VERTICAL DISTRIBUTION AND DEVELOPMENT OF LARVAL FISHES IN THE NORTH PACIFIC CENTRAL GYRE DURING SUMMER

VALERIE J. LOEB¹

ABSTRACT

Abundance data are presented on the mesopelagic fish larvae taken in 60 opening/closing bongo net samples from the North Pacific central gyre in late summer. Vertical abundance and size-depth distributions are described for 43 species of gonostomatids and myctophids and two sternoptychid genera. Developmental stages at which these fishes leave the surface layers (either moving deeper or beginning extensive vertical migration) are estimated from sizes of captured larvae.

Over 96% of the estimated larval water column abundance occurred within the upper 100 m. Maximum abundance and diversity were at 25-50 m, possibly related to the bottom of the seasonal mixed layer. Most of the abundant species had distinct depths of maximum abundance within one of the 25 m depth intervals sampled and demonstrated changes in size composition with depth. Different larval distributional patterns were found within and between the Gonostomatidae, Sternoptychidae, and Myctophidae. Larvae of the two myctophid subfamilies had significantly different overall vertical distribution patterns; Myctophinae larvae were more deeply distributed than Lampanyctinae larvae. The myctophids exhibited two patterns of ontogenetic migration: one group of species remains in the surface layers until transformation; the other leaves the surface layers in early stages of photophore development.

Mesopelagic fish species dominate the fish fauna in oceanic regimes, both in terms of numbers of species and numbers of individuals. The adults are important components of oceanic communities. The vertically migrating and more active species are known predators upon other nekton and upon zooplankton (Pearcy and Laurs 1966; Legand and Rivaton 1969; Merrett and Roe 1974). We know much about the depth distributions and diurnal migrations of adult fish species; comparatively little is known of the vertical distributions of their early life stages.

The larvae of most mesopelagic fish species are found within the upper several hundred meters of the water column (Ahlstrom 1969) where they are part of the zooplankton. This larval fish fraction of zooplankton assemblages is called the ichthyoplankton. Ahlstrom's (1959) study of vertical distributions of larval fishes in the California Current included some mesopelagic species. He found that the majority of the species occurred within the mixed layer and upper thermocline and that each species had a characteristic depth distribution; these depth distributions, however, varied with the highly variable (10-90 m) mixed layer depth. Larval fishes grow and develop within the upper levels until some point of development when the individuals leave the plankton and adopt juvenile-adult roles. Changes in depth distribution with larval development and the stage(s) of development at which the young leave the upper levels and either descend to juvenile depths or begin extensive vertical migrations have not previously been reported.

The North Pacific central gyre is an excellent area in which to examine the vertical distribution of ichthyoplankton. Physically the upper several hundred meters are horizontally monotonous and vertically well stratified (McGowan and Hayward 1978; Gregg et al. 1973). In contrast to the California Current, the summertime mixed layer depth (ca. 40 m) is quite constant. The ichthyoplankton is composed of a diverse and rather equitably distributed assemblage of mesopelagic fish species. Overall species composition and relative abundance relations of larvae taken in integrating 0-300 m Isaacs-Kidd plankton trawl samples are similar from tow to tow within and between summers (Loeb 1979b); repeated patterns of species composition and abundance relations also occur in replicated bongo samples taken within the same depth interval (Loeb 1979a).

In this study I present catch information on a large number of larval fish species taken in 60

¹Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093.

opening/closing bongo net samples during a stratified sampling program in the North Pacific central gyre (Scripps Institution of Oceanography 1974). I describe the vertical abundance and sizedepth distributions of the more abundant families (Gonostomatidae, Sternoptychidae, and Myctophidae) and species. I also present estimates of the predescent stages of development of species for which there are sufficient catch data.

METHODS

All depth stratified samples were obtained during Climax I expedition (19-28 September 1968; Scripps Institution of Oceanography 1974) near lat. 28° N, long. 155° W. The physical, chemical, and biological properties at this locale have been shown to be stable over large time and space scales (McGowan and Walker in press) and are expected to be representative of the central gyre (Scripps Institution of Oceanography 1974). During this cruise, round-the-clock sampling was done with opening/closing bongo nets (Scripps Institution of Oceanography 1966) between a set of parachute drogues placed at 10 m depth about 10 km apart. The drogues traveled 346 km during the 10 days of sampling. The main depth intervals sampled were: 0-25 m, 25-50 m, 50-75 m, 75-100 m, 100-350 m, and 350-600 m; other intervals were also sampled. Paired 505 μ m nets on the 70 cm diameter frames each had a mouth area of 0.396 m². They were opened at the bottom of the desired depth range and fished obliquely upward, closing near the top of the range. Maximum tow depths were determined by Benthos² depth-telemetering pinger and/or wire angle. The nets were closed automatically by a calibrated flowmeter after 400 m³ of water had been filtered per net. Ship speed was nominally 2.5 kn.

All fishes were sorted from 60 samples representing 38 separate tows (one sample equals the catch from one of the paired nets). Samples included: ten each from 0-25 m, 25-50 m, 50-75 m, and 75-100 m; six from 100-225 m; six from 100-350 m; and eight from 350-600 m (Table 1).

To reduce biases due to net avoidance by larger individuals and more agile species (Bridger 1956; Ahlstrom 1959) most analyses were of "night" samples (taken between 2000 and 0600 local time). To provide enough replicate samples to allow statistical analyses of strata deeper than 50 m, I found it necessary to include 11 "day" samples; these were selected from tows taken as close to dawn or dusk as possible. As a result, this study does not include aspects of diurnal changes in depth distributions. Ahlstrom (1959) and Badcock and Merrett (1976) showed that the larvae of some midwater fishes (size or stage of development unreported) do undergo limited diurnal migrations.

I identified all fishes caught to the lowest taxon possible. These were categorized to stage of development (i.e., larval, metamorphic, postmetamorphic or juvenile, adult), enumerated and measured to the nearest 0.1 mm standard length (SL) (notochord length was measured for preflexion larvae). The data presented in this paper (unless otherwise noted) are based on larval to early

TABLE 1.—Opening/closing bongo net samples used for larval fish depth distribution analyses. Samples taken near lat. 28° N, long. 155° W in the North Pacific central gyre during September 1968. L and R designate left or right sample from paired net assembly. Mean and standard deviations of temperature at upper (T_U) and lower (T_L) limits of each interval based on 10 day and 7 night 0-500 m STD lowerings.

Depth	Date (Sept			Temperat	ture (C°)
(m)	1968)	Time	Net	τ _U	TL
0-25	21 22 23 26 27	0250-0325 0408-0445 0247-0330 2118-2137 0040-0103		27.10±0.20	26.85±0.24
25-50	27 21 22 23 24 26 27 27	0341-0404 0250-0325 0408-0445 0247-0330 0507-0540 2118-2137 0040-0103 0341-0404	L&R L&R L&R L&R R R	26.85±0.24	24.94±1.01
50-75	21 22 26 26 27 27 27	0250-0325 0408-0445 1859-1922 2206-2230 0126-0156 0449-0510 0804-0838	- R R L&R L&R L & R L B	24.94±1.01	21.45±0.31
75-100	21 22 24 26 26 27 27	0250-0325 0408-0445 0413-0500 1859-1922 2206-2230 0126-0156 0449-0510	R R L&R L&R L&R R L&R	21.45±0.31	20.51±0.21
100-225	21 21 22 24	0529-0600 1638-1656 0214-0234 0046-0111	L L & R L & R L	20.51±0.21	15.28±0.30
100-350	26 27 27	2010-2033 0237-0255 0606-0633	L & R L & R L & R	20.51±0.21	10.52±0.27
350-600	26 26 27 27	2010-2033 2328-2351 0237-0255 0606-0633	L&R L&R L&R L&R	10.52±0.27	Not avail- able

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

metamorphic stages only; juvenile and adult information is provided separately. I was able to identify most of the abundant larvae to species. Some of the larvae, however, could not be identified with certainty. For these I assigned "probable" and "possible" species names. These designations were based on the accumulation of enough larvae to establish developmental links to known adult species (Loeb 1979b, >29,000 larval identifications) and a list of adult central gyre mesopelagic fish species and their relative abundances (Barnett 1975).

For analyses of abundance distributions with depth, the larval fish catches from each sample were converted to numbers per 1,000 m³. These were averaged for each depth interval and then summed to provide estimated water column abundance. Individual species distributions are expressed as percent of their estimated water column abundance caught within each of the main depth intervals sampled. The 100-225 m catches were used in calculations only if they contained species not present in 100-350 m or 350-600 m samples. The 100-225 m and 100-350 m samples were compared to assess whether larval abundance was concentrated in the upper portion of the larger depth range.

