencies of the Cobb trawl and the 10 foot Isaacs-Kidd midwater trawl for myctophids and gonostomatids in Pacific equatorial waters, Kuba (1970) reports that the Cobb trawl samples approximately 50 times more water per tow than the 10 foot IKMT when both are towed at the same speed. Primarily because of the larger volume of water filtered, the Cobb trawl, towed at 2 knots, provided much better estimates of species diversity than the IKMT, even when the latter was towed at 4 knots. Samples from  $12\frac{1}{2}^{\circ}\text{N}$ ,  $7\frac{1}{2}^{\circ}\text{N}$ , and  $3\frac{1}{2}^{\circ}\text{S}$  were compared. The total number of myctophid species captured at these latitudes was 12, 11 and 12, respectively. At  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$

all species were captured by the Cobb trawl while the IKMT took only 4 species at each latitude. Of the 12 species captured at  $3\frac{1}{2}^{\circ}\text{S}$ , 10 species were taken by the Cobb trawl and 7 by the IKMT.

Temperature and salinity measurements were regularly taken during the cruise. Bathythermograph casts to 300 m were made at approximately 50 km intervals between  $14^{\circ}\text{N}$  and  $3^{\circ}\text{N}$  and at approximately 16 km intervals between  $3^{\circ}\text{N}$  and  $3^{\circ}\text{S}$ . Salinity-temperature-depth casts to 500 m were made at 1 degree intervals from  $14^{\circ}\text{N}$  to  $3^{\circ}\text{N}$  and at approximately 32 km intervals from  $3^{\circ}\text{N}$  to  $3^{\circ}\text{S}$ . Surface salinity was determined from surface water samples taken approximately every 50 km and titrated using the Knudsen method.

#### PHYSICAL OCEANOGRAPHY OF THE SAMPLING AREA

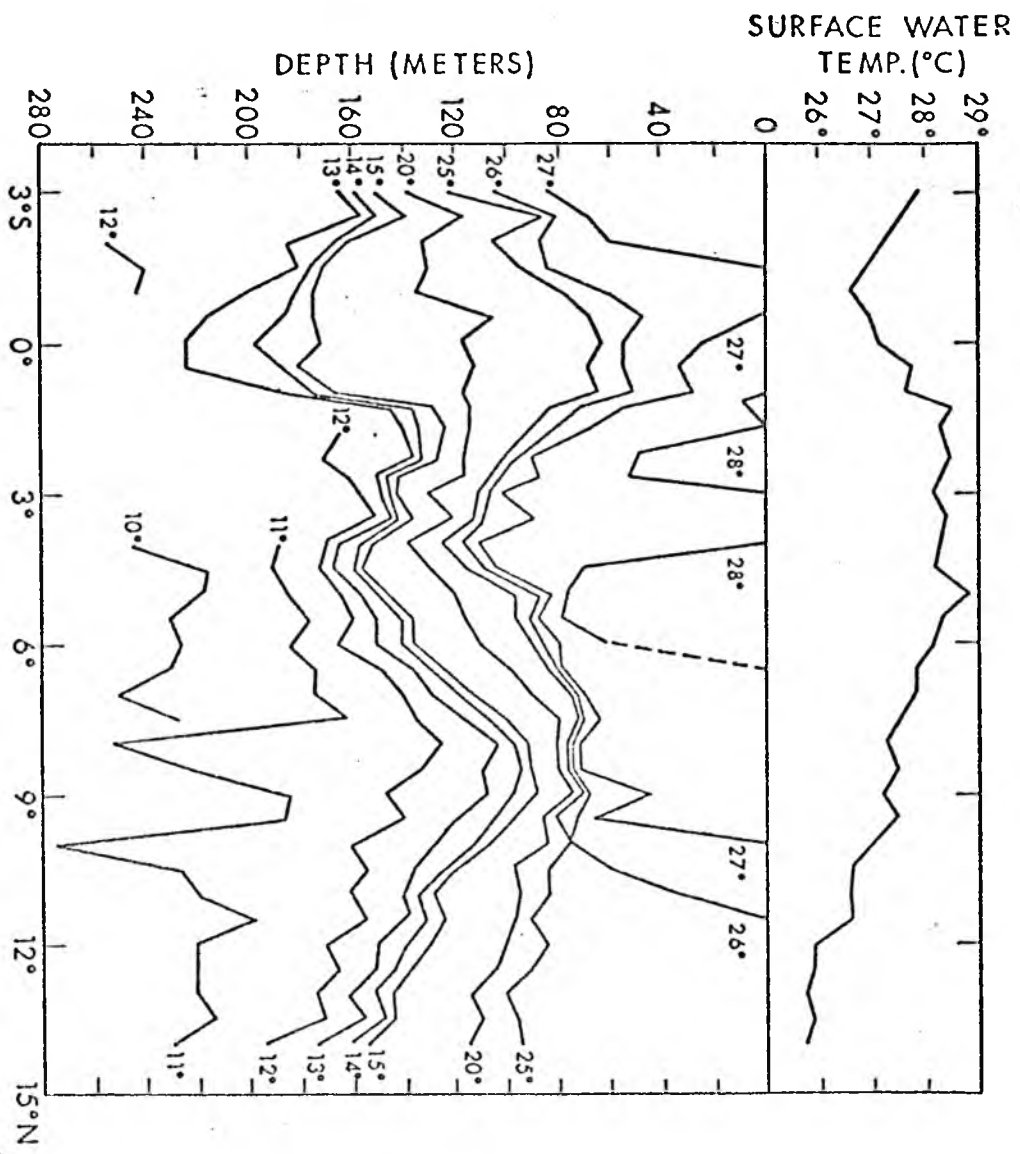
The general pattern of surface circulation in the central equatorial Pacific has been described by Sverdrup *et. al.* (1942), Cromwell (1951), and others. The equatorial current system is highly variable, the major currents often shifting their positions by several degrees of latitude as the result of seasonal meteorological changes. It is thus important, when working in this area, to know the precise location of the various currents.

Figure 1 is a temperature profile of the sampling area compiled from data collected during cruise 43. The North Equatorial Current is indicated by isotherms sloping downward to the north from  $09^{\circ}\text{N}$  to  $13\frac{1}{2}^{\circ}\text{N}$ . From  $04^{\circ}\text{N}$  to  $09^{\circ}\text{N}$ , the isotherms sloping down to the south indicate the eastward flowing Equatorial Countercurrent. From  $04^{\circ}\text{N}$  to the southern limit of the sampling area is the South Equatorial Current, flowing west. The eastward flowing Cromwell Current extended

## FIGURE 1

Top- Surface temperature across the equator  
along  $145^{\circ}\text{W}$  longitude from  $03^{\circ}\text{S}$  to  $14^{\circ}\text{N}$

Bottom- Temperature-depth profile across the equator  
along  $145^{\circ}\text{W}$  longitude from  $03^{\circ}\text{S}$  to  $14^{\circ}\text{N}$



from 50 m to 225 m in depth at the equator. It can be seen in Figure 1 as the oval area between the doming of the  $26^{\circ}$  isotherm and the depression of the  $13^{\circ}$  isotherm.

Meridional circulation in the region of the equator has been described by Cromwell (1953). Horizontal divergence at or near the equator induces upwelling which brings nutrient rich water to the surface. During the southeast trade winds, there is a net transport of water across the equator to the north. Upwelled water is carried to a zone of convergence between  $02^{\circ}\text{N}$  and  $04^{\circ}\text{N}$ , forming a thin band of highly productive water just north of the equator. This zone of upwelling is indicated in Figure 1 by a decrease in surface temperature around  $01^{\circ}\text{S}$ .

