DISTRIBUTION AND ABUNDANCE OF BILLFISH LARVAE (PISCES: ISTIOPHORIDAE) IN THE GREAT BARRIER REEF LAGOON AND CORAL SEA NEAR LIZARD ISLAND, AUSTRALIA

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ABSTRACT

Istiophorid larvae were relatively common in plankton samples from the Lizard Island region in November to early March 1980-85. Black marlin, blue marlin, and sailfish larvae were captured. Larvae of all three taxa were most concentrated and abundant in the Coral Sea immediately seaward (= windward) of the outer ribbon reefs. Concentration and abundance within the Great Barrier Reef Lagoon were not usually different from those more than 0.25 nautical miles offshore in the Coral Sea. Size-frequency data combined with the distributional information suggest that spawning or at least hatching of eggs was concentrated in the area within 0.25 nautical mile seaward of the reef crest. Preflexion larvae of blue marlin and sailfish were essentially confined to the upper 6 m of the water column (and perhaps the upper half of that), but not the neuston. Preflexion larvae of all three species dominated the oblique bongo net tows (98%), while postflexion larvae dominated the neuston samples (76%). This suggests an upward ontogenetic movement.

The horizontal distribution of istiophorid larvae is probably the result of spawning close to the reef front, an area of supposed downwelling, combined with the proclivity of the larvae to occupy surface waters. This should lead to retention of larvae in the forereef area. Some caveats about accepting this hypothesis as a complete explanation for the horizontal distribution of istiophorid larvae are discussed.

Near-reef areas appear to be important in the early life history of istiophorids at least in the Coral Sea and for the three taxa studied.

The billfishes of the family Istiophoridae are large, high trophic level, pelagic fishes of considerable sport and commercial importance throughout tropical and subtropical oceans (Nakamura 1985). Information on their early life history is limited and investigations have been hampered by the relative rarity of the larvae. Studies on the distribution of istiophorid larvae in the Indo-Pacific have dealt with distributions over very broad areas and have not examined distributions on a small scale, particularly those very close to reefs. (The considerable Japanese work was summarized by Nishikawa et al. 1985 and the Russian work by Gorbunova 1976.) Size of larvae in relation to horizontal distribution has only rarely been considered. Aside from reports that istiophorid larvae had been captured in neuston tows (e.g., Bartlett and Haedrich 1968; Gorbunova 1976) the only published information on vertical distribution of istiophorid larvae was provided by Ueyanagi (1964), who concluded billfish larvae were largely confined to surface waters during the day and dispersed through the upper 50 m at night.

During studies on the distributional ecology of the larvae of reef fishes in the vicinity of Lizard Island in the northern region of the Great Barrier Reef, Australia, two of us (Leis and Goldman) have sampled extensively in the Great Barrier Reef Lagoon and the near-reef waters of the Coral Sea. In our samples, we captured a relatively large number of istiophorid larvae. This has provided information which sheds light on little known aspects of the early life history of istiophorids and in view of the widespread interest in istiophorid biology, we have prepared this summary on the horizontal and vertical distribution of istiophorid larvae over relatively small scales and how these relate to development of the larvae. Because istiophorid larvae are difficult to identify, we have collaborated to insure accuracy in identification of the larvae.

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MATERIALS AND METHODS

All samples considered here were taken in an area between Lizard Island, approximately midway across the Great Barrier Reef Lagoon, to 10 nmi seaward of the outer ribbon reefs of the Great Barrier Reef in the Coral Sea (Fig. 1).

The Great Barrier Reef Lagoon is modally 30 m deep in this region (range 25-40 m). The outer ribbon reefs are located along the shelf break, and the bottom falls off sharply with distance into the Coral Sea reaching depths >2,000 m within 6 nmi (Fig. 1).