Significance of differences in size composition with depth were determined, where sample sizes permitted, using the Kolmogorov-Smirnov test (Conover 1971) on cumulative size-frequency distributions of 0.5 mm (SL) categories of the total larvae taken (all samples combined) within each depth interval. A one-tailed probability of the maximum difference between cumulative sizefrequency distributions in two depth strata ≤ 0.05 was deemed "significant." Rejection of the null hypothesis of no difference indicates that one of the size distributions being compared is significantly larger than the other. The results of these tests are in no case altered by the exclusion of larvae from the "day" samples in their calculation.

Descriptions of the developmental stages of myctophid larvae in the plankton include additional information obtained from six other central gyre cruises in the vicinity of lat. 28° N, long. 155° W. These cruises utilized Isaacs-Kidd plankton trawls (IKPT) fished obliquely from the surface to about 300 m (Loeb 1979b). Those data (24,500 identified larvae) provide a broader range of larval sizes and developmental stages, and development from early larvae to metamorphosis (transformation) has been traced for many species. I used this information as an aid for estimating levels of development reached while larvae are still in the upper water column, prior to descent to deeper juvenile-adult depths.

RESULTS

I identified a total of 5,448 larvae (Table 2). These included 94 generic and species identifications from 36 families, and one ordinal grouping. Three families (Gonostomatidae, Sternoptychidae, and Myctophidae) together contributed 91% of the individuals and 50% of the species.

Larvae were taken throughout the 600 m depth range (Figure 1a); however, over 97% of the estimated water column abundance was in the upper 100 m. Only 13 of the 95 kinds of larvae appeared to have maximum abundance below 100 m. Maximum larval abundance (and diversity, or number of species) occurred within the 25-50 m interval (Figure 1a); the bottom of the summer mixed layer (ca. 40 m) is within this interval (Figure 1b). Total larval abundance (Figure 1a) as well as individual species abundances were highly variable from tow to tow within each interval. Despite this variability, most species demonstrated a definite peak of abundance (generally >60% of their estimated water column abundance) and



FIGURE 1.—Vertical distribution of ichthyoplankton in relation to late summer thermal structure in the North Pacific central gyre. (a) Mean and range of total numbers of larvae per 1,000 m³ caught in replicate samples within each depth interval (bracketed values are numbers of replicate samples). (b) Temperature profile of upper water column during Climax I, based on average values from 10 day and 7 night STD lowerings.

 TABLE 2.—Total numbers of individuals (N) and rank of numerical abundance (R) of larval fish species caught (n samples combined) within each of seven depth intervals in the North Pacific central gyre during late summer.

<u></u>	0-	25 m	25-50 m 50-75 m		75-100 m · 100-225 m		100-350 m		350-600 m		Total					
Species	N	R	N.	 	N	R	<u></u>	R	N	R 8	//	R	N	R	N	R
Gonostomatidae:	- <u>-</u>		······		÷							- -				
Cyclothone alba	580	(1)	687	(1)	171	(1)	17	(12)	3	(131⁄2)					1,458	(1)
C. sp. A (prob. pseudopallida)	49	(5)	9	(261/2)	2	(37)									60 1	(19)
C. spp.	76	(30)	78	(10)	28	(11)	4	(271/2)			2	(11)	5	(1)	193	(7)
Diplophos taenia	13	(11)	1	(54)				,					-		14	(421/2)
Gonostoma atlanticum							30	(6)	9	(3)	2	(11)			41	(29)
G. elongatum							10	(14)	2	(18//2)	2	(11)			14	(4272)
Margrethia obtusirostra							'	(10)	4	(101/2)					4	(731/2)
Valenciennellus tripunctulatus									6	(6)	з	(71/2)			9	(52)
Vinciguerria nimbaria	6	(18)	376	(2)	99	(2)	25	(8)	7	(4)	1	(19)			514	(2)
V. poweriae	_		•••		2	(37)	60	(2)	5	(81/2)	4	(5)			71	(16)
V. Spp. Woodsia sp	3	(251/2)	90	(9)	61	(5)	34	(5)	3	(131/2)	13	(1)			204	(6)
Sternoptychidae:							-	(2772)		(2072)					5	(07)
Argyropelecus spp.											1	(19)	4	(2)	5	(67)
Sternoptyx diaphana									14	(1)	5	(3)			19	(381/2)
S. pseudobscura							1	(461/2)	4	(101/2)		(5)	1	(4)	6	(61)
S. spp. Myctophidae									0	(0)	4	(5)			10	(50)
Lampanyctinae:																
Bolinichthys distofax			27	(17)											27	(30)
B. longipes	177	(2)	47	(11)	1	(46)									225	(5)
B. spp.	30	(6)	21	(21)	47	(6)	2	(25)		(2614)					51	(23%2)
Diaphus anderseni	84	(3)	40	(13)	5	(25)	2	(35)		(2092)	1	(19)			130	(12)
D. "slender B" (D. mollis B?)	•	(0)	2	(441/2)	7	(21)	2	(35)			•	(,			11	(48)
D. "slender C" (D. mollis A?)	12	(12)	95	(8)	9	(171/2)	2	(35)					1	(4)	119	(13)
D. brachycephalus	6	(18)	30	(16)	14	(15)	1	(461/2)		(001/)					51	(231/2)
D. siender spp." D. elucens (= perspicillatus)	10	(1492)	164	(4)	46	(23)	2	(35)	1	(2672)					230	(38%2)
D. rolfbolini (= phillipsi)	2	(281/2)	97	(7)	27	(12)	5	(24)	2	(18½)	1	(19)			134	(10)
D. "stubby C" (D. schmidti?)	5	(21)	11	(241/2)	7	(21)	•	()	-	()		()			23	(341/2)
D. "stubby spp."	_						1	(461⁄2)							1	(100)
Lampadena anomala	5	(21)	3	(39)				(4614)							8	(551/2)
Lampanyctus "bio snout"		(13)	16	(23)	2	(37)		(4072)							18	(40)
L. "lacks pectorals"			4	(331/2)	33	(9)	7	(18)	1	(261/2)					45	(26)
L. nobilis	1	(38)	23	(19)	2	(37)		(· -/		(,					26	(31)
L. steinbecki	3	(251⁄2)	123	(6)	12	(16)									138	(9)
L. spp.			7	(291⁄2)	20	(10)	26	(7)	2	(1916)			1	(4)	- 8 57	(55½) (21)
Notolychnus valdiviae					20	(37)	40	(4)	2	(1072)	2	(11)			44	(27)
Triphoturus nigrescens	6	(18)	128	(5)	8	(19)	4	(271/2)							146	(8)
Myctophinae:		• •		•••						(~	(
Benthosema suborbitale							48	(3)	11	(2)	6	(2)			65	(17½)
Centrobranchus andrae							1	(461/2)								(100)
C. choerocephalus							5	(24)							5	(67)
Diogenichthys atlanticus							8	(151/2)	2	(18½)	2	(11)			12	(45)
Hygophum proximum			26	(18)	95	(3)	11	(13)		(0014)					132	(11)
n. reinnarati Myctophum brachygnathum			17	(22)	45	(30%)	19	(11)	,	(2072)					65 21	(17/2)
M. lychnobium			32	(15)	18	(13)	8	(151/2)							58	(20)
M. nitidulum					1	(46)	6	(21)							7	(581/2)
M. selenops					5	(25)			•			(10)			5	(67)
M. spp. Symboloobarys overmanni			۵	(261/4)	76	(4)	22	(0)	2	(18½)	1	(19)			109	(78½)
Other Larvae			3	(20%)	10	(4)	22	(9)		(2072)					100	(14)
Congridae:																
Ariosoma sp.	1	(38)													1	(100)
Nemichthyidae:		(00)		(5.4)												
Nemichthys scolopaceus	1	(38)	1	(54)											2	(84%)
Bathvlagus bericoides											1	(19)			1	(100)
B. longirostris									з	(131⁄2)	1	(19)			4	(721/2)
Stomiatoid fishes ¹	2	(281⁄2)	22	(20)	16	(14)	2	(35)							42	(28)
Idiacanthidae:							-	(4.5)							-	(= < : :
rolacanthus lasciola Paralepididee					Т	(46)	7	(18)							8	(551⁄2)
Type A (prob. Lestidium nudum)	2	(281/2)	1	(54)	2	(37)									5	(67)
Type B (like L. interpacificum)	7	(16)	7	(291/2)	2	(37)									16	(41)
Type D (prob. Gen. nov. sp. nov.)				, in the second s	4	(28)									4	(73½)
Paralepis atlantica Stomonopudia		(28)		(2014)		(00)			2	(181⁄2)					2	(841/2)
Stemonosuois macrura	1	(30)	4	(33/2)	4	(∠6)									9	(52)

LOEB: VERTICAL DISTRIBUTION OF LARVAL FISHES

TABLE 2.—Continued.