Figure 2 is a salinity profile of the sampling area compiled from cruise data. Salinity is quite uniform in the upper layer north of the equator, varying between  $34.8\text{‰}$  and  $35.0\text{‰}$ . South of the equator, salinity is higher and less uniform, ranging from  $34.8\text{‰}$  to  $35.8\text{‰}$ . This general increase and greater variability is caused by a tongue of high salinity water with its core at about 100 m, which penetrates the equatorial region from the South Pacific and extends to just north of the equator. The presence of this tongue is shown by the increasing surface salinity between  $01^{\circ}\text{N}$  and the equator.

## RESULTS

Figure 3 shows the average number of total myctophids captured per 50 m tow at each latitude. Total numbers increased steadily from  $12\frac{1}{2}^{\circ}\text{N}$  to the equator, then decreased sharply between the equator and

## FIGURE 2

Top- Surface salinity across the equator  
along  $145^{\circ}\text{W}$  longitude from  $03^{\circ}\text{S}$  to  $18^{\circ}\text{N}$

Bottom- Salinity-depth profile across the equator  
along  $145^{\circ}\text{W}$  longitude from  $03^{\circ}\text{S}$  to  $18^{\circ}\text{N}$

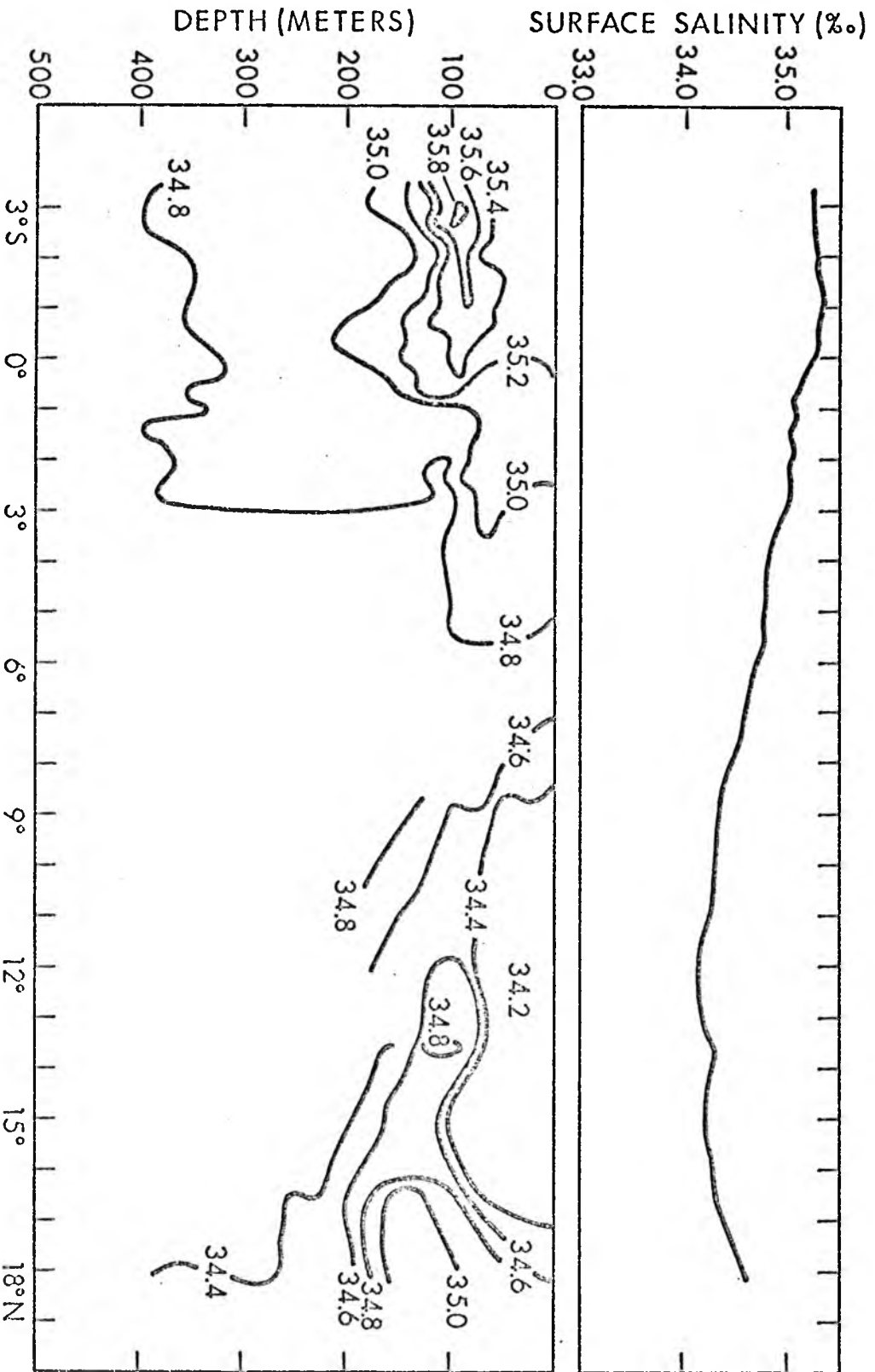
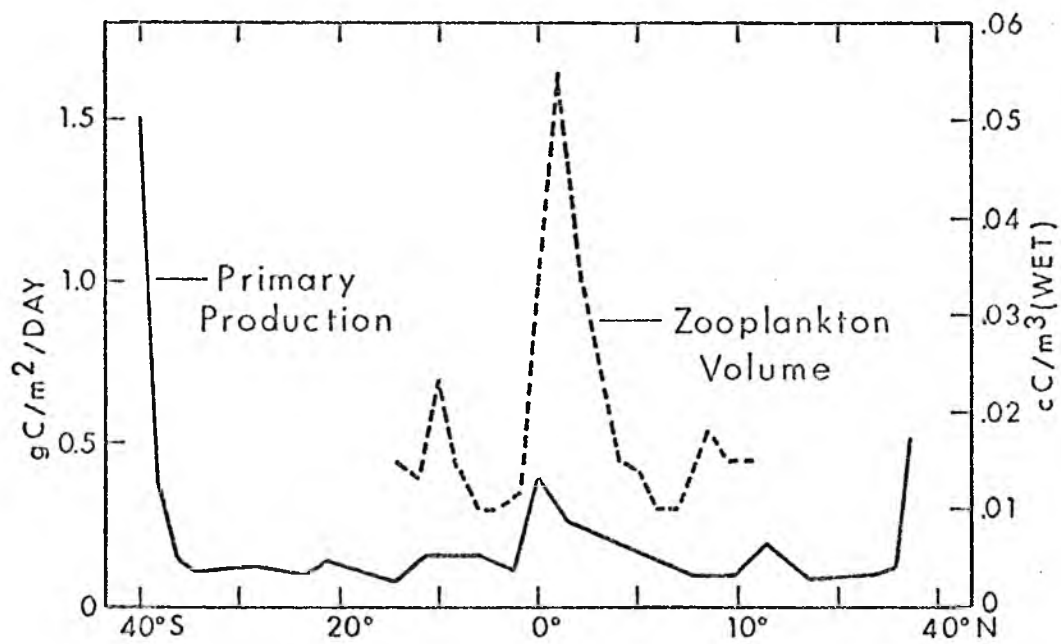
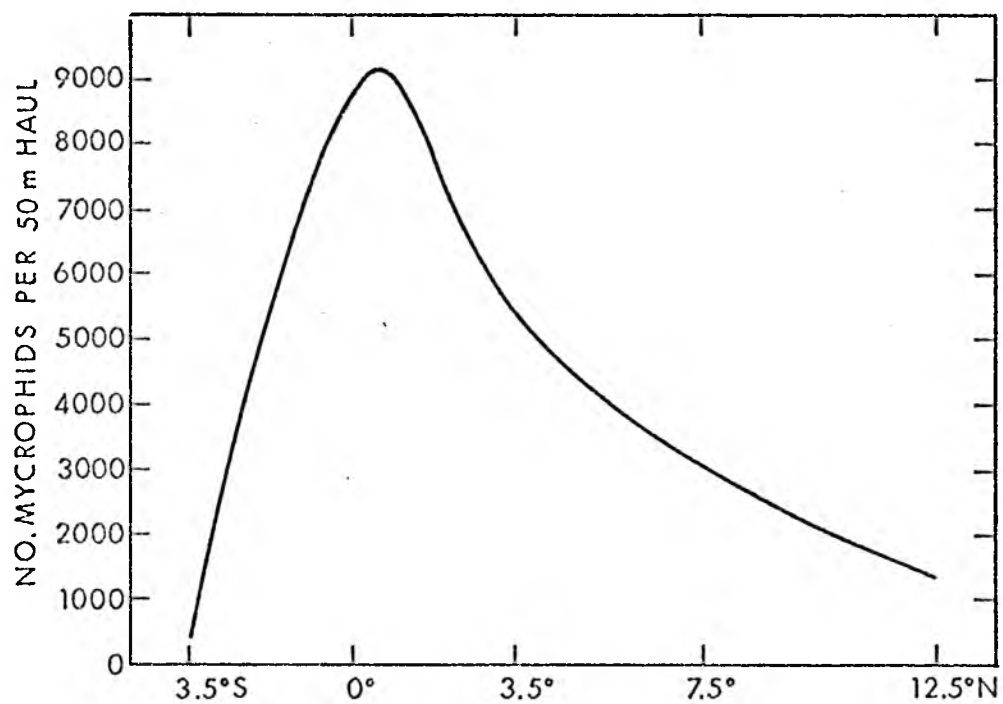