The samples immediately to windward of Lizard Island were taken from a 7 m boat with a net of 0.4 m^2 mouth area (see Leis 1986 for further details of sampling). Other samples were taken from RV *Sunbird*, a 14 m catamaran. The neuston net, with mouth dimensions of 1 × 0.3 m and 0.5 mm mesh, was towed between the bows of the catamaran, and normally fished to a depth of 0.1 m. Bongo nets of 0.85 m diameter and fitted with a depressor were towed in a double-oblique pattern to study horizontal distribution or in opening-closing mode to study vertical distribution. Nets were towed at approximately 1 m/second, were of 0.5 mm mesh, and were equipped with a flowmeter. During the vertical distribution study, a depth sensor with a deck display was fitted to the net. At other times, a mechanical depth-distance recorder was used.

The neuston net, when used, fished during the bongo net tow. The oblique bongo net tows were done to the greatest calculated depth that was

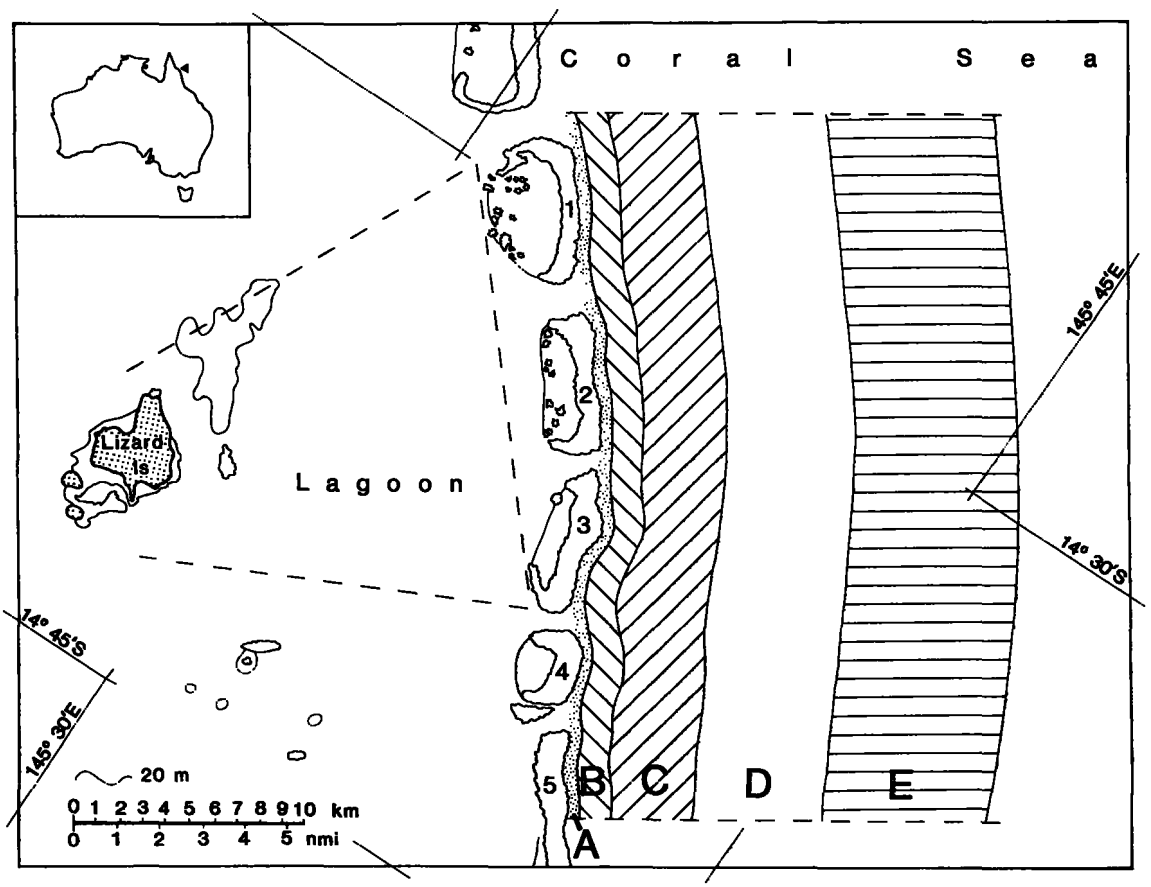

FIGURE 1.—Map of the study area. One sampling block is the Great Barrier Reef Lagoon beween Lizard Island and the ribbon reefs, this is delineated by the broken lines. In the Coral Sea, there are five sampling blocks A-E as defined in the text. Depths in the Lagoon range from 20 to 40 m. Depths to 400 m are encountered in Coral Sea block A, to 1,000 m in block B and >1,500 m in C-E. Outer ribbon reefs are 1) Day, 2) Carter, 3) Yonge, 4) No Name, and 5) Number 10 Ribbon. None of the outer reefs are emergent.