	0	-25 m = 10	2	5-50 m = 10	5	0-75 m 1 = 10	75-100 m n = 10		100-225 m n = 6		100-350 m n = 6		350-600 n	n	Total
Species	N	R	N	R	N	R	N	R	N	R	N	R	NR	N	R
Sudis atrox Uncisudis advena			2	(44½) (54)	2	(37) (37)	2 5	(35) (24)						6 8	(61) (55½)
Unidentified Paralepidids Alepisauridae:			1	(54)	2	(37)	_	(07)						3	(78½)
Alepísaurus ferox Evermannellidae:				(3	(30½)	2	(35)						5	(67)
Evermannella Indica Odontostomops normalops Unidentified evermannellids	2	(28½)	4 44 2	(33½) (12) (44½)	1 7	(46) (21)								5 53 2	(67) (22) (84½)
Scopelarchus spp. Notosudidae:							4	(271⁄2)	з	(131⁄2)	4	(5)		11	(48)
Ahliesaurus brevis Scopeloseurus smithi	10 14	(14½) (9%)	1 8	(54) (28)			3	(30)						11 25	(48) (32)
Neoscopelidae: Scopelengys sp. (prob. clarkei)		()	2	(441/2)			•	(-0)						2	(841/2)
Giganturidae: Bathyleptus IIsae			1	(54)										1	(100)
Melanocetidae: Melanocetus johnsoni	4	(231/2)			1	(46)								5	(67)
<i>M.</i> sp. Oneirodidae:	1	(38)	•	(00)										1	(100)
Dolopicntnys longicornis Oneirodid A (poss. Lasiognathus sp	o.) 1	(38)	3	(39)										3	(78½) (100)
Gigantactinidae:		(38)	3	(3314)										3	(7892)
Ceratiidae: Ceratiis holboelli	•	(30)	1	(54)										1	(100)
Cryptopsaras couesi Caulophrvnidae:	5	(21)	4	(331/2)										9	(52)
Caulophryne jordani Unidentified ceratioids	4	(231/2)	3	(39)	1	(46)								1 7	(100) (58½)
Bregmacerotidae: Bregmaceros spp.					5	(25)	76	(1)	6	(6)	1	(19)		88	(15)
Ophidiidae: Brotulid (poss. Lamprogrammus nig	ger)		1	(54)										1	(100)
Macrouridae: Mesobius berryi Exocoatidae:											1	(19)		1	(100)
Unidentiified exocoetids			3	(39)	1	(46)								4	(731⁄2)
Melamphaes simus M. sp. A (prtb. indicus)			1	(54)			6 1	(21) (46½)						6 2	(61) (84½)
M. spp. Scopeloberyx spp.							1 20	(46½) (10)	1	(261⁄2)	з	(71/2)		1 24	(100) (33)
Scopelogadus mizolepis mizolepis Unidentified melamphaeids							2 1	(35) (46½)						2 1	(84½) (100)
Anoplogasteridae: Anoplogaster cornuta Zoidao:			1	(54)										1	(100)
Unidentified zeid Trachinteridae									1	(261/2)				1	(100)
Trachipterus sp. Stylephoridae:			1	(54)										1	(100)
Stylephorus chordatus Apogonidae:											1	(19)		1	(100)
Howella sp. Bramidae:	1	(38)	39	(14)	9	(171⁄2)								49	(25)
Brama japonica Coryphaenidae:	1	(38)	2	(44½)										3	(781⁄2)
Coryphaena sp. (prob. equiselis) Chiasmodontidae:	1	(38)												1	(100)
Gempylidae:	1	(38)		(2214)	2	(37)		(4614)						1	(100)
Gempyius serpens Trichiuridae: Diolosoinus multistristus	14	(972)	4	(5392)	2	(37)	ر م	(40½) (21)	1	(2614)				21	(36½) (45)
Type A (poss. Aphanopus carbo) Unidentified trichiurid Scombridae:			•	(34)	7	(20)	1	(21) (46½)	1	(261/2)				12	(45) (100) (100)
Acanthocybium sp. Katsuwonus pelamis	1 1	(38) (38)	2	(441/2)										1 3	(100) (78½)
Nomeidae: Cubiceps caeruleus	1	(38)												1	(100)

TABLE 2.-Continued.

	0-25 n =	m 10	25-50 n =	0 m 10	50-75 n =	im 10	75-10 n ==	00 m 10	100-2 n :	225 m = 6	100-3 // 1	350 m = 6	350-6 n =	600 m = 8	Tot	al
Species	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R
Total larvae identified Unidentified larvae Total larvae	1,190 143 1,333		2,583 347 2,930		932 89 1,021		557 106 663		111 22 133		63 11 74		12 8 20		5,448 726 6,174	
Number of rankings	41		60		49		50		31		24		7		112	

¹Stomiatoid fishes include Astronesthidae, Malacosteidae, Melanostomiatidae, and Stomiatidae.

frequency of occurrence within one of the 25 m depth intervals. For many of the more abundant species, the catches in replicate tows within this

interval were significantly greater (Mann-Whitney U test, $P \leq 0.05$) than those in adjacent intervals (Table 3).

TABLE 3.—Gonostomatidae, Sternoptychidae, and Myctophidae: Total estimated water column abundance of larval species during late summer in the North Pacific central gyre, based on summation of mean estimated abundances (numbers/1,000 m³) from each depth

			0-25 m			25-50 m				50-75 m				
	Total			Mediar)			Median)			Mediar)	
• •	no. per	F		length	Range	F		length	Range	F.		length	Range	
Species	1,000 m ³	(10)	%	(mm)	(mm)	(10)	%	(mm)	(mm)	(10)	%	(mm)	(mm)	
Gonostomatidae:												÷		
Cyclothone alba	365.0	10	39.7	5.6	3.2-12.6	10	47.0	4.5	2.5-12.2	10	11.7	7.9	2.2-12.4	
C. sp. A	15.0	9	181.7	5.9	3.2-13.8	6	15.0	7.6	4.9-13.9	2	3.3	9.4	5.0-13.7	
C. atraria	0.2	1	100.0	4.6										
Diplophos taenia	3.5	7	192.9	11.0	5.2-26.8	1	7.1	12.6						
Gonostoma atlanticum	8.3													
G, elongatum	3.3													
Ichthyococcus ovatus	3.8													
Margrethia														
obtusirostra	1.7													
Valenciennellus														
tripunctulatus	1.2													
Vinciquerria nimbaria	127.0	5	1.2	9.0	6.8-11.9	10	174.1	7.2	3.7-14.5	10	19.5	14.0	3.7-17.5	
V. poweriae	17.2									2	2.9	8.8	7.2-10.3	
Woodsia sp.	1.4													
Sternoptychidae:														
Aravropelecus spp.	1.7													
Sternoptyx spp.	4.3													
Myctophidae:														
Lampanyctinae:														
Bolinichthys distofax	6.8					5	100.0	5.7	3.2-8.8					
B. lonaipes	56.2	10	178.7	4.6	3.1-8.4	8	20.9	5.1	3.4-8.2	1	0.4	8.7		
Ceratoscopelus warmingi	75.2	4	5.0	4.0	3.2-4.7	10	178.2	5.0	2.7-7.7	10	15.6	6.3	4.8-8.3	
Diaphus anderseni	32.7	10	164.3	4.2	2.7-6.5	7	30.6	4.5	3.2-7.1	2	3.8	7.0	5.3-11.6	
D. "slender B"	2.8					2	18.2	3.6	2.5-4.6	2	63.6	5.6	3.5-6.3	
D. "slender C"	29.8	3	10.1	3.8	2.6-5.0	9	179.7	4.5	2.3-6.5	4	7.6	4.9	4.5-6.3	
D. brachycephalus	12.8	3	11.8	4.0	3.7-4.6	6	58.8	4.2	2.6-5.9	5	27.4	5.4	4.3-8.7	
D. elucens	57.5	8	7.8	3.5	2.8-4.8	10	171.3	4.0	2.6-8.7	6	20.0	5.5	2.6-8.6	
D. rolfbolini	33.2	1	1.5	3,4	3.3-3.5	10	¹ 73.1	4.0	2.7-6.6	8	20,4	4,7	2.9-7.7	
D. "stubby C"	5.8	2	21.7	3.5	3.2-3.8	2	47.8	3.7	3.0-4.2	2	30,4	3.6	3.3-3.8	
Lampadena anomala	2.0	5	62.5	5.1	3.4-5.8	3	37.5	3.7	2.9-6.2					
L. luminosa	5.8	4	47.8	5.0	3,7-5.9	4	47.8	6.8	3.4-8.6					
Lampanyctus "big snout"	4.5					7	¹ 88.9	4.0	2.8-7.1	2	11.1	5.6	3.9-7.4	
L. "lacks pectorals"	11.4					3	8.8	4.0	3.5-5.9	9	172.2	4.4	2.6-6.2	
L. nobilis	6.5	1	3.8	5.4		5	88.5	4.8	2.9-10.5	2	7.7	7.8	5,4-10.2	
L. steinbecki	34.5	3	2.2	3.2	3.2-4.2	10	¹ 89.1	3.4	2.1-5.5	4	8.7	4.4	2.9-6.9	
Lobianchia gemellari	14.6									8	49.7	4.4	2.8-5.8	
Notolychnus valdiviae	11.3									2	4.4	4.0	3.1-10.5	
Triphoturus nigrescens	36.5	4	4.1	5.0	2.3-7.4	10	¹ 87.7	4.4	2.7-8.1	4	5.5	6.7	5.2-7.9	
Myctophinae:														
Benthosema suborbitale	14.5													
Centrobranchus andrae	0.2													
C. brevirostris	0.2													
C. choerocephalus	1.2													
Diogenichthys														
atlanticus	2.8													
Hygophum proximum	33.0					9	19.7	3.8	2.8-5.9	10	172.0	4.5	2.3-8.7	
H. reinhardti	16.4								-	9	¹ 68.5	6.5	3.8-9.4	
Myctophum brachygnathum	5.2					6	81.0	2.9	2.3-4.1	2	14.3	3.9	2.5-4.8	
M. lychnobium	14.5					7	55.2	3.7	2.8-5.6	5	31.0	3.6	2.5-4.6	
M. nitidulum	1.8									1	14.3	3.9		
M. selenops	1.2									2	100	4.7	3.4-5.4	
Symbolophorus evermanni	27.2					3	8.3	5.5	3. 9- 6.2	9	¹ 69.9	4.5	2.8-5.6	