FIGURE 3

Average number of myctophid fishes per trawl at 50 m  
along  $145^{\circ}\text{W}$  longitude  
from  $12\frac{1}{2}^{\circ}\text{N}$  to  $3\frac{1}{2}^{\circ}\text{S}$  during May-June, 1969

FIGURE 4

Rate of primary production (Galathea) and volume of zooplankton  
(after King and Demond, 1953) across the equator  
along  $160^{\circ}$ - $170^{\circ}\text{W}$  during January-March



$3\frac{1}{2}^{\circ}\text{S}$ . Other investigators report similar distributions for primary production (Neilsen and Jensen, 1957), zooplankton biomass (King and Demond, 1953; King and Hida, 1957), forage organisms (King and Iversen, 1962), and large fishes (Sette, 1955; Murphy and Shimura, 1958). Figure 4 shows variations in the rate of primary production and zooplankton volumes on a longitudinal section across the equator in the central Pacific. Comparison of Figures 3 and 4 clearly demonstrates that the overall abundance of myctophid fishes, primarily zooplankton feeders, is closely related to zooplankton biomass distribution and to the pattern of primary production in the vicinity of the equator.

Catch results for species are summarized in Table 2. Table 3 is a list of the "dominant species" at each latitude and depth. A species was considered "dominant" at a given latitude and depth if it made up 15% or more by number of the total myctophids.

In the following discussion, catch results for each of the genera are considered separately. Species presence and absence, vertical zonation, and variations in abundance are considered. It is noted when results agree with other studies which have been conducted in the same general area.

#### HYGOPHUM

Hygophum proximum was the only species collected in this genus. It was taken at every latitude and depth and was present in all but one sample. It was one of the few species which exhibited no marked decline in abundance in the generally barren waters at  $3\frac{1}{2}^{\circ}\text{S}$  and was the

TABLE 2

Number of individuals of each species taken per tow for stations in Table 1

Station number	12 <sup>1</sup> / <sub>2</sub> <sup>0</sup> N					7 <sup>1</sup> / <sub>2</sub> <sup>0</sup> N				
	20m			50m		20m			50m	
	8	12	16	10	14	24	28	22	26	30
<u>Hygophum proximum</u>	8	--	3	170	30	111	51	206	274	98
<u>Diogenichthys atlanticus</u>	--	--	--	9	1	--	--	5	7	12
<u>Diogenichthys laternatus</u>	--	2	--	1139	173	3	--	214	150	168
<u>Symbolophorus evermanni</u>	1491	334	270	62	75	446	745	514	359	927
<u>S. evermanni</u> (form A)	647	55	57	12	5	10	17	13	13	18
<u>S. evermanni</u> (form B)	21	5	1	--	2	5	3	6	38	48
<u>S. evermanni</u> (form C)	118	73	10	5	3	71	41	26	28	4
<u>Myctophum asperum</u>	--	--	--	--	--	2	13	13	26	77
<u>Myctophum brachygnathum</u>	--	--	--	--	--	--	--	--	--	--
<u>Myctophum lychnobium</u>	1	--	--	--	--	12	1	14	4	104
<u>Myctophum nitidulum</u>	6	2	12	4	1	13	3	10	11	3
<u>Myctophum spinosum</u>	--	--	--	--	--	--	--	--	--	--
<u>Gonichthys tenuiculus</u>	2	4	4	1	--	--	--	1	1	--
<u>Centrobranchus choerocephalus</u>	--	--	--	--	--	--	1	--	--	--

(continued)

	$3\frac{1}{2}^{\circ}\text{N}$					$0^{\circ}$					$3\frac{1}{2}^{\circ}\text{S}$			
	20m			50m		50m					20m		50m	
Station number	36	40	44	38	42	46	48	50	52	54	55	59	57	61
<u>Hygophum proximum</u>	17	58	52	35	26	91	40	176	64	196	55	117	175	157
<u>Diogenichthys atlanticus</u>	1	--	14	60	52	26	4	22	12	32	--	2	27	19
<u>Diogenichthys laternatus</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Symbolophorus evermanni</u>	92	141	161	220	92	1216	819	968	1984	1244	43	4	75	62
<u>S. evermanni</u> (form A)	16	23	18	4	6	--	9	--	40	76	5	--	3	7
<u>S. evermanni</u> (form B)	--	4	--	--	5	32	18	11	24	11	--	--	4	--
<u>S. evermanni</u> (form C)	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Myctophum asperum</u>	3	3	7	1	16	3	43	253	236	26	--	--	2	3
<u>Myctophum brachygnathum</u>	--	2	--	--	3	--	--	11	32	24	--	--	--	--
<u>Myctophum lychnobium</u>	4	23	6	3	5	3	7	33	48	16	--	1	--	--
<u>Myctophum nitidulum</u>	2	--	3	2	1	2	1	--	24	20	--	--	--	--
<u>Myctophum spinosum</u>	--	1	--	--	--	2	--	22	--	4	--	--	--	--
<u>Gonichthys tenuiculus</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Centrobranchus choerocephalus</u>	--	--	--	1	--	--	--	--	--	--	--	--	--	--

(continued)

Station number	12 <sup>1</sup> / <sub>2</sub> °N					7 <sup>1</sup> / <sub>2</sub> °N				
	20m			50m		20m			50m	
	8	12	16	10	14	24	28	22	26	30
<u>Notolychnus valdiviae</u>	--	--	--	--	--	--	--	--	--	--
<u>Triphoturus nigrescens</u>	--	2	--	--	--	7	7	1	9	18
<u>Lampanyctus hubbsi</u>	--	--	--	--	--	--	1	1	1	1
<u>Lampanyctus nobilis</u>	--	--	1	193	520	--	2	177	105	126
<u>Lampanyctus omostigma</u>	12	127	17	83	39	2	20	34	17	3
<u>Lampanyctus parvicauda</u>	--	--	--	--	1	--	--	--	--	--
<u>Lampanyctus steinbecki</u>	--	--	--	--	20	--	--	--	--	26
<u>Lepidophanes longipes</u>	--	--	--	--	2	--	--	2	15	333
<u>Ceratoscopelus warmingi</u>	--	--	--	--	8	--	--	96	192	2289
<u>Notoscopelus resplendens</u>	--	--	--	9	26	--	--	4	--	--
<u>Diaphus brachycephalus</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus effelgens</u>	--	--	--	--	--	--	--	--	--	3
<u>Diaphus elucens</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus fragilis</u>	--	--	--	--	1	--	--	15	66	259
<u>Diaphus garmani</u>	--	--	--	114	63	--	--	1085	359	485