considered safe in the lagoon and close to the windward face of the reef. Because of the great variations in bottom topography in the latter area, the net actually hit bottom upon occasion. Further offshore, bongo net tows were done with a standard amount of wire out which ensured a maximum sampling depth in excess of 100 m.

Position fixing in the Coral Sea was by radar reflection of the waves breaking on the reef crest when close to the reef. This meant that actual distance off the reef varied somewhat (~100 m) depending on sea state and tide. Four cruises were made to investigate horizontal distribution: 1) 2-5 November 1984, 2) 17 and 20-22 November 1984, 3) 30 January-2 February 1985, and 4) 9-13 February 1985. On each cruise, six samples were taken between Lizard Island and the outer reef on one day (Fig. 1), and three days were spent in the Coral Sea running a transect each day and starting at opposite ends of the transect on alternate days. On each transect, two randomly located samples were taken in each of five offshore blocks defined by distance (nmi) from the outer reef crest (Fig. 1): A, 0-0.25 nmi; B, 0.25-1.0 nmi; C, 1.0-3.0 nmi; D, 3.0-6.0 nmi; E, 6.0-10.0 nmi. Therefore, six samples were taken in each block on each cruise. The three transects on a cruise were each centered off a different reef (i.e., either of Day, Carter, Yonge, No Name, or Number 10 Ribbon Reefs). Bad weather and high volumes of floating pumice precluded the routine use of the neuston net. There were some variations in this plan owing to weather or equipment problems, the most serious of which was missing 4 of 6 samples in block A on the second cruise. Larvae from other samples taken with similar methods in November 1983 were also included where appropriate. Funding limitations prevented processing of samples from block D.

The vertical distribution samples were taken in the lee of Carter Reef primarily in the Great Barrier Reef Lagoon, but partially in the pass to the north of Carter Reef (Fig. 1). Samples were taken in sets; each set consisted of a neuston tow and 3 bongo net (0-6 m, 6-13 m, and 13-20 m) tows. The 0-6 m stratum was sampled in the undisturbed water flowing between the hulls of the catamaran. In February-March 1983, 22 such sets were taken, 8 each in morning and afternoon and 6 at night.

Additional samples from within the Great Barrier Reef Lagoon as reported by Leis and Goldman (1984, 1987) and Leis (1986) were used for seasonality information. Samples in the Lagoon were taken in all months but May, June, August, September, and December. Samples were taken in the Coral Sea in October, November, January, and February.

Oblique bongo net tows typically filtered 1,000-1,500 m^3 and horizontally stratified tows filtered 400 m^3. Neuston tows typically travelled 1,200-2,000 m. All nets were carefully washed after each tow and the sample preserved in 5-10% seawater-formalin.

In the laboratory, samples were sorted using a dissection microscope (~10×) and all larvae removed. Samples from both sides of the bongo net were fully sorted except for the Great Barrier Reef Lagoon samples from February-March 1983 and November 1984 when only side was sorted because of high plankton volume. Larvae were placed in 70% ethanol prior to measurement. Identification of larvae followed Ueyangi (1963, 1974a, b). Larvae were measured using an eyepiece micrometer of a dissection microscope to the nearest 0.1 mm. Notochord length and standard length were measured for preflexion and postflexion larvae, respectively (Leis and Rennis 1983). Larvae from these samples are deposited in the Australian Museum, Sydney.

Numbers of larvae per sample were converted to numbers per volume (concentration) and numbers per area (abundance) using standard methods (Leis 1986). In analysis of vertical distribution data, only positive sets (i.e., those in which at least one larva was captured) were considered. Statistical methods followed Conover (1971) and Zar (1974). References to the Student-Newman-Keuls (SNK) test refer to the version based on ranks (Zar 1974).