Designates abundances which, based on abundances within replicate tows, are significantly greater (Mann-Whitney U-test, P <0.05) than in any other depth ²Denotes use of 100-225 m instead of 100-350 m samples.

Gonostomatid and myctophid larvae made up most of the ichthyoplankton in the upper 100 m

(Figure 2). The "other larvae" were a low, constant percent of the total from the surface to 75 m, but

their percent contribution was markedly increased between 75 and 350 m. Below 350 m most

of the larvae were sternoptychids and gonostomatids.

Family Gonostomatidae

The gonostomatids (8 genera, 12 species) composed 48% of the identified larvae. The family was an important fraction of the total larvae in all strata (Figure 3a); 97% of the estimated family abundance occurred above 100 m. Maximum abundance was at 25-50 m due to concentrations of the two most abundant species Cyclothone alba

interval; and frequency of occurrence (F) in (n) samples, percent of total estimated water column abundance, median length, and size range (mm standard length) within each depth interval.

		7	5-100 m			10	00-350 m	350-600 m				
0	 F	~	Median length	Range	F		Median length	Range	F		Median length	
Species	(10)	%	(11111)	(mm)	(6)	%	(mm)	(mm)	(8)	%	(mm)	
Gonostomatidae:	-											
Cyclothone alba	5	1.2	9.2	3.7-14.7	-22	0.3	4.1	3.8-4.7				
C. sp. A												
C. atraria												
Diplophos taenia	_		• •	0 7 40 0		40.0						
Gonostoma atlanticum	7	90.0	6.1	2.7-16.3	1	10.0	0.5	2.7-12.9				
G. elongatum	5	75.1	5.4	3.7-12.2	2	24.9	6.5	4.3-8.2				
Ichthyococcus ovatus	3	45.7	8.0	5.8-13.2	-3	54.3	11.0	4.0-16.3				
Margrethia					20	100	40	0000				
ODIUSITOSITA Malana la ana liva					-3	100	4.0	2.0-0.2				
Valenciennellus					•	100		7100				
tripunctulatus	•		14.0	20170	2	100	0.0	7.1-9.9				
Vinciguerria nimparia	9	4.9	14.2	3.9-17.0	1	0.3	4.0	5.1-1.1				
V. poweriae	9	87.4	10.0	0.0-19.2	24	9.7	2.1	0.0-19.7				
Woodsia sp.	2	/0.4	5.9	3.7-0.2	-1	29.0	3.2					
Stemoptychidae:						25.2			•	76.9		
Argyropelecus spp.		6 0			4	2J.2			-	70		
Mustanhidae:		5.0			4	07.0				1.6		
l ampenyetinge:												
Bolizichthue distofev												
B longines												
Ceretosconelus werminai	2	0.7	10.7	86-128	21	0.5	11.8					
Dianhus anderseni	-	•		0.0 12.0	i	1.3	10.5					
D "slender B"	2	18.2	8.8	6 2-10 0	•							
D. "slender C"	2	1.7	6.6	4.3-8.9					1	1.0	4.9	
D. brachvcenhalus	1	2.0	6.1									
D. elucens	ź	0.9	6.8	4.8-8.9								
D. rolfbolini	3	3.8	6.9	4.9-9.9	1	1.3	4.7	2.9-7.8				
D. "stubby C"												
Lampadena anomala												
L. luminosa	1	4.4	12.7									
Lampanyctus "big snout"												
L. "lacks pectorals"	4	15.3	5.7	3.2-6.8	² 1	3.7	4.3					
L. nobilis												
L. steinbecki												
Loblanchia gemellari	9	44.6	3.8	3.2-7. 9	²2	5.7	4.0	3.7-4.2				
Notolychnus valdiviae	8	¹ 88.3	5.2	3.3-8.0	2	7.3	6.2	6.1-6.4				
Triphoturus nigrescens	2	2.7	7.6	6.2-11.8								
Myctophinae:												
Benthosema suborbitale	4	82.8	3.6	2.5-7.8	3	17.2	3.9	1.8-8.0				
Centrobranchus andrae	1	100	5.9									
C. brevirostris	1	100	5.3									
C. choerocephalus	3	100	6.2	3.4-7.1								
Diogenichthys												
atlanticus	4	70.7	4.9	4.3-5.8	2	29.3	4.2	3.8-4.6				
Hygophum proximum	5	8.3	5.5	2.2-10.8								
H. reinhardti	- 7	28.9	6.5	2.4-13.1	21	2.6	4.6					
Myctophum brachygnathum	1	4.7	7.5									
M. lychnoblum	3	13.8	3.6	2.2-4.2								
M. nitidulum	3	85.7	3.7	2.7-4.9								
M. selenops												
Symbolophorus evermanni	8	20.2	4.4	3.3-10.5	² 1	1.6	4.7					



FIGURE 2.—Percent contribution of major families and "other larvae" to the total ichthyoplankton caught within each depth interval of the North Pacific central gyre during summer.

and Vinciguerria nimbaria (Figure 3b). Maximum diversity occurred at 75-225 m.

CYCLOTHONE SPP.—Cyclothone alba is a numerous larval fish species in the central gyre throughout the year, ranking second in abundance only to Vinciguerria nimbaria (Loeb 1979b). It was the most abundant species taken during this cruise (27% of all larvae), and was present in all samples from 0 to 75 m; below 75 m it was rare (Table 2). Eighty-seven percent of the estimated water column abundance was from the upper 50 m, with highest concentrations at 25-50 m (Figure 3b). Abundances in replicate tows within the 0-25 m and 25-50 m intervals were not significantly different from each other; they were, however, significantly greater (Mann-Whitney U test, P < 0.01) than those in deeper intervals.

A wide range of larval lengths was found within each depth interval from 0 to 75 m and the cumulative size-frequency curves differed significantly (Kolmogorov-Smirnov test, P < 0.05) between all three intervals (Figure 4). There was no simple



FIGURE 3.—Vertical distributions of larval gonostomatids in the North Pacific central gyre during summer. Concentrations of (a) gonostomatid larvae (12 species combined) and of (b) *Cyclothone alba* and *Vinciguerria nimbaria* larvae by depth interval.

increase in standard length with depth: smaller sizes dominated at 25-50 m, larger lengths at 50-75 m, and intermediate sizes at 0-25 m. Although median standard length was largest in the 75-100 m interval, the cumulative size-frequency curve was not significantly different from that at 50-75 m, possibly because of the paucity of larvae captured at 75-100 m. The three largest larvae present in 75-100 m samples (11.6-14.7 mm) were in the prometamorphic (white photophore) stage (Ahlstrom and Counts 1958) of development. Only three small larvae were caught between 100 and 350 m, and 57 metamorphosed individuals were caught at 350-600 m.