(continued)

Station number	$3\frac{1}{2}^{\circ}\text{N}$					$0^{\circ}$					$3\frac{1}{2}^{\circ}\text{S}$			
	20m		50m			50m					20m		50m	
	36	40	44	38	42	46	48	50	52	54	55	59	57	61
<u>Notolychnus valdiviae</u>	--	--	--	4	2	312	4	--	12	144	--	--	--	13
<u>Triphoturus nigrescens</u>	2	4	3	259	82	1670	1526	1232	1308	1824	--	--	--	21
<u>Lampanyctus hubbsi</u>	--	--	1	259	43	175	45	33	44	--	--	--	--	--
<u>Lampanyctus nobilis</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Lampanyctus omostigma</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Lampanyctus parvicauda</u>	--	--	--	1	--	--	--	--	--	--	--	--	--	--
<u>Lampanyctus steinbecki</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Lepidophanes longipes</u>	2	--	--	108	11	566	158	99	148	136	--	--	--	--
<u>Ceratoscopelus warmingi</u>	2	--	6	5103	1907	1391	1764	1232	2024	4016	--	--	71	186
<u>Notoscopelus resplendens</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Diaphus brachycephalus</u>	--	--	--	--	--	13	--	--	--	--	1	21	2	1
<u>Diaphus effulgens</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Diaphus elucens</u>	34	--	--	39	32	--	--	--	--	--	--	--	--	--
<u>Diaphus fragilis</u>	14	--	--	--	90	13	81	99	20	168	--	--	40	54
<u>Diaphus garmani</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--

(continued)

Station number	$12\frac{1}{2}^{\circ}\text{N}$					$7\frac{1}{2}^{\circ}\text{N}$				
	20m			50m		20m			50m	
	8	12	16	10	14	24	28	22	26	30
<u>Diaphus jenseni</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus malayanus</u>	--	--	--	--	--	--	--	--	1	19
<u>Diaphus "mollis"</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus problematicus</u>	--	--	--	--	--	--	--	1	15	382
<u>Diaphus regani</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus signatus</u>	--	--	--	--	--	--	--	--	--	--
<u>Diaphus splendidus</u>	--	--	--	--	--	--	--	--	1	106

Station number	$3\frac{1}{2}^{\circ}\text{N}$					$0^{\circ}$					$3\frac{1}{2}^{\circ}\text{S}$			
	20m			50m		50m					20m		50m	
	36	40	44	38	42	46	48	50	52	54	55	59	57	61
<u>Diaphus jenseni</u>	--	--	--	53	46	7	5	11	4	60	--	--	--	--
<u>Diaphus malayanus</u>	--	--	7	1190	638	156	270	1694	112	800	--	--	--	--
<u>Diaphus "mollis"</u>	--	--	--	46	37	91	495	154	212	280	--	--	--	--
<u>Diaphus problematicus</u>	--	--	--	--	--	--	--	--	--	--	--	--	--	--
<u>Diaphus regani</u>	--	--	--	--	1	65	18	--	32	64	--	--	--	--
<u>Diaphus signatus</u>	--	--	--	112	4	604	2025	2299	4400	3804	--	--	--	--
<u>Diaphus splendidus</u>	--	--	11	--	--	--	--	--	--	--	--	--	--	--

TABLE 3

Myctophid species comprising 15% or more of the total myctophids caught at each depth and latitude

<u>Latitude</u>	<u>Depth</u>	<u>Species</u>	<u>% total myctophids</u>
12½°N	20m	<u>S. evermanni</u>	91%
	50m	<u>D. laternatus</u>	48%
		<u>L. nobilis</u>	26%
7½°N	20m	<u>S. evermanni</u>	83%
	50m	<u>C. warmingi</u>	27%
		<u>D. garmani</u>	20%
		<u>S. evermanni</u>	19%
3½°N	20m	<u>S. evermanni</u>	56%
		<u>H. proximum</u>	18%
	50m	<u>C. warmingi</u>	66%
		<u>D. malayanus</u>	17%
0°	50m	<u>D. signatus</u>	29%
		<u>C. warmingi</u>	23%
		<u>T. nigrescens</u>	17%
3½°S	20m	<u>H. proximum</u>	70%
		<u>S. evermanni</u>	19%
	50m	<u>H. proximum</u>	28%
		<u>S. evermanni</u>	15%

most abundance species at that latitude, comprising 70% and 37% of the myctophid population at 20 m and 50 m respectively.

At the four southernmost latitudes, abundance of H. proximum was only slightly higher at the 50 m depth than at 20 m. At  $12\frac{1}{2}^{\circ}\text{N}$ , however, abundance at 50 m was 25 times higher than at 20 m due to a marked decrease in abundance at 20 m. At this latitude, Symbolophorus evermanni, normally occurring in greater numbers at 50 m, was found mainly at 20 m. Here, S. evermanni was much more abundant than elsewhere and was the dominant species, making up 91% of the total myctophids. The decrease in abundance of H. proximum at the same location may have been related to the great increase in numbers and change of depth distribution of S. evermanni.

#### DIOGENICHTHYS

The genus Diogenichthys was represented in the waters sampled by two species: D. atlanticus and D. laternatus. D. atlanticus was present at all latitudes sampled, though in relatively low numbers. Peak abundance occurred at  $3\frac{1}{2}^{\circ}\text{N}$  and decreased to north and south. At all latitudes, abundance was higher at 50 m.

These results disagree with those of King and Iversen (1962), who found D. atlanticus only in waters of the South Equatorial Current. This disagreement may be the result of differences in sampling gear. In 157 one hour hauls with a 10 foot IKMT, King and Iversen report that this species occurred in only 3% of the hauls with an average catch of one specimen per haul. Kuba (1970) reports that D. atlanticus is undersampled by the 10 foot IKMT. Results of the present study indicate that D. atlanticus is fairly abundant in waters of the South

Equatorial Current and rare in waters of the North Equatorial Current and Equatorial Countercurrent. Thus, it was probably collected by King and Iversen only where it was relatively abundant.

D. Laternatus was restricted to the two northernmost latitudes, with greatest abundance occurring at  $12\frac{1}{2}^{\circ}\text{N}$ . D. laternatus was the dominant species there, comprising 48% of the total myctophids at 50 m. The species occurred almost exclusively at 50 m.

#### SYMBOLOPHORUS

S. evermanni, the only representative of this genus in central equatorial waters, is a complex of three very similar forms (Wisner, MS). These forms can be differentiated only on the basis of the structure of the supracaudal glands of adult males. In forms A and B, the concavities of the supracaudal glands face anteriorly, but the structure of the individual luminous scales differs notably. In form C, the concavities of the supracaudal glands face posteriorly.

S. evermanni occurred at all 24 stations. It was a "dominant species" in six of the nine latitude-depth areas sampled. Between  $7\frac{1}{2}^{\circ}\text{N}$  and  $3\frac{1}{2}^{\circ}\text{S}$ , abundances at 20 m and 50 m were similar. At  $12\frac{1}{2}^{\circ}\text{N}$ , however, abundance at 20 m was markedly higher than at 50 m. Here, the 20 m abundance was also much higher than the 20 m abundance at any other latitude.

It was possible to separate the three morphological forms from among the adult males captured. Forms A and B were present at all five latitudes. The range of form C, however, included only the two northernmost latitudes. Thus, S. evermanni probably consists of all three morphological forms at  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ , and forms A and B at the three southernmost latitudes.