RESULTS

Identification

We captured larvae of black marlin, *Makaira indica*; blue marlin, *Makaira mazara*; striped marlin, *Tetrapturus audax*; and Indo-Pacific sailfish, *Istiophorus platypterus*. The larvae here identified as black marlin correspond to the "non-pigmented" sailfish of Ueyanagi (1974a, b). This type of istiophorid larva has been captured only in the seas off northern Australia and the southern portion of the Indonesia-New Guinea archipelago (Ueyanagi 1974a, b). In our Coral Sea samples these larvae were found almost exclusively during November, the time when large

numbers of gravid female black marlin occur in the area (B. Goldman pers. obs.; J. Pepperell[4]). A major sport fishery is based on this apparent spawning migration and the catches are made primarily just off the windward reef faces in the northern Coral Sea. When sampling in November 1984, our research vessel was frequently operating in the midst of the sport fishing fleet. This circumstantial evidence suggested the possibility that the "non-pigmented" sailfish larva was in fact the larva of the black marlin, and led us to recheck these "non-pigmented" sailfish larvae. Two specimens (5.6 and 9.7 mm) were cleared and stained for bone and cartilage (Potthoff 1984); both specimens had vertebral formulae of 11+13=24. This confirms that they are of the genus *Makaira* (Nakamura 1985). These larvae can be distinguished from those of the only other Indo-Pacific member of the genus, the blue marlin, by head profile and depth and minor pigment differences. Therefore, we concluded that the "non-pigmented" sailfish larva captured in the present study were black marlin. A more detailed treatment of the identity of "non-pigmented" sailfish larvae will be given separately (Ueyanagi and Leis in prep.).

The larvae identified here as sailfish are normally pigmented sailfish larvae which had not previously been reported from the Coral Sea (Ueyanagi 1974a, b). Only a few striped marlin larvae were captured, and because nearly all were small and only tentatively identified, they are not considered further.

Seasonal Occurrence

Sailfish larvae were taken only in January, February, and March. Blue marlin larvae were taken in mid-November, January, February, March, and April, although only one larva was taken in April. Black marlin larvae were taken throughout November, and three were taken in January-February.

A sequence of occurrence of larvae and presumably of spawning in the area begins with the appearance of black marlin larvae in late spring-early summer, followed by blue marlin in summer-autumn, and finally sailfish in late summer-early autumn.

Horizontal Distribution

Black marlin larvae were most concentrated in block A adjacent to the seaward side of the reef on all cruises (Table 1). Concentrations elsewhere were low, with median values usually of zero. However, data from only one cruise could be tested statistically. The distribution of abundance was similar to that of concentration, with the exception that abundance in the two near-reef blocks could not be shown to be significantly different during the first cruise. During the first two (November) cruises, black marlin larvae were taken in 7 of 8 samples from the near-reef area (block A). Only three black marlin larvae were taken on cruises three and four (January-February), all in block A. Black marlin larvae were present in only 13 of 96 samples taken elsewhere, and of these areas, block B (0.25-1.0 nmi offshore) had the highest frequency of occurrence, 5 of 24 samples.

Clearly, black marlin larvae were consistently found in greatest numbers closest to the seaward side of the reef. The offshore extent of this high density zone of black marlin larvae was very limited, extending at most to 1 nmi seaward (block B) of the reef crest, but more likely to only 0.25 nmi.

Blue marlin larvae were less abundant than black marlin in our samples but had a similar distributional pattern. Again, data from only one cruise (the third) could be tested statistically. Except for the second cruise, blue marlin larvae were both most concentrated and abundant in block A, the area closest to the seaward face of the reef (Table 1). Further, 8 of the 13 occurrences were in this block. During the second cruise, blue marlin larvae seemed most concentrated and abundant at block B (0.25-1.0 nmi off), but only six larvae were captured on this cruise and only two samples were taken in block A so the significance of these results is questionable. Blue marlin were, with the possible exception of the second cruise, consistently found in greatest numbers closest to the seaward side of the reef. This is similar to the pattern for black marlin. However, small numbers of blue marlin larvae were captured in block E, the most offshore segment of the transect, and this offshore area had the second highest frequency of occurrence of blue marlin larvae (Table 1).