FIGURE 4.—Cumulative size-frequency curves for *Cyclothone* alba larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

Most of the smallest C. alba larvae apparently occur near the bottom of the mixed layer, and move first up and then downward with increasing size and development; the most advanced stage attained in 0-100 m is prometamorphic. A rapid descent may then occur, indicated by the near absence of any individuals in 100-225 m and 100-350 m samples. Photophore completion and metamorphosis probably occur at depths >350 m, in agreement with Ahlstrom's (1974) report that only the white photophore stage of Cyclothone spp. is found above 200 m, and that more advanced stages occur deeper in the water column.

Kobayashi (1973) gives a 300-1,000 m depth range for adult Pacific C. alba. He found that the individuals occurring in the range of maximum abundance (400-600 m) were smaller than those occurring shallower or deeper; intermediate-sized adults were shallower and largest adults were deeper. This size distribution of the adults parallels that found herein for the larvae, although shifted well downwards in the water column.

Cyclothone sp. A is probably the larval form of C. pseudopallida, and is the only other larval Cyclothone species found in abundance in the central gyre (Loeb 1979b). Fifty-nine of the sixty larvae caught were from the upper 50 m, and maximum abundance was at 0-25 m (Table 3). Median standard lengths increased with depth but, due to the small sample sizes, significance of differences in size-frequency distributions could not be tested. No metamorphic stages were taken either in the stratified tows or among the 365 Cyclothone sp. A larvae taken in 0-300 m IKPT samples during other gyre cruises. Most of early larval development may occur at 0-50 m, with a subsequent rapid descent to the juvenile-adult depth ranges (500-900 m; Kobayashi 1973).

VINCIGUERRIA SPP.—Vinciguerria nimbaria was the second most abundant species caught (9% of all larvae). On a year-round basis it is the most abundant larval fish species taken in the gyre (Loeb 1979b). The larvae occurred in samples from 0 to 350 m (Figure 3b), but were consistently present (29 out of 30 samples) only between 25 and 75 m. Ninety percent of the estimated water column abundance was between 25 and 75 m (74% at 25-50 m). Abundances in replicate tows within the 25-50 m depth interval were significantly greater (P < 0.01) than in any other interval (Table 3).

Samples from 25 to 100 m contained a wide range of larval sizes. However, median standard length increased with depth (Table 3) and cumulative size-frequency curves from 25-50 m and 50-75 m (Figure 5) were significantly different from each other. The proportion of metamorphosing individuals increased below 50 m (Table 4). These included the prometamorphic (white photophore), midmetamorphic (rapid body shape change), and postmetamorphic (photophore completion and body pigmentation) stages described by Ahlstrom and Counts (1958). All V. nimbaria present in 0-25 m samples were early larvae, as were most in the 25-50 m samples (only 3% from 25-50 m were pro- or midmetamorphic). In contrast, 75% from 50-75 m were in metamorphic stages. Size distribution at 75-100 m was essentially bimodal: 40% of the larvae were very small (3.5-6.0 mm) and 50% were metamorphic (10.5-17.5 mm). No juveniles or adults were taken.

Vinciguerria poweriae was much less abundant, and had a deeper distribution than did its congener; it occurred from 50 to 350 m (Table 3), with maximum abundance at 75-100 m. There was a trend for increased size with depth (Table 3). Only four metamorphosing individuals were caught.



FIGURE 5.—Cumulative size-frequency curves for Vinciguerria nimbaria larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

TABLE 4.—Abundance of metamorphic stages of *Vinciguerria nimbaria* by depth during late summer in the North Pacific central gyre.

Depth	Total	Pro-	Mid-	Post-	Percent	
_(m)	duals	meta	morphic	metamorphic		
0-25	6					
25-50	376	5	6		2.9	
50-75	99	25	15	34	74.7	
75-100	25	2	4	7	52.0	
100-350	1					

OTHER GONOSTOMATIDS.—The eight other gonostomatid species caught were rare; together <4% of the family total (Tables 2, 3). Diplophos taenia had the shallowest distribution of any gonostomatid species, occurring mostly at 0-25 m. Gonostoma atlanticum, G. elongatum, Ichthyococcus ovatus, and Woodsia sp. were present in the 75-350 m range, with maxima at 75-100 m. Margrethia obtusirostra and Valenciennellus tripunctulatus were caught only at 100-225 m and 100-350 m.

Family Sternoptychidae

The Sternoptychidae is the third most abundant family in the central gyre in terms of total larval abundance on a year-round basis (Loeb 1979b). Peak abundances occur during winter months, when this family makes up more than 6% of the total larvae. Minimal catches occur in late summer, so the 40 individuals taken during the present (late summer) cruise can provide only a very sketchy description of the vertical distributions of this otherwise abundant family.

The two genera (Sternoptyx and Argyropelecus) almost always occurred deeper than 100 m (Figure 2) and were abundant relative to other larvae in the 100-600 m depth range. Sternoptyx spp. appeared to have a shallower distribution than Argyropelecus spp. (Table 2). All but 2 of the 35 Sternoptyx larvae were taken between 100 and 350 m, with largest catches at 100-225 m (24 larvae distributed among all six samples). Four of the five Argyropelecus larvae were caught at 350-600 m. This is in contrast with the depth distributions



FIGURE 6.—Vertical distributions of larval myctophids in the North Pacific central gyre during summer. (a) Concentrations of myctophid larvae (31 species combined) by depth interval. (b) Percent of estimated water column abundances of Lampanyctinae and Myctophinae larvae in each depth interval.

found in the eastern Atlantic (Badcock and Merrett 1976) where *Argyropelecus* larvae were found from 100 to 500 m and *Sternoptyx* from 500 to 1,000 m.

A variety of developmental stages of both genera were found in the stratified samples. Sternoptyx diaphana from 100 to 225 m ranged from early larvae (3.8 mm) to larvae with abdominal and isthmal photophores (7.7 mm). The four Argyropelecus spp. from 350-600 m ranged from very small undeveloped larvae to one individual with an almost complete photophore complement.

Family Myctophidae

The myctophids (14 genera, 31 species) contributed over 42% of the total larvae. Over 98% of the estimated water column abundance was in the upper 100 m with maximum abundance at 25-50 m (Figure 6a). Diversity was highest (21 to 23 species) between 25 and 100 m (Table 2). The larval depth distributions of the two subfamilies differed (Figure 6b). Ninety-four percent of the Lampanyctinae estimated water column abundance was in the upper 75 m, with peak abundance at 25-50 m; only two (Lobianchia gemellari and Notolychnus valdiviae) of the 19 species were not taken in the 25-50 m interval (Table 3). This subfamily contributed 78% of the myctophid individuals and therefore greatly influenced the shape of the family distribution curve (Figure 6a). Myctophinae larvae were never caught in the upper 25 m. and contributed only 7% of the total myctophid larvae in the 25-50 m interval. The subfamily was most abundant from 50-225 m, contributing 49%, 58%, and 71% of the total myctophid larvae in the 50-75 m, 75-100 m, and 100-225 m intervals, respectively; peak abundance occurred at 50 75 m (Figure 6b). Only 4 of the 12 myctophine species taken were found at 25-50 m, while 7 were taken at 50-75 m and 11 at 75-100 m (Table 3). Significant differences were found between the cumulative frequency versus depth distributions of the two subfamilies (Kolmogorov-Smirnov test, P << 0.01).

Aspects of abundance, size distributions, and development of the more abundant species are considered below. For some species a variety of developmental stages was found. Because of the diverse patterns of photophore development exhibited by myctophid larvae (Moser and Ahlstrom 1970) only very general terminology is used to denote these stages. These include: early larvae (= no photophore development); early photophore development larvae (= photophores developing); late photophore development larvae (= lacking full photophore complement and still having larval morphology); transforming, or metamorphosing, individuals (= those completing photophore development and undergoing changes in pigmentation and morphology); and transformed, or early juvenile, stages (= adult morphology and photophore patterns, but still lightly pigmented). Additional information from other gyre cruises on developmental stages is included here.