MYCTOPHUM

The genus Myctophum was represented by six species in the waters sampled. Although species' ranges varied in latitudinal extent, all species were present in the highly productive waters at  $3\frac{1}{2}^{\circ}\text{N}$  and at the equator. M. aurolaternatum and M. lychnobium were present at all five latitudes. M. asperum ranged from  $7\frac{1}{2}^{\circ}\text{N}$  to  $3\frac{1}{2}^{\circ}\text{S}$ . M. spinosum and M. brachygnathum were taken exclusively in the highly productive waters at  $3\frac{1}{2}^{\circ}\text{N}$  and at the equator.

All species occurred in relatively low abundances within their ranges and showed no obvious peaks of abundance at any one latitude. All species occurred in roughly similar numbers at 20 m and 50 m.

GONICHTHYS

G. teniculus, the only species taken in this genus, was represented by only 11 specimens. All specimens were captured at the two northernmost latitudes, nine at  $12\frac{1}{2}^{\circ}\text{N}$  and two at  $7\frac{1}{2}^{\circ}\text{N}$ . G. teniculus occurred at both 20 m and 50 m.

CENTROBRANCHIUS

The genus Centrobranchus was represented by one species, C. choerocephalus, and only 2 individuals. One was taken at  $7\frac{1}{2}^{\circ}\text{N}$  at 20 m and one was taken at the equator at 50 m.

NOTOLYCHNUS

N. valdiviae, the only species in this genus, occurred in greatest abundance at the equator. A few individuals were taken at  $3\frac{1}{2}^{\circ}\text{N}$  and  $3\frac{1}{2}^{\circ}\text{S}$ . All specimens occurred at 50 m.

TRIPHOTURUS

T. nigrescens, the single species taken in this genus, was present

at all latitudes sampled, but varied greatly in abundance with latitude. Peak abundance occurred at the equator where it was a "dominant species", and decreases sharply to the north and south.

The depth of capture of T. nigrescens increased toward the southern limit of the sampling area. The only specimen captured at  $12\frac{1}{2}^{\circ}\text{N}$  was taken at 20 m. At  $7\frac{1}{2}^{\circ}\text{N}$ , abundances at 20 m and 50 m were nearly equal. At  $3\frac{1}{2}^{\circ}\text{S}$ , abundance was markedly higher at 50 m.

### DIAPHUS

The genus Diaphus, represented by 12 species, was the most speciose genus of myctophids encountered in the waters sampled. Six species were relatively abundant within at least part of their ranges, while six other species were rare. The genus was characterized by limited ranges, with 11 of the 12 species present at only one or two latitudes. All species but two occurred almost exclusively at 50 m.

The only Diaphus species to occur at all five latitudes was D. fragilis. It was represented at  $12\frac{1}{2}^{\circ}\text{N}$  by a single individual, but abundance was high and relatively consistent over the remainder of its range.

Eight species were distributed at two latitudes only. D. garmani occurred only at the two northernmost latitudes and was a "dominant species" at  $7\frac{1}{2}^{\circ}\text{N}$ . Five species: D. signatus, D. regani, D. jenseni, D. malayanus and an unnamed species closely related to D. mollis (Wisner, MS), were found exclusively at  $3\frac{1}{2}^{\circ}\text{N}$  and at the equator. D. malayanus and S. signatus were "dominant species" at  $3\frac{1}{2}^{\circ}\text{N}$  and at the equator, respectively. D. splendidus was present at  $7\frac{1}{2}^{\circ}\text{N}$  and  $3\frac{1}{2}^{\circ}\text{N}$ . Its abundance was low at both latitudes. D. brachycephalus occurred at

the equator and at  $3\frac{1}{2}^{\circ}\text{S}$ . Abundance was low at both latitudes. This was the only species of Diaphus with greater abundance at 20 m than 50 m.

The remaining three species occurred at one latitude only.

D. problematicus was taken at  $7\frac{1}{2}^{\circ}\text{N}$  and D. elucens occurred exclusively at  $3\frac{1}{2}^{\circ}\text{N}$ . D. effulgens was represented by a single specimen taken at  $7\frac{1}{2}^{\circ}\text{N}$ .

#### LAMPANYCTUS

The genus Lampanyctus was represented by 4 or 5 species: L. steinbecki, L. nobilis, L. omostigma, L. hubbsi and possibly L. parvicauda.

L. omostigma, L. nobilis, and L. steinbecki had similar latitudinal ranges. All were taken at  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$  with higher abundances at  $12\frac{1}{2}^{\circ}\text{N}$ , where L. nobilis was a "dominant species". Variations, however, occurred in their vertical distributions. L. omostigma was captured in roughly equal numbers at 20 m and 50 m while L. steinbecki and L. nobilis occurred mainly at 50 m.

The distribution of L. hubbsi was centered in the waters at  $3\frac{1}{2}^{\circ}\text{N}$  and at the equator. A few specimens were taken at  $7\frac{1}{2}^{\circ}\text{N}$ , but the species was not present in significant numbers. L. hubbsi occurred almost exclusively at 50 m.

Two damaged individuals have been tentatively identified as L. parvicauda. One was captured at  $12\frac{1}{2}^{\circ}\text{N}$  and one at the equator. Both were taken at 50 m.

#### LEPIDOPHANES

A single species, L. longipes (= L. pyrosobolus) was taken in

this genus and was present at all latitudes north of the equator, but absent at  $3\frac{1}{2}^{\circ}\text{S}$ . Peak abundance occurred at the equator with slightly lower numbers at  $3\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ . Only two specimens were taken at  $12\frac{1}{2}^{\circ}\text{N}$ . L. longipes occurred almost exclusively at 50 m.

#### CERATOSCOPELUS

C. warmingi, the only species taken in this genus, was captured at all five latitudes where it occurred almost exclusively at 50 m. Highest numbers were taken at  $3\frac{1}{2}^{\circ}\text{N}$  and declined to north and south. C. warmingi was a "dominant species" at all latitudes but  $12\frac{1}{2}^{\circ}\text{N}$ . At  $3\frac{1}{2}^{\circ}\text{N}$  it comprised 66% of the total myctophids and provided the highest number of individuals of a single species captured in a single tow.

#### NOTOSCOPELUS

N. resplendens, the only species of this genus captured, was confined to the northernmost latitudes where it occurred exclusively at 50 m. Grandperrin and Rivaton (1966), sampling with a five foot IKMT did not find this species west of  $110^{\circ}\text{W}$ . Kuba (1970) captured this species at  $145^{\circ}\text{W}$ , but reported it was taken only by the Cobb trawl and never by the IKMT. Apparently, the IKMT badly under-samples N. resplendens.

### DISCUSSION AND CONCLUSIONS

The surface waters in the Pacific equatorial region are highly uniform in terms of temperature and salinity. In the waters sampled during this study, surface temperature varied by only  $2.7^{\circ}\text{C}$  and surface salinity by only 1.2‰ between  $12\frac{1}{2}^{\circ}\text{N}$  and  $3\frac{1}{2}^{\circ}\text{S}$ .

Commenting on the physical uniformity of the equatorial currents in the Pacific, Knauss (1963) states "...there is no change of water mass, water color, or marked change in surface temperature as one moves out of one current and into the next. At least in the Pacific, there is no surface phenomenon of any kind that gives indirect but conclusive evidence of entering or leaving one of the equatorial currents."