Only 13 sailfish larvae were taken, and the data are too sparse to indicate much more than all but 1 of the 7 occurrences were in the two blocks nearest the reef front (A and B). Sailfish larvae

[4]J. Pepperell, Fisheries Research Institute, N.S.W. Department of Agriculture, Cronulla, N.S.W., Australia, pers. commun. 1986.

TABLE 1.—Distribution of istiophorid larvae based on transects from the Great Barrier Reef Lagoon into the Coral Sea. Co, concentration (larvae/1,000 m^3); Ab, abundance (larvae/100 m^2); f, frequency (i.e., number of positive hauls). Values for Co and Ab are medians, and parenthetically, ranges. P is for Kruskal-Wallis test. For tested data sets, values with the same superscript symbol (# or †) are not significantly different ($P > 0.05$, SNK Test). NT, not tested statistically: T, because only 2 samples were taken in block A; F, because too few larvae were taken. Normally, 6 samples were taken in each block on each cruise. No larvae were taken on the cruises not listed.

		Coral Sea blocks				
	Great Barrier Reef Lagoon	A (0-0.25 nmi)	B (0.25-1.0 nmi)	C (1.0-3.0 nmi)	E (6.0-10.0 nmi)	P
Black marlin						
1st cruise						
Co	0 (0-4.4)#	3.8 (0-11.3)	0.8 (0-1.9)#	0 (0-1.9)#	0 (0-0.5)#	0.04
Ab	0 (0-10.9)#	15.0 (0-56.5)†	10.5 (0-33.0)#†	0 (0-47.1)#	0 (0-13.0)#	0.06
f	1	5	4	2	2	
2d cruise						
Co	0 (0-1.4)	2.8 (1.1-4.5)	0 (0-0.5)	0 (0-1.2)	0	NT, T
Ab	0 (0-3.4)	12.8 (5.1-20.4)	0 (0-6.9)	0 (0-14.9)	0	
f	2	2 (of 2)	1	1	0	
3d cruise						
Co	0	0 (0-0.7)	0	0	0	NT, F
Ab	0	0 (0-2.0)	0	0	0	
f	0	2	0	0	0	
4th cruise						
Co	0	0 (0-1.2)	0	0	0	NT, F
Ab	0	0 (0-1.8)	0	0	0	
f	0	1	0	0	0	
Blue marlin						
2d cruise						
Co	0	0	0 (0-2.2)	0 (0-0.6)	0	NT, T, F
Ab	0	0	0 (0-23.0)	0 (0-7.2)	0	
f	0	0 (of 2)	2	1	0	
3d cruise						
Co	0#	1.5 (0-8.4)	0 (0-0.5)#	0#	0 (0-0.6)#	0.02
Ab	0#	12.6 (0-25.2)	0 (0-5.2)#	0#	0 (0-7.0)#	0.02
f	0	5	1	0	2	
4th cruise						
Co	0	0.33 (0-2.4)	0	0	0 (0-1.8)	NT, F
Ab	0	1.0 (0-7.7)	0	0	0 (0-21.1)	
f	0	3	0	0	2	
Sailfish						
3d cruise						
Co	0	0 (0-4.2)	0 (0-0.6)	0	0	NT, F
Ab	0	0 (0-12.6)	0 (0-6.1)	0	0	
f	0	1	2	0	0	
4th cruise						
Co	0	0 (0-2.6)	0 (0-0.8)	0 (0-0.7)	0	NT, F
Ab	0	0 (0-10.4)	0 (0-9.3)	0 (0-7.8)	0	
f	0	2	1	1	0	

may have a distribution similar to that of blue marlin and black marlin larvae (Table 1).