Subfamily Lampanyctinae

BOLINICHTHYS SPP.—Bolinichthys longipes was the fifth-ranked species taken, occurring primarily in the upper 50 m, with peak abundance at 0-25 m; abundances in replicate tows within the 0-25 m interval were significantly greater (Mann-Whitney U test, P < 0.01) than in other depth intervals (Table 3). Median standard lengths increased with depth (Table 3) and 0-25 m and 25-50 m cumulative size-frequency curves were significantly different from each other. The largest specimen (8.7 mm, from 50-75 m) was still in early photophore development. The largest B. longipes larva (10.8 mm) of the 670 taken from IKPT samples was also in early photophore development. No transforming individuals were taken, although juveniles ≥ 12.8 mm were caught.

Bolinichthys distofax had a narrower distribu-

tion than did *B. longipes*; all individuals came from 25-50 m (Table 3). Larval size ranges and developmental stages found in bongo and IKPT samples were comparable with those of *B. lon*gipes.

CERATOSCOPELUS WARMINGI.-Ceratoscopelus warmingi was the third-ranked species, >5% of total larvae, and is also third-ranked species on a year-round basis (Loeb 1979b). Although present at 0-225 m (Figure 7), 94% of the estimated water column abundance was at 25-75 m. Abundances in replicate samples within the 25-50 m interval were significantly greater (P < 0.01) than in other intervals; the species made up 9% of the total larvae in this interval. Median standard lengths increased with depth and cumulative size-frequency curves for 0-25 m, 25-50 m, 50-75 m, and 75-225 m (Figure 8) were all significantly different from each other. The three largest larvae (8.6-12.8 mm), taken at 75-225 m, were still in early photophore development stages. No later photophore development stages or transforming specimens of C. warmingi were found among the 1,806 larvae (to 16.7 mm) examined from 0-300 m IKPT samples; a few early juveniles $(\geq 18.0 \text{ mm})$ were taken.

DIAPHUS SPP.—Seven Diaphus species were taken on this cruise. They fell into the two morphological categories described by Moser and Ahlstrom (1974): the "slender" form (which as adults possess a suborbital photophore) and the







FIGURE 8.—Cumulative size-frequency curves for *Cerato-scopelus warmingi* larvae taken in 10 samples each from 0-25 m, 25-50 m, 50-75 m, and in combined samples from 75-100 m (10) and 100-225 m (6) of the North Pacific central gyre during summer.

"stubby" form (without this photophore). The presence of transforming specimens of most of these species in plankton samples facilitated their probable identifications. The "slender" species were *D. anderseni*, *D. brachycephalus*, and the *D.* mollis complex. The "stubby" species were *D. elu*cens, *D. rolfbolini*, and the possible larvae of *D.* schmidti.

Diaphus anderseni had the shallowest distribution among Diaphus species, with 96% of the abundance from the upper 50 m and significant (P < 0.05) peak abundance at 0-25 m (Figure 7b; Table 3). Median standard lengths increased slightly from 0-25 m to 25-50 m, with a much greater increase between 25-50 m and 50-75 m (Table 3); cumulative size-frequency curves were significantly different for all three intervals. The largest individuals (11.3 and 11.6 mm), caught at 50-75 m, were transforming. One recently transformed (10.5 mm) individual was taken at 100-350 m. The entire developmental sequence of D. anderseni was found in 0-300 m IKPT samples; transforming individuals were 11.3-11.8 mm.

Diaphus "slender C" (probably the "B" form of D. mollis; Clarke 1973), D. brachycephalus, D. elucens, and D. rolfbolini all had similar distributions centered around maximum abundances at 25-50 m (Figure 7b); for all but D. brachycephalus the abundances in replicate tows within this interval were significantly greater than in other depth intervals (Table 3). Within the 25-50 m interval,

D. elucens, D. rolfbolini, and D. "slender C" ranked 4, 7, and 8, respectively, in total larval abundance; D. elucens was the fourth-ranked species taken overall during this cruise (Table 2). For each species, median standard lengths increased with depth (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other.

No transforming individuals of these species were taken in tows considered here, although a transforming D. "slender C" (10.5 mm) was caught in a 0-100 m sample, and one recently transformed D. elucens (11.8 mm) was caught at 0-25 m. Oblique IKPT hauls (ranging in depth from 0-180 m to 0-360 m) on other central gyre cruises have caught late larval, transformational, and early juvenile stages of all four species. Transforming individuals of D. brachycephalus were 9.8-10.5 mm; D. elucens, 10.3-11.7 mm; D. "slender C," 11.2-12.7 mm; and D. rolfbolini, 11.7-12.5 mm.

The two other *Diaphus* species taken were both rare in stratified tows (Table 2). Most of *D*. "slender B" (probably the "A" form of *D*. mollis; Clarke 1973) occurred at 50-75 m, the deepest distribution of the genus (Figure 7b). Transforming specimens (10.0-11.3 mm) have been caught in 0-300 m IKPT hauls. *Diaphus* "stubby C" may be the larval form of *D*. schmidti; the larvae have been taken in the central gyre only in small numbers and sizes. Most were caught at 25-50 m during this cruise.

LAMPADENA SPP.—Lampadena anomala and L. luminosa were caught in low numbers within the upper 50 m. Eleven L. luminosa larvae occurred in four tows from both 0-25 m and 25-50 m; one large larva (12.7 mm) was also taken at 75-100 m (Table 3). There was a trend for increased size with depth. Lampadena anomala was taken (one per sample) in five 0-25 m and three 25-50 m samples (Table 3). All Lampadena spp. individuals were in early stages of photophore development. No late-stage specimens of these relatively rare central gyre species have been taken in any of the samples examined.

LAMPANYCTUS SPP.—Lampanyctus steinbecki, most abundant of the larval Lampanyctus species taken, ranked ninth for this cruise (Table 2). It was caught at 0-75 m, but 89% of the estimated water column abundance was at 25-50 m; abundances in replicate samples within this interval were significantly higher (P < 0.01) than in other intervals (Table 3). Only early-stage larvae (2.1-6.9 mm) were taken. Median standard length increased only slightly with depth (Table 3).

The three other Lampanyctus species caught in stratified tows were rare. These included: L. "big snout," probably of the L. niger complex; L. "lacks pectorals," a larval stage of an undescribed Lampanyctus species (E. H. Ahlstrom³); and L. nobilis. The larvae of L. "big snout" and L. nobilis were most abundant at 25-50 m, while L. "lacks pectorals" was taken mostly at 50-75 m (Table 3). All three species showed a trend for increased size with depth (Table 3); only early photophore development stages were taken. No late larval or transformational stages of any Lampanyctus species were found in 0-300 m IKPT samples (1,477 specimens examined).

LOBIANCHIA GEMELLARI—The larvae of L. gemellari occurred deeper than most lampanyctine species, only at depths >50 m (Table 3). Over 94% of the estimated water column abundance was between 50 and 100 m; larvae were similar in frequency of occurrence in samples and in abundance at 50-75 m and 75-100 m. Cumulative sizefrequency curves for 50-75 m and 75-100 m were significantly different from each other and indicated more small and fewer large individuals in the deeper interval. The largest larvae taken in stratified tows (6.7 and 7.9 mm) were in early photophore development. Stages from early larvae through transformation (10.8-12.7 mm) were caught in 0-180 m IKPT hauls.

NOTOLYCHNUS VALDIVIAE.—Both the adult and larval N. valdiviae differ from other lampanyctine species in several respects, and Moser and Ahlstrom (1974) suggested placement of the species in a separate subfamily. The larvae are also unusual in their depth distributions as compared with other lampanyctine species (Figure 7a). Notolychnus valdiviae was absent at 0-50 m and rare at 50-75 m; maximum abundance (40 of the 44 larvae caught) occurred at 75-100 m where the species ranked fourth (Table 2).

All stages of development of N. valdiviae were found between 50 and 100 m. The largest pretransformation specimen (8.0 mm) was from 75-100 m. A 10.5 mm transforming specimen plus nine other individuals ranging from recently transformed to adult (10.8-21.8 mm) were caught at 50-75 m. Three other metamorphosed individuals were found in other intervals: a recently transformed individual (11.3 mm) at 25-50 m; and two juveniles (15.7 and 17.3 mm) at 75-100 m.

TRIPHOTURUS NIGRESCENS.—Triphoturus nigrescens was the fourth-ranked myctophid (eighth ranked species overall) taken. The larvae were distributed from 0 to 100 m, with 88% of the estimated water column abundance at 25-50 m: abundances in replicate samples within this interval were significantly greater (P < 0.01) than in other intervals (Table 3). Median standard lengths increased below 50 m (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other. The 11.8 mm larva, from 75-100 m (Table 3), was one of the largest T. nigrescens larvae taken in any central gyre plankton sample; it still lacked photophore development. Nine metamorphosed individuals were also caught in stratified tows: six (14.7-17.0 mm) at 25-50 m; one (17.9 mm) at 50-75 m; and two (17.0 and 21.3 mm) at 75-100 m. No late-stage larvae have been found among the 612 specimens collected from central gyre IKPT samples.