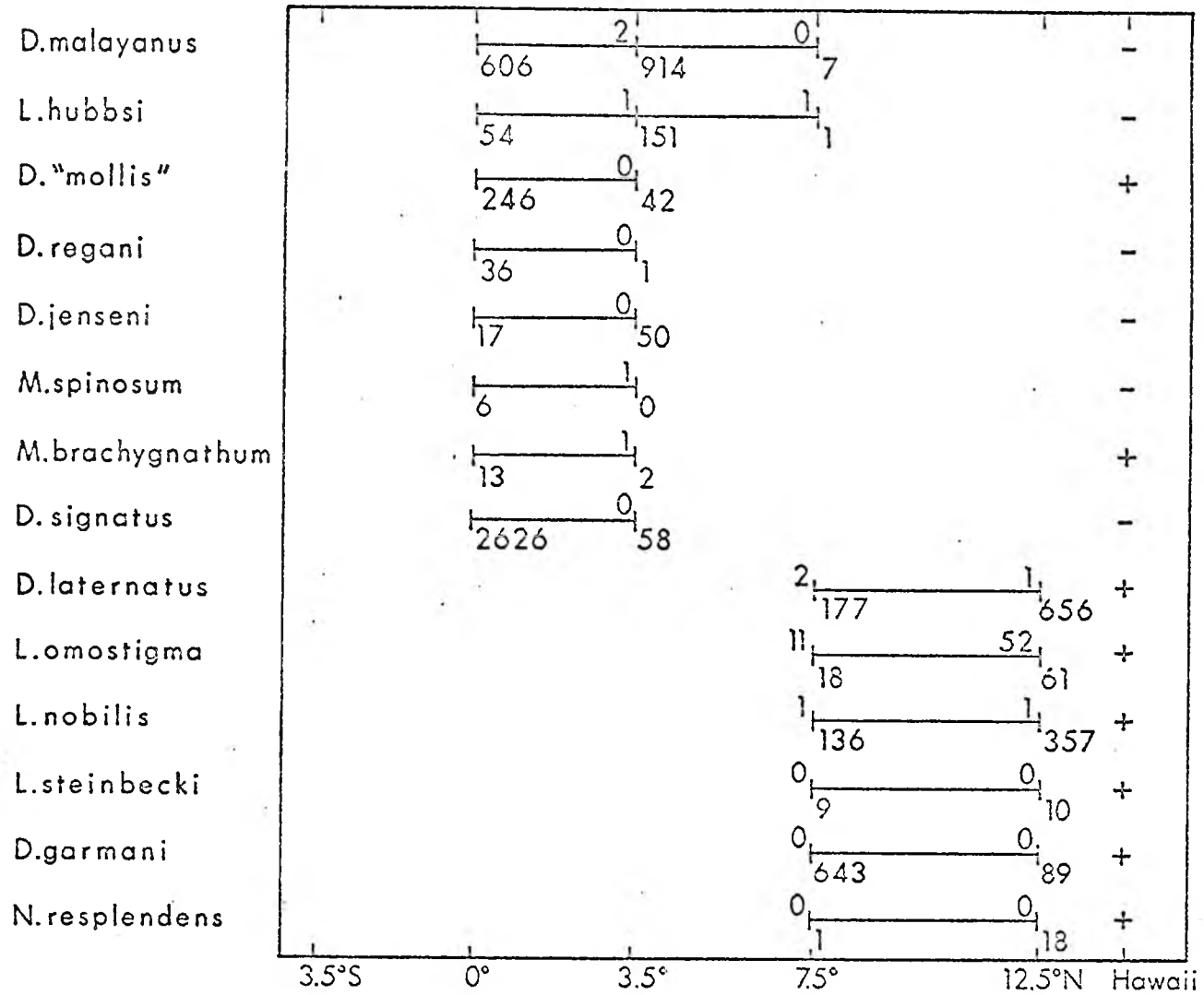
In spite of this uniformity, there were marked latitudinal variations in the abundance and composition of the equatorial myctophid populations (Fig 5). These variations were not directly related to the different equatorial currents except possibly in the case of N. valdiviae. In most cases, species' ranges either crossed major current boundaries or were restricted to one sector within a current. Patterns of distribution showed the best correlation with primary productivity and zooplankton biomass.

The equatorial zone of high primary productivity effectively divides the surface layers above the Pacific Equatorial Water mass into 3 zones: a southern zone characterized by low levels of primary production, an equatorial zone of high productivity associated with upwelling, and a northern zone with productivity levels that are low, but generally higher than those in the southern zone.

The total numbers of myctophids correlated well with the zones based on primary production and zooplankton biomass (Figs 3 and 4). Highest figures occurred at the equator, decreasing gradually to the north and sharply to the south. Abundance patterns and ranges of most species also correlated well with the zones based on productivity (Fig 5).

## FIGURE 5

Latitudinal ranges of myctophid species along  $145^{\circ}$ W longitude  
from  $3\frac{1}{2}^{\circ}$ S to  $12\frac{1}{2}^{\circ}$ N during May-June, 1969.  
Numbers above and below each line indicate average numbers of  
each species captured per haul at each locality at 20 m and  
50 m respectively.  
Species known to occur in Hawaiian waters are indicated by a+.



<i>H. proximum</i>	86	42	81	4	+
	166	114	31	193	100
<i>S. evermanni</i>	24	131	596	698	+
	69	1246	156	600	69
<i>D. atlanticus</i>	1	5	0	0	+
	23	14	56	8	5
<i>M. aurolaternatum</i>	1	7	2	2	-
	0	12	18	14	1
<i>M. lychnobium</i>	1	3	7	1	-
	0	21	4	9	0
<i>T. nigrescens</i>	0	3	7	1	+
	11	1512	171	9	1
<i>C. warmingi</i>	0	3	0	0	+
	129	2085	3505	859	4
<i>D. fragilis</i>	0	5	0	0	+
	47	76	45	113	1
<i>L. longipes</i>		1	0	0	+
		221	60	117	1
<i>M. nitidulum</i>		2	8	7	+
		9	2	8	3
<i>N. valdiviae</i>	0	0			+
	7	94	3		
	3.5°S	0°	3.5°	7.5°	12.5°N Hawaii

Most of the myctophid species collected in equatorial waters could be divided among three groups: those whose ranges extended across the entire sampling area, those who were restricted to the northern zone of low primary productivity, and those who were restricted to the highly productive upwelled water at the equator.

Nine species occurred only northward of the equatorial zone of high productivity, i.e. at  $7\frac{1}{2}^{\circ}\text{N}$  and  $12\frac{1}{2}^{\circ}\text{N}$ . Seven of these: D. laternatus, G. tenuiculus, L. omostigma, L. nobilis, L. steinbecki, D. garmani, and N. resplendens were captured at both  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ .

Because the northern limits of the above species' ranges extended beyond the sampling area, maps of species' distributions compiled by Wisner (MS) were examined to determine what parameters might be limiting to the different species in the north. Although the southern range limits for all of the above species clearly coincided with the northern boundary of the zone of high productivity, the northern range limits varied. Examination of Wisner's (MS) distributional maps indicates that the northern range limits of D. laternatus, G. tenuiculus, L. omostigma, L. nobilis and D. effulgens occur between  $10^{\circ}\text{N}$  and  $20^{\circ}\text{N}$  in the central Pacific while N. resplendens, D. garmani, and L. omostigma range northward to approximately  $35^{\circ}\text{N}$ . The range of D. problematicus is not well delineated at present.

The sudden disappearance of the above species coincident with the zone of upwelling around  $3\frac{1}{2}^{\circ}\text{N}$  indicates that the level of primary production is an important factor affecting their distributions. The fact that this boundary does not coincide with the boundary of the Pacific Equatorial Water mass indicates that productivity may be more

important than physico-chemical parameters in determining the range of these species.

Examination of Figure 4 shows that primary production levels decline steadily between the equator and  $15^{\circ}$ - $20^{\circ}$ N, and with the exception of a slight increase around  $23^{\circ}$ N, remain at relatively low levels until they increase sharply around  $35^{\circ}$ N. Sette (1955) reports that vertical movement resulting from eddies and wakes created within the North Equatorial Current as it flows past the Hawaiian group bring some nutrient rich water into the mixed layer, resulting in increased primary production to the lee of the islands.