Sizes of Larvae From Bongo Net Tows

Black marlin larvae ranged from 2.5 to 6.8 mm with a strong mode at 2.8-2.9 mm (Table 2a). Statistical comparison of the size-frequency data between areas could only be undertaken for the first cruise. Data from block A were compared with data from all other areas pooled. The size-frequency distributions were possibly different (Kolmogorov-Smirnov test, $P = 0.07$): a greater proportion of the larvae were of the smaller size classes (<4 mm) in block A than in the other blocks. Inspection of the limited size-frequency data from the other cruises indicates a similar situation. More than one cohort of larvae was present because larvae on the second cruise were not larger than those on the first.

Blue marlin larvae ranged from 2.5 to 8.3 mm with a weak mode at 3.1 mm (Table 2b). Too few blue marlin larvae were captured to allow rigorous analysis of the size-frequency data, but there did not appear to be any difference in the size

TABLE 2.—Size frequency of a) black and b) blue marlin and c) sailfish larvae. If a block or cruise is not listed, no larvae were taken there. X indicates a hiatus in the size sequence. A few larvae too badly damaged to be measured were omitted. Blanks indicate zero.

a. Black marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	X	5.6	5.7	5.8	5.9	6.0	X	6.8
E	1st		1 1												
C	1st		1 1 1			1									
	2d		1 1												
B	1st		1 1 1 1			1	1					1			1
	2d		1 1												
A	1st		3 2 8 6 4 3 2 1 3 4	3 1	1	1			1	1					
	2d	1	3 1 2 3												
	3d		1												
	4th		1 1												
Lagoon	1st			1 1			1								
	2d		1 1												

b. Blue marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	5.5	X	8.3
E	3d		2							
	4th		1		1 1 1					1
C	2d		1							
B	2d	1 1 1				1				
	3d				1					
A	3d	2	1 1	4 2 1 2	1 1	1 1	1 1			
	4th			1		1	1	2		

c. Sailfish

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0
C	4th				1
B	3d		1 1		
	4th		1		
A	3d	2 3	1		
	4th		1 1 1		

composition of the larvae between areas. Larvae on the fourth cruise were apparently larger than those on the third, however it is doubtful that only one cohort was involved because of the small size difference between the two cruises which were about 10 days apart (Table 2b).

Sailfish larvae ranged from 2.5 to 3.8 mm, with a mode at 2.6 mm (Table 2c). Only 12 larvae were captured, but there is a suggestion that smaller larvae were taken nearest the windward reef face, and that the size of larvae increased with distance into the Coral Sea.

Vertical Distribution

Our information on vertical distribution comes primarily from samples taken within the Great Barrier Reef Lagoon. It is limited, but it is consistent.

In the sampling with opening-closing bongo net and neuston net, larvae of two species, sailfish and blue marlin, were captured. No istiophorid larvae were present in the neuston tows of the vertical distribution sets. Sailfish larvae were captured in 7 of 16 day-time vertical sets and none of the 6 night-time sets. All the sailfish larvae were captured in the 0-6 m stratum with the exception of two larvae, one from each of the two deeper strata, which came from two sets taken in one of the turbulent interreef channels during a falling tide (Table 3). Even with the inclusion of the data from the interreef channel, sailfish larvae were most concentrated in the 0-6 m stratum while concentrations in the other strata did not differ (Friedman test, SNK test, $P < 0.05$). Blue marlin larvae were captured in only three of the day-time vertical sets. All the blue marlin larvae were captured in the 0-6 m stratum, with the

TABLE 3.—Day-time vertical distribution of sailfish and blue marlin larvae in the vicinity of Carter Reef in February and March 1983. *N* refers to number of vertical sets (i.e., a tow in each stratum) that contained at least one larva of that species.