Subfamily Myctophinae

BENTHOSEMA SUBORBITALE.—Benthosema suborbitale occurred at 75-350 m, and was an important component of the deeper ichthyoplankton, ranking third in 75-100 m samples and second in 100-225 m and 100-350 m samples (Table 2). Largest numbers occurred at 75-100 m, but 46 of the 48 larvae from this interval came from only 2 of 10 samples; frequency of positive samples was highest at 100-225 m (five of six samples). Size ranges, median lengths, and cumulative size-frequency curves were similar for all depth intervals. The largest larva (8.0 mm) was in early photophore development. Seven recently transformed juveniles were caught: five (11.1-12.1 mm) at 25-50 m and two (10.8 and 12.7 mm) at 50-75 m. Developmental stages to early transformation (10.8-11.3 mm) were found in 0-300 m IKPT samples.

CENTROBRANCHUS SPP.—Three species of Centrobranchus were caught at 75-100 m (Table

³E. H. Ahlstrom, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. 1977.

3). Centrobranchus andrae and C. brevirostris were represented by single specimens. The five C. choerocephalus individuals (3.4-7.1 mm) occurred in three samples. All specimens were early photophore stage larvae.

DIOGENICHTHYS ATLANTICUS.—The 12 D. atlanticus larvae (all early photophore stage larvae) were caught between 75 and 350 m; 8 came from 75-100 m (Table 2). During other central gyre cruises, D. atlanticus was abundant in IKPT samples, and developmental stages from early larvae to transformation (11.3-12.8 mm) were found.

HYGOPHUM SPP.—Hygophum proximum was the most numerous larval myctophine (Table 2). It occurred from 25 to 100 m, with maximum abundance and significantly larger catches in replicate tows (P < 0.01) at 50-75 m (Table 3). Median standard length increased with depth (Table 3) and 25-50 m and 50-100 m size-frequency curves were significantly different from each other. The largest larva (10.0 mm, from 75-100 m) was in early photophore development. No late-stage H. proximum larvae have been found among the 490 examined from 0-300 m IKPT samples.

Hygophum reinhardti larvae were more deeply distributed than those of *H. proximum*, occurring from 50 to 225 m. As with its congener, maximum estimated water column abundance and significantly larger catches ($P \le 0.05$) were at 50-75 m, but the larvae were also frequently taken (7 of 10 samples) at 75-100 m (Figure 7c). There were no apparent trends in size with depth (Table 3). No late photophore development larvae were caught, but two recently transformed individuals (12.3-13.3 mm) were found in 0-300 m IKPT samples from other cruises.

MYCTOPHUM SPP.—Four Myctophum species were caught (Table 2). The 58 M. lychnobium larvae occurred between 25 and 100 m, with maximum abundance at 25-50 m; M. brachygnathum had a similar distribution. All five M. selenops were caught at 50-75 m, and six of the seven M. nitidulum at 75-100 m. All of the larvae were small (<8.0 mm) and in early photophore development; only those of M. brachygnathum appeared to have increased size with depth (Table 3). A total of 393 Myctophum larvae, of all four species, have been examined from central gyre IKPT samples; none exceeded 10.0 mm or were in advanced stages of photophore development.

SYMBOLOPHORUS EVERMANNI.-Symbolophorus evermanni occurred from 25 to 225 m; over 90% of the estimated water column abundance was between 50 and 100 m; abundances in replicate samples within the 50-75 m interval were significantly greater (P < 0.05) than in other intervals (Table 3). Although the largest larva (10.5 mm) was from 75-100 m, the median standard length was smaller there than at shallower depths (Table 3). The 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other, indicating decreased size with increased depth. Only early photophore development stages were caught by stratified tows. This was also the case for all 0-300 m IKPT samples examined, where the largest prejuvenile (15.5 mm) of 369 individuals was in the earliest stages of photophore development.

Other Larvae

Other families contributed only 9% of the identified larvae and included a wide assortment of mesopelagic fishes; only 3 of the 33 families identified were epipelagic. These "other larvae" were found in samples taken from 0 to 350 m (Figure 2). Total abundance was low in the upper 75 m, but increased greatly below 75 m (due primarily to peak abundances of two families), and made up 25% and 19% of the ichthyoplankton in 75-100 m and 100-350 m samples, respectively. Maximum diversity occurred at 25-50 m.

None of these "other" species was abundant. Of the 49 kinds of larvae represented only 3 were caught in even moderate numbers: *Bregmaceros* spp. (Bregmacerotidae), *Odontostomops normalops* (Evermannellidae), and *Howella* sp. (Aponogonidae). Only *Bregmaceros* spp. is abundant in the central gyre ichthyoplankton on a year-round basis (Loeb 1979b). Together these three kinds made up 39% of the other larvae; the remaining 61% was contributed by 1 order and 30 families (42 species). Catch information on the other larvae is presented in Table 2; more detailed distributional data is provided in Loeb (1979a).

DISCUSSION AND CONCLUSIONS

The overall vertical distribution pattern of central gyre ichthyoplankton conforms to that described by Ahlstrom (1959) for the California Current. Most species and individuals were in the upper 100 m, with maximum abundance and diversity at 25-50 m, possibly related to the bottom of the mixed layer. A distinct change in species composition and relative abundances occurred below 75 m. This involved a shift from dominance by Cyclothone alba, Vinciguerria nimbaria, and lampanyctine myctophids to other gonostomatid species, myctophine myctophids, and other families. Ahlstrom (1959) previously had found groups of species (in the California Current) to be either predominantly within the mixed layer and upper thermocline or mostly within or below the thermocline.

None of the abundant larvae were taken only in one 25 m interval, and most were found over at least a 75 m depth range. However, almost all species taken in the upper 100 m had distinct maxima of catch frequency and abundance within one of the 25 m depth intervals sampled; for many species, despite high catch variability due to patchiness, the abundances in replicate tows within this interval were significantly higher than in any other interval. Almost twice as many larvae and half again as many kinds were found in 100-225 m samples as in 100-350 m samples, indicating that most deeper species may be distributed above 225 m.

Significant changes were found in cumulative size-frequency distributions with depth for many of the abundant species. There was a general trend for those species with peak abundance in the upper 50 m to have significant increases in larval size with depth. Species with maximum abundance below 50 m tended to exhibit no size-depth changes, or had significant decreases in size with depth. With these deeper larvae, the apparent lack of size change with depth may be the product of small sample sizes outside the depth of maximum abundance and the broader depth ranges sampled below 100 m.

The gonostomatids exhibited two different distributional patterns. Cyclothone spp., V. nimbaria, and Diplophos taenia occupied the topmost 50 m. The other seven species were distributed below 75 m, with maximum abundances in the 75-225 m range. The nighttime depth distribution patterns of juveniles and adults (from Clarke 1974) of the migratory gonostomatid species relative to each other are, with the exception of Gonostoma elongatum, generally the same as for the larvae (Figure 9). Both larval and adult Diplophos taenia had the shallowest distribution and Valenciennellus tripunctulatus the deepest distribution within the family. Also, except for G. elongatum,



FIGURE 9.—Larval (upper bar) and adult (lower bar) nighttime depth distributions for migratory gonostomatid species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates intervals where >90% of the estimated water column abundance occurred. Adult depth distributions from Clarke (1974).

the upper depth distributions of the adults (usually small adults; Clarke 1974) tend to overlap the lower ranges of peak larval abundance. Although Clarke's (1974) adult information is from a different oceanic regime (offshore Hawaiian waters), his general patterns of depth distribution may still be valid for the central gyre adults.

The night depth patterns of larval and adult myctophid species are more complex than those of the gonostomatids. The larvae of subfamily Lampanyctinae generally occupy shallower depths than do those of subfamily Myctophinae (Figure 6b). The opposite is generally true of the night distributions of the adults from the two subfamilies. Clarke (1973) presented adult depth distributions for 46 myctophid species taken near Hawaii. Of the 15 myctophine species he listed, 8 had upper night distribution limits at 0-25 m (5 of these were taken in substantial numbers by dip nets): 2 others occurred at 25-50 m. In contrast, only 10 of the 31 lampanyctine species listed by Clarke (1973) were caught in the upper 50 m. Ahlstrom and Stevens (1976) also found that neuston (surface) samples taken in the California Current caught only myctophine juveniles and adults and lampanyctine larvae.