Distributions of the above nine species apparently terminate in the south coincident with the boundary of the zone of high primary productivity. Since primary production levels decline steadily between this zone and  $15^{\circ}$ - $20^{\circ}$ N, the northern limits of those species whose ranges extend to  $10^{\circ}$ - $20^{\circ}$ N may be affected by the very low production levels of the central gyre. This general area is also the transition zone between the Pacific Equatorial and North Pacific Central Water masses, but as Ebeling (1962) points out, the boundary between these biologically and physically similar water masses is relatively weak. It is difficult, therefore, to determine what factors are affecting the distributions of those species at the northern ends of their ranges. Since the physical gradients associated with this boundary are extremely weak and appear less pronounced than the productivity gradients, it seems unlikely that the physical parameters constitute a barrier to myctophid distributions.

Those species whose ranges extend to  $35^{\circ}$ N are apparently able to

tolerate the low productivity levels of the central gyre. The northern limits of their ranges, however, coincide with the sudden increase in productivity associated with the southern boundary of the Subarctic Pacific Water mass. (Marked changes in physical parameters also occur at this boundary.) These species, then, are bounded both in the north and in the south by high levels of primary production.

Eight species were taken exclusively, or nearly so, within the zone of upwelling at the equator and at  $3\frac{1}{2}^{\circ}\text{N}$ . These included M. spinosum, M. brachygnathum, D. regani, D. jenseni, D. signatus, and an unnamed species closely related to D. mollis. A few specimens of D. malayanus and L. hubbsi were captured at  $7\frac{1}{2}^{\circ}\text{N}$ , but their distributions were clearly centered to the south. It is surprising, in fact, that more species did not overlap the narrow zone of high productivity to some extent.

Wisner (MS) indicates a very limited distribution for all of the Diaphus species except the one related to D. mollis and for L. hubbsi. All are said to occur between Hawaii and the equator. The results of this study, however, indicate a normal range even more limited in latitudinal extent. Perhaps the specimens taken north of the zone of high productivity represent expatriates. Clarke (pers. comm.) has found none of these species as far north as Hawaii.

Maximum wind velocity and consequently maximum intensity of upwelling in the central equatorial Pacific occurs around  $120^{\circ}\text{W}$  (Sette, 1955). Just  $10^{\circ}$  downcurrent from this area, Grandperrin and Rivaton (1966), sampling along the equator, found the highest levels of primary production in the central equatorial Pacific between approxi-

mately 130°W and 165°W. The importance of primary productivity levels in affecting species' ranges is most obvious here. The ranges of D. regani, D. jenseni, D. signatus, D. malayanus, and L. hubbsi coincide in both longitudinal and latitudinal extent with the most highly productive water in the central equatorial Pacific.

The biological uniqueness of this small but highly productive area has been pointed out by several investigators. Sette (1955) found the highest abundance of tuna along the equator between 150°W and 170°W. Grandperrin and Rivaton (1966) found the highest numbers of both individuals and species of mesopelagic fishes along the equator in the same area. These consisted mainly of myctophids of the genera Diaphus and Lampanyctus.

Eight species were distributed across the entire sampling area. These included H. proximum, D. atlanticus, S. evermanni, M. auro-laternatum, M. lychnobium, T. nigrescens, C. warmingi, and D. fragilis. Though not taken at 3½°S during cruise 43, L. longipes will be included in this group because it was taken at 3½°S in low numbers by Kuba (1970) during cruise 47.

Examination of Wisner's (MS) distributional maps indicates that with the exception of D. atlanticus, these species have continuous distributions which include equatorial waters of both high and low productivity. The ranges of most of these species also extend into Central Water in the north. All but M. aurolaternatum and M. lychnobium are regularly taken in Hawaiian waters (Clarke, pers. comm.).

Although clearly not affected by the zone of high productivity, the ranges of most of the species in this group seem to be bounded by

areas of low productivity. The northern limits of their distributions appear to coincide with the low productivity levels of Central Water. In the south, where productivity levels decline more rapidly, their ranges extend approximately to the southern boundary of the Pacific Equatorial Water mass. The distribution of M. aurolaternatum follows the boundaries of the Pacific Equatorial Water mass more closely than the other species in this group, extending from approximately  $10^{\circ}$ - $15^{\circ}$ N to  $5^{\circ}$ - $10^{\circ}$ S.

D. atlanticus has a disrupted distribution related to zones of high productivity. It occurs in the upwelling zones along the coasts of California and Peru-Chile and in equatorial waters between  $130^{\circ}$ W and  $165^{\circ}$ W (Wisner, MS). Unlike the species endemic to the equatorial zone of high productivity, however, the range of D. atlanticus extends significantly beyond the zones of high productivity in which its populations are apparently centered. Along the coasts of California and Peru-Chile it has been taken as far as  $25^{\circ}$  of longitude from the coast (Wisner, MS). In the present study, it occurred in highest numbers in the upwelling region, but extended into the less productive waters to the north and south. D. atlanticus is also taken regularly in Hawaiian waters (Wisner, MS; Clarke, pers. comm.).

The 50 m abundance of six of the nine species which ranged across the entire sampling area showed a strong positive correlation with the changing levels of productivity across the sampling area. These were: D. atlanticus, S. evermanni, C. warmingi, M. aurolaternatum, T. nigrescens, and L. longipes. All were taken in highest numbers within the zone of upwelling and all but S. evermanni and L. longipes decreased

step-wise in abundance with the declining levels of productivity to the north and south.

Legand et. al. (1970) report similar results from the western Pacific. Sampling along 170°E from 4°N to 20°S, they found that as a general rule, abundance figures averaged over four or five degrees of latitude showed two marked peaks at the ends of the transect, i.e. at 4°N-0° and at 15°-20°S. Minimum values generally occurred between 4°S and 14°S. The high values at the northern end were undoubtedly related to the equatorial zone of high productivity. To the south, there is a marked increase in primary productivity along 170°E southward of 15°S in the vicinity of New Caledonia (El-Sayed, 1970; Koblentz-Mishke et. al., 1970). Legand et. al. (1970) also report that the northward increase in abundance figures is never observed at more than two or three consecutive latitudes between 0° and 2°N. In the present study high abundance figures associated with equatorial upwelling extended to at least 3½°N and possibly farther. Since the latitudinal extent of the zone of high productivity decreases from east to west, however, the latitudinal extent of the high abundance figures associated with this zone would also be expected to decrease accordingly.

The relative abundance between species also showed a high degree of correlation with changing productivity levels in some cases. Examination of Table 3 shows that the relative abundance of S. evermanni at 20 m is inversely proportional to primary productivity levels. It was the dominant species at 12½°N, 7½°N and 3½°N, but comprised a steadily lower proportion of the total myctophid population in areas

of progressively higher primary productivity. The absence of this species from Table 3 at the equator is probably due to the fact that no 20 m samples were taken at the equator.

The relative abundance of C. warmingi showed the opposite trend, i.e. its relative abundance was directly proportional to the level of primary production. This species comprised the highest proportion of the total myctophid population at  $3\frac{1}{2}^{\circ}\text{N}$ . Relative abundance declined to both north and south. At  $12\frac{1}{2}^{\circ}\text{N}$ , only one specimen was taken. Clarke (pers. comm.), however, found that in Hawaiian waters, where productivity levels again increase, C. warmingi is the most abundant species in the upper 100 m at night.

Although the above nine species have wide ranges, the importance of the zone of convergence around  $3\frac{1}{2}^{\circ}\text{N}$  as a faunal boundary is apparent for many of the other species. This is perhaps best demonstrated by two cases of replacement by closely related species. D. garmani and L. omostigma, both fairly abundant at  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ , dropped out and were replaced in the zone of upwelling by two species which were nearly identical morphologically; D. malayanus and L. hubbsi.