Sailfish (*N* = 7)

Depth stratum	Concentration (larvae/400 m³) Median	Range	Number of positive hauls (of 7)
Neuston	0	0-0	0
Bongo net			
0-6 m	1.7	0-7.8	6
6-13 m	0	0-1.6	1
13-20 m	0	0-1.0	1

Blue marlin (*N* = 3)

Depth stratum	Concentration (larvae/400 m³) Median	Range	Number of positive hauls (of 3)
Neuston	0	0-0	0
Bongo net			
0-6 m	1.8	1.8-4.3	3
6-13 m	0	0-0	0
13-20 m	0	0-1.0	1

exception of a single larva from 13 to 20 m from one of the interreef channel sets. In the three positive sets, blue marlin larvae were always most concentrated in the 0-6 m stratum, but there were too few data for rigorous testing.

Blue marlin and sailfish larvae occurred in one vertical set taken on the windward side of Lizard Island in January 1980 (see Leis 1986). One larva of each species was taken in each of the 0-1 m and the 3-4 m tows, while none were taken in the 6-7 m tow.

Istiophorid larvae from our neuston samples were developmentally more advanced (older) than those from bongo net samples. In all our samples, the bongo net captured 160 istiophorid larvae (black marlin, blue marlin, sailfish), three of which were postflexion stage, while the neuston net captured 17 istiophorid larvae (black marlin and blue marlin), 13 of which were postflexion stage (chi square, $P < 0.001$).

During the day preflexion blue marlin and sailfish larvae inhabit the upper 6 m, and possibly the upper half of that, but not the neuston. It appears that once the caudal fin is formed, istiophorid larvae move upward even more and enter the neuston.

DISCUSSION

Distribution of istiophorid larvae over such a small scale has not been studied previously, nor have such high concentrations of larvae been reported. Our results were surprising. Highest concentrations and abundances of istiophorid larvae in our study area were consistently found in the Coral Sea very close to the windward side of the ribbon reefs at the outer edge of the Great Barrier Reef. The size-frequency data (see below) suggest that this near-reef environment was a spawning area or just down wind of one for the three types of billfishes considered here.

Concentration and abundance of istiophorid larvae in the Great Barrier Reef Lagoon (hereafter referred to as the Lagoon) were always lower than in block A when both areas were sampled, but lagoonal numbers were generally not different from those further offshore in the Coral Sea. We cannot exclude the possibility that some istiophorid spawning takes place within the Lagoon, but believe it is more likely that the larvae were advected into the Lagoon through the interreef channels, as are larvae of many other oceanic fishes (Leis 1986; Leis and Goldman 1987). Still, concentrations of istiophorid larvae were high at times in the Lagoon (e.g., February-March 1983), and the relative survival of the larvae in the Lagoon vs. the Coral Sea is an open question.

The marginally significant difference between areas in size frequency of black marlin larvae suggests that hatching of the eggs takes place very near the windward face of the reefs. This also suggests that black marlin larvae found elsewhere were largely the result of dispersal away from the near-reef area, and these dispersed larvae had grown somewhat during their dispersal. Spawning could either be concentrated in the near-reef area or more widely spread, in which case the eggs would have become concentrated in the near-reef area through wind-induced surface drift and forereef downwelling (see below). Alternatively, larval growth rates could be higher or mortality lower in the areas further from the reef. Our data do not allow us to distinguish between these alternatives, but we believe the first is the most likely.

The data on blue marlin larvae gave no indication of differences in size frequency between areas. The lack of difference in size-frequency distribution could indicate that spawning in blue marlin was more evenly spread than in black marlin. If so, the increase in numbers nearest the windward side of the reef would be attributable to concentration and retention of larvae there. We cannot differentiate between this possibility and

the alternative that spawning is most intense near the reef.

Too few sailfish larvae were taken to make any firm statements on distribution of larvae of different sizes. However, they appeared to have a pattern of size distribution with location similar to that of black marlin larvae.

The vertical distribution data show that, at least during the day, preflexion larvae of blue marlin and sailfish concentrate in the upper few meters (perhaps upper 3 m) of the water column, but not in the neuston. However, postflexion larvae of blue marlin and black marlin are neustonic. This ontogenetic vertical migration has not been noted previously. The somewhat different results from the limited interreef channel samples could have been caused by turbulence due to strong tidal currents in these narrow passes.