Different night adult and larval depth patterns are apparent for the two subfamilies (Figure 10). Lampanyctine adults, generally overlap, or are distributed below, their depths of maximum larval abundance. The shallowest lampanyctine individuals (which share the larval depth range) are usually small adults or juveniles (Clarke 1973). This contrasts strongly with myctophine adults



FIGURE 10.—Larval (upper bar) and juvenile and adult (lower bar) nighttime depth distributions for the more abundant lampanyctine and myctophine (Myctophidae) species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates depth intervals where $\geq 90\%$ of the estimated water column abundance occurred. Adult depth distributions from Clarke (1973).

(except for *Hygophum* spp.), wherein all sizes tend to be distributed above the depths of maximum larval abundance. In most cases the largest adults of both subfamilies are vertically separated from the larvae, and, where overlap occurs, the smallest juveniles are in similar depth ranges with the largest larvae.

A variety of patterns of early developmental stages were found. Among the gonostomatids, metamorphic stages of Cyclothone alba and Vinciguerria spp. were found in stratified samples. Apparently C. alba leaves the larval depth range once it has reached the prometamorphic stage of development. Vinciguerria spp. go through all early metamorphic stages while in the larval depth range and presumably descend to greater depths once the postmetamorphic stage is completed. For both C. alba and V. nimbaria the advanced stages of larval development were found in the lower portion of the larval depth range. Gradual downward migration with development, as seen in V. nimbaria, may also occur in Valenciennellus tripunctulatus and Gonostoma spp. (Badcock and Merrett 1976).

The myctophid species exhibited different levels of photophore development before descending to juvenile depths. Developmental series from early larvae to transforming individuals were found from \leq 350 m for 11 of the 31 myctophid species taken in Climax I. These include: six of the seven Diaphus species (all but D. schmidti), Lobianchia gemellari, Notolychnus valdiviae, Benthosema suborbitale, Diogenichthys atlanticus, and Hygophum reinhardti. At least some individuals of Diaphus spp., L. gemellari, N. valdiviae, and D. atlanticus complete transformation before descent to juvenile depths or else begin extensive migrations before transformation. The presence of lightly pigmented juveniles of D. anderseni, D. elucens, N. valdiviae, B. suborbitale, and H. reinhardti in the upper 100 m at night indicated that, if these are not predescent individuals, some members of these species may undergo early juvenile migration.

No late photophore stage larvae were found for Bolinichthys spp., Ceratoscopelus warmingi, Lampadena spp., Lampanyctus spp., Triphoturus nigrescens, H. proximum, Myctophum spp., or Symbolophorus evermanni in either the Climax I samples or 0-300 m IKPT samples taken on other gyre cruises. These larvae appear to leave the upper 300 m of the water column at varying levels of early photophore development prior to transformation. The late stages of photophore development probably occur at the juvenile day depth range for each species. The developmental state at descent appears to be a generic characteristic within both subfamilies. Except for Hygophum spp., congeners achieved similar levels of photophore development while in the upper 300 m.

Due to small numbers of other larvae captured. little can be ascertained about their distributional patterns. Most species occurred in the upper 100 m, with greatest numbers of species at 25-50 m. Basic trends in depth distribution appeared to exist on a familial or ordinal level: Notosudidae were most abundant at 0-25 m; five families of ceratioid fishes occurred in the upper 50 m; four families of stomiatoid fishes and the Evermannellidae occurred most frequently at 25-75 m; Bregmacerotidae and Melamphaeidae were most abundant at 75-100 m; and Scopelarchidae, Bathylagidae, and Sternoptychidae occurred below 100 m. The paralepidids (much like the myctophids) exhibited a variety of depth distributions through the upper 225 m.

The depth distributions described are for the late summer central gyre ichthyoplankton assemblage. Surface temperature is $6^{\circ}-7^{\circ}$ C lower in winter and the mixed layer depth increases from ca. 40 m in late summer to 110-140 m in winter (McGowan and Williams 1973). There are also

definite seasonal changes in larval fish species composition and abundance relations. As larval depth distributions are apparently affected by temperature distribution and mixed layer depth (Ahlstrom 1959) spatial patterns in winter gyre waters may be different from those portrayed here.

ACKNOWLEDGMENTS

This work was supported by grants from the Institute of Marine Resources of Scripps Institution of Oceanography and the Oceanic Biology Program (Code 484) of the Office of Naval Research. Ship time was in part supported by the U.S. National Science Foundation and the Marine Life Research Program of the State of California. I greatly appreciate the assistance in larval fish identification provided by E. H. Ahlstrom and Betsy Stevens of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, Calif. Special thanks go to Eric Shulenberger of the Office of Naval Research for his excellent editorial advice. Thanks also to John A. McGowan and R. H. Rosenblatt of Scripps Institution of Oceanography for their editorial suggestions.

LITERATURE CITED

AHLSTROM, E. H.

- 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.
- 1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Rep. 13:39-44.
- 1974. The diverse patterns of metamorphosis in gonostomatid fishes—an aid to classification. *In J. H. S. Blaxter* (editor), The early life history of fish, p. 659-674. Springer-Verlag, N.Y.

AHLSTROM, E. H., AND R. C. COUNTS.

1958. Development and distribution of Vinciguerria lucetia and related species in the eastern Pacific. U.S. Fish Wildl. Serv., Fish. Bull. 58:363-416.

AHLSTROM, E. H., AND E. STEVENS.

1976. Report of neuston (surface) collections made on an extended CalCOFI cruise during May 1972. Calif. Coop. Oceanic Fish Invest. Rep. 18:167-188.

BADCOCK, J., AND N. R. MERRETT.

1976. Midwater fishes in the eastern North Atlantic. I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog. Oceanogr. 7:3-58.

BARNETT, M. A.

1975. Studies on the patterns of distribution of mesopelagic fish faunal assemblages in the central Pacific and their temporal persistence in the gyres. Ph.D. Thesis, Scripps Institution of Oceanogpraphy, Univ. California, San Diego, 145 p.

BRIDGER, J. P.

- 1956. On day and night variation in catches of fish larvae. J. Cons. 22:42-57.
- CLARKE, T. A.
 - 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.
 - 1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. Fish Bull., U.S. 72:337-351.
- CONOVER, W. J.
 - 1971. Practical nonparametric statistics. John Wiley and Sons, N.Y., 462 p.
- GREGG, M. C., C. S. COX, AND P. W. HACKER.
 - 1973. Vertical microstructure measurements in the central North Pacific. J. Phys. Oceanogr. 3:458-469.

KOBAYASHI, B. N.

1973. Systematics, zoogeography, and aspects of the biology of the bathypelagic fish genus *Cyclothone* in the Pacific Ocean. Ph.D. Thesis, Scripps Institution of Oceanography, Univ. California, San Diego, 487 p.

LEGAND, M., AND J. RIVATON.

1969. Cycles biologiques des poissons mésopélagiques de l'est de l'Océan Indien. Trosième note: action predatrice des poissons micronectoniques. Cah. O.R.S.T.O.M. Sér. Océanogr. 7:29-45.

LOEB, V. J.

- 1979a. The icthyoplankton assemblage of the North Pacific central gyre: spatial and temporal patterns. Ph.D. Thesis, Scripps Institution of Oceanography, Univ. California, San Diego, 220 p.
- 1979b. Larval fishes in the zooplankton community of the North Pacific central gyre. Mar. Biol. (Berl.) 53:173-191.
- MCGOWAN, J. A., AND T. L. HAYWARD.
 - 1978. Mixing and oceanic productivity. Deep-Sea Res. 25:771-793.
- MCGOWAN, J. A., AND P. W. WALKER.
 - In press. Structure in the copepod community of the central North Pacific gyre. Ecol. Monogr.
- MCGOWAN, J. A., AND P. M. WILLIAMS.
 - 1973. Oceanic habitat differences in the North Pacific. J. Exp. Mar. Biol. Ecol. 12:187-217.

MERRETT, N. R., AND H. S. J. ROE.

1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. (Berl.) 28:115-126.

MOSER, H. G., AND E. H. AHLSTROM.

- 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narroweyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.
- 1974. Role of larval stages in systematic investigations of marine teleosts: The Myctophidae, a case study. Fish. Bull., U.S. 72:391-413.

PEARCY, W. G., AND R. M. LAURS.

1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

SCRIPPS INSTITUTION OF OCEANOGRAPHY.

- 1966. A new opening closing paired zooplankton net. Scripps Inst. Oceanogr., SIO Ref. 66-23, 56 p.
- 1974. Physical, chemical and biological data. Climax I Expedition, 19 September 28 September 1968. Scripps. Inst. Oceanogr., SIO Ref. 74-20, 41 p.