The zone of convergence near  $3\frac{1}{2}^{\circ}$  also marked a change in the composition of the population of S. evermanni. At  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ , the populations of this species consisted of all three morphological forms. In waters to the south, however, form C dropped out leaving only forms A and B. The disappearance of form C from the population here seemed particularly significant since it ranked either first or second in abundance among adult males of the three forms at both depths at the two northernmost latitudes.

N. valdiviae was the only species to be taken almost exclusively at the equator. The highest abundance of this species occurred at  $0^{\circ}$  with a few individuals captured to the north and south. Grandperrin and Legand (1967) have described the influence of equatorial circulation on the reproductive cycle of N. valdiviae in the Pacific. The species reproduces in the western equatorial Pacific. Larvae then drift eastward in the Cromwell Current and as they approach  $140^{\circ}\text{W}$ , descend into the Deep Equatorial Current and drift back to their spawning grounds. This reproductive cycle should keep the breeding population of N. valdiviae in close proximity to the equator.

Although there are scattered records of N. valdiviae from  $30^{\circ}\text{N}$ - $30^{\circ}\text{S}$  in the Pacific (Wisner, MS), no specimens were taken farther than  $3\frac{1}{2}^{\circ}$  of latitude from the equator either during the present study or during the study by Kuba (1970). King and Iversen (1962) report taking N. valdiviae only in the waters of the South Equatorial Current, the Equatorial Countercurrent and in Hawaiian waters. T. Clarke (pers. comm.) regularly captures this species near Hawaii.

The distribution of N. valdiviae, then, though clearly related to equatorial circulation in the central Pacific, may also be affected by areas of high to moderate productivity. If this is so, the enrichment of the mixed layer around Hawaii apparently increases productivity sufficiently to provide a suitable habitat for this species there. It seems likely, however, that the population of N. valdiviae occurring in Hawaiian waters must form a separate breeding population with a reproductive cycle differing from that of the equatorial population of the same species. The scattered records of this species

may represent expatriates from one or both populations.

The distributional patterns of most myctophid species in equatorial waters were more closely related to biological parameters of primary production and zooplankton biomass than to physico-chemical parameters. The ranges of many myctophid species were limited to well defined zones within the boundaries of the physically uniform Pacific Equatorial Water mass. These faunal zones correlated closely with zones based on primary productivity. Most species were distributed either within the highly productive water between the equator and  $3\frac{1}{2}^{\circ}\text{N}$  or in the less productive water between  $12\frac{1}{2}^{\circ}\text{N}$  and  $7\frac{1}{2}^{\circ}\text{N}$ . Where species' distributions crossed zones of differing productivity, abundances were generally proportional to levels of primary production.

Similar results have been obtained by other investigators. Ebeling (1962) found that the ranges of species of the genus Melamphaes (Family Melamphaidae) generally followed water masses, but where they departed it was usually to follow contours of productivity. He suggests that areas of increased primary productivity generally support faunas which are distinct from those of adjacent, less productive areas. Backus et. al. (1969) have described a major change in the mesopelagic fish fauna of the Sargasso Sea which coincides with a marked thermal front as well as a marked change in productivity levels. Gibbs and Hurwitz (1967) report that surface water movements associated with the Frontal Zone, around  $10^{\circ}\text{S}$  in the Indian Ocean, maintain a productive situation to the north of  $10^{\circ}\text{S}$ , while waters to the south rapidly become sterile. Nafpaktitis and Nafpaktitis

(1969), describing the distribution of myctophid fishes in the western Indian Ocean indicate that the majority of these species are distributed either in the northern or southern Indian Ocean. In almost every case, the distributions of these species are limited between  $10^{\circ}\text{S}$  and  $20^{\circ}\text{S}$ . Bieri (1959) found that spatial variations in numbers of arrow worms were related to changing levels of productivity within their ranges. Murphy and Shomura (1958) have demonstrated that temporal variations in the abundance of yellowfin tuna in the zone of upwelling at the equator are related to temporal variations in phosphate levels and zooplankton volumes.

The close relationship between the ranges of the myctophid species taken during the present study and levels of primary production within the mixed layer is not surprising since most species spend a large percentage of their life cycles within the mixed layer. Adults of all the species sampled migrate to depths within the mixed layer at night, presumably to feed. The larvae and young of many species may live and feed entirely within the mixed layer.

The larvae and young of many mesopelagic and bathypelagic fishes live within narrow depth ranges near the surface and are geographically limited to localized conditions to which they are specifically adapted (Ebeling, 1962). Ahlstrom (1959; 1971) found that the larvae of most myctophid species in the California Current were distributed within the upper mixed layer or in the upper part of the thermocline between the surface and 125 m. Nafpaktitis (1968) found that the distributions of the larvae of the most common myctophid species in the North Atlantic were confined to the upper mixed layer.

Larvae and breeding adults generally have the narrowest physiological tolerance limits for environmental parameters and as a result, they may limit the distribution of a whole species (Ebeling, 1962). Those adults which are carried from the area where conditions for breeding and larval survival are optimal may survive, but are often reproductively lost to the population (Nafpaktitis, 1968).

Beklemishev and Parin (1960) believe that the shallow, planktonic existence of bathypelagic fish larvae may be responsible for the correlation between surface phenomena and the distribution of all growth stages. Bolin (in Ebeling, 1962) suggests that the narrow ranges of many myctophid species may be related to the special requirements of their larvae. Ebeling (1967) feels that the larvae of many midwater fishes are concentrated by current gyres and eddies in the tropical water masses where they may be dependent upon a particular food supply or temperature regime.

Since latitudinal variations in the level of primary production are such a marked and constant feature of the central Pacific equatorial waters and since the mixed layer provides the major food resource for most larval and adult myctophids, it is not surprising that species distributions are correlated with levels of food concentration and productivity within the mixed layer. Backus et. al. (1969) have concluded that the concept of adaptation to certain levels of productivity may largely explain the distribution of most fishes in the world ocean.

The correlation between abundance and levels of productivity is also not surprising. An increase in productivity should result

in an increase in zooplankton biomass, hence in the number of myctophids that a given volume of water can support. Vinberg and Koblenz-Mishke (1966), however, have shown that an increase in levels of productivity is accompanied not only by an increase in zooplankton biomass, but also by an increase in the ratio of zooplankton biomass to primary production. As a result, a given increase in production levels should cause an even greater increase in food concentration for zooplankton feeders.

Koblenz-Mishke et. al. (1970) have suggested that the increase in the ratio of zooplankton biomass to productivity as productivity increases may result from an increase in the efficiency of the utilization of productivity by zooplankton because as food density increases, less energy must be expended in obtaining food. If this is so, this increase in feeding efficiency may also apply to higher trophic levels, i.e. the ratio of the biomass of zooplankton feeders to the biomass of zooplankton should also increase as productivity increases. The combined effects of the increases in both the ratio of zooplankton biomass to productivity and in the ratio of the biomass of zooplankton feeders to zooplankton may largely explain the great increase in the abundance of myctophids which is associated with latitudinal increases in primary production.

The correlation between levels of primary production and the distribution of myctophid species may be more marked in the tropics than in higher latitudes. According to Fager (1963), the biological aspects of the environment become increasingly important in affecting species' ranges in areas where the physical aspects of the environment

are stable. In the physically controlled community where physical conditions fluctuate widely and unpredictably, organisms must give adaptive priority to the physical regime. In the biologically accommodated community, however, biological interactions are refined and organisms are able to make subtle distinctions about the biological aspects of the environment (Sanders, 1969).

Ebeling (1962) reports that agreement between species' ranges and water masses is poorest in the central tropical regions of the oceans, i.e. within the equatorial and central water masses. In the uniform and physically stable waters of the tropics, then, biological parameters may be of primary importance in affecting the distributions of species, particularly of those species whose life cycles and migration habits are closely tied to the mixed layer where variations in biological parameters are most pronounced.

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