Using nonclosing nets, Ueyanagi (1964) studied vertical distribution of istiophorid larvae (all taxa combined) over the upper 50 m and concluded that during the day larvae were most often caught at the surface and frequency of capture decreased with depth. At night catches of larvae were approximately evenly distributed over the upper 50 m. More recent data (Ueyanagi unpubl. data) confirmed this pattern for blue marlin, striped marlin, spearfish, and sailfish larvae.

It is possible that the observed horizontal distribution of istiophorid larvae in the Lizard Island area results solely from a concentration of spawning or at least hatching of eggs close to the windward side of the reefs. However, it is likely that additional factors are involved. The southeast trade winds push surface water against the windward sides of these reefs and although some of the water flows across the reefs into the Lagoon, downwelling (anstau conditions) should occur seaward of the reef. An organism which maintains a position near the top of the water column, as do the istiophorid larvae (or positively bouyant fish eggs), would accumulate in such a downwelling zone. A similar situation has been described off the windward reef at Lizard Island where larvae of a number of reef fishes with shallow-living larvae were apparently retained (Leis 1986). However, the istiophorid larvae apparently disperse away from the surface at night (Ueyanagi 1964) whereas the larvae retained off windward Lizard Island tended to maintain their day-time vertical distribution at night (Leis 1986). If they did leave the surface, the istiophorids might be advected away from the reef front. A further caveat against accepting the "anstau hypothesis" as a full and simple explanation for the distribution of istiophorid larvae in the area involves the trade winds. During the time the near-reef peak in istiophorid larvae was best developed (2-5 November), the winds varied from 0 to 10 kt and from northeast to southeast while on the other cruises, the wind was stronger and varied from 10 to 30 kt and from east to southeast. Finally, preliminary analysis of data from the samples in which the istiophorids were captured revealed that high abundances of a number of reef fish larvae also occur off the windward reef face. Many of these were not near-surface dwelling larvae. Further study of larval fish distributions and their causes in this area is clearly required.

Whatever the causes for the distributions of the istiophorid larvae very near the windward reef face, it is somewhat surprising that the larvae of epipelagic, oceanic fishes should be so abundant in such a narrow band along the reefs. Sailfish are known to spawn relatively close to land masses rather than in the open ocean (Ueyanagi 1974c) and black marlin are often found nearshore (Nakamura 1985); blue marlin are truly oceanic fishes (Nakamura 1985; Nishikawa et al. 1985). Yet larvae of all three were concentrated in a narrow band only 0.25 nmi (possibly to 1 nmi) off the reef crest. If pelagic fishes such as istiophorids concentrate their spawning very close to reefs or if the larvae are retained there, it will be essential for such areas to be included in studies of the larval biology of these fishes. The assumption that open oceanic areas are the important nursery areas for epipelagic fishes seems at best questionable for istiophorids in the Coral Sea and similar factors may apply to other taxa in this and other areas. For example, Miller (1979) reported much higher concentrations of yellowfin tuna larvae, *Thunnus albacares*, in areas 200 m off the Oahu shoreline than had been reported elsewhere.

Nearshore or near-reef areas may provide more favourable habitats for fish larvae, including those of many pelagic species, than do oceanic areas. The larvae of jack mackerel, *Trachurus symmetricus*, an epipelagic (albeit, neritic) fish, are spread widely over oceanic and coastal areas off California, yet larval mortality due to starvation in oceanic areas can be much higher than in coastal areas, presumably because of insufficient concentrations of food offshore (Theilacker 1986). This may apply to other pelagic fishes as well and

is a further indication that very nearshore (and near-reef) areas must not be excluded from studies of the larvae of epipelagic fishes.

In summary, we found the highest concentrations and abundances of istiophorid larvae of three taxa very close to the windward face of the Great Barrier Reef in the Coral Sea in late spring and summer. Size-frequency analysis suggested that these high concentrations of larvae were due to spawning or at least hatching of eggs very close to the reef. The larvae might be retained in this forereef area of supposed downwelling because, at least during the day, they concentrate in the upper few meters of the water column as preflexion larvae and in the neuston as postflexion larvae. These results have potentially important implications for the study of the larval biology of epipelagic fishes.

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