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VERTICAL AND ONSHORE-OFFSHORE DISTRIBUTION OF TUNA LARVAE (PISCES, SCOMBRIDAE) OFF OAHU, HAWAII

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ABSTRACT

The seasonal and spatial distribution of larval scombrids in waters off the Hawaiian island of Oahu were studied in September and December 1985 and April and June 1986 to determine patterns of vertical and onshore-offshore distribution. Transects on the windward (east) and leeward (west) sides of the island consisted of three stations, each between 1.8 and 28.0 km offshore. Resolution of vertical distribution was provided by sampling with MOCNESS and Manta nets in eight depth strata (0-80 m) at the nearshore stations and nine depth strata (0-200 m) at the four offshore stations. Scombrid larvae were abundant in all months except December.

Collections in September and June were dominated by *Thunnus* spp., of which about half were large enough to be identified to species; these were predominantly *T. albacares*. *Thunnus* spp. larvae generally were most abundant at the station closest to shore on the leeward side of the island. Larval *Thunnus* were not taken at depths greater than 60 m, were most abundant in the upper 20 m, and were captured in the neuston at night but rarely in daytime. The other two dominant larval scombrids, *Katsuwonus pelamis* and *Auxis* spp., were most abundant in slightly deeper water. *Katsuwonus pelamis* were most abundant at offshore stations, but *Auxis* spp. showed no clear onshore-offshore pattern. In April, *Auxis* spp. were most abundant and comprised over 99% of all larval scombrids.

Temperature and, to a lesser extent salinity appear to play important roles in the spatial and temporal distribution of larvae. Seasonal patterns of spawning may be dependent upon availability of appropriate thermal habitat. Larval *Thunnus* and *Katsuwonus*, in particular, are abundant only in June and September when temperatures are relatively warm. *Auxis* larvae are found over a wider range of temperature than are the other genera.

INTRODUCTION

Most studies on the distribution of tuna larvae have been conducted at scales of >10 km, in an attempt to document tuna spawning aggregations and locations (Matsumoto 1958; Kohno et al. 1985). Typically, these studies have used ring nets or other plankton gear and sampled obliquely or strictly in shallow water; the resultant densities of larvae were generally quite low (Matsumoto 1958; Strasburg 1960; Conand and Richards 1981). In the open ocean, tunas may aggregate for spawning (Batalyants 1989; Koido and Suzuki 1989), and very high densities of early larval bluefin tunas, *Thunnus maccoyii*, have been observed in a localized study site (Young and Davis 1990). Sampling of vertical distribution has not received a great deal of interest. Recent research has shown that tuna larvae are confined to the upper mixed layer and disperse throughout that layer at night (Davis et al. 1990).

Another important facet of larval tuna distribution related to spatial abundance is its relationship to land masses, particularly islands in tropical regions. Densities of larval yellowfin tuna, *T. albacares*, are up to two orders of magnitude greater near leeward Oahu, Hawaii, than in offshore waters, and a mechanism has been proposed by which the larval concentrations might be maintained in island waters (Miller 1979). Similarly high concentrations of tuna larvae were noted in waters near islands in French Polynesia by Leis et al. (1991) who suggested that spawning in waters near islands may be an important feature for some species, particularly in the genus *Thunnus*. This may reach an extreme case for *T. tonggol*, where larvae are found only in nearshore waters (Nishikawa and Ueyanagi 1991).

The present study was undertaken to provide detailed information on the seasonal, vertical, and onshore-offshore distribution of larval scombrids in relatively nearshore waters around Oahu. This paper represents the first of a series describing the patterns of vertical and onshore-offshore distribution.

MATERIALS AND METHODS

Four ichthyoplankton surveys were conducted aboard the NOAA ship *Townsend Cromwell*: 6-15 September 1985, 12-20 December 1985, 8-18 April 1986, and 24 June-2 July 1986. East-west transects were established offshore from Kahe Point on the leeward (west) side and Kaoio Point on the windward (east) side of Oahu at latitudes 21°21'N and 21°32'N, respectively. Sampling stations were located 1, 5, and 15 nmi from shore along the leeward side (L1, L5, and L15, respectively) and 2, 5, and 15 nmi from shore along the windward side (W2, W5, and W15, respectively) (Fig. 1). Larvae were sampled below the surface with a 1 m^2 multiple opening-closing net and environmental sensing system (MOCNESS) (Wiebe et al. 1985) and at the sea surface with a 0.49 m^2 Manta net modified to take surface samples to a depth of 0.7 m; both types of sampling gear were equipped with nets of 0.333 mm mesh. Volume estimates for both nets were based on mechanical flowmeter readings. Samples were taken in eight depth strata (neuston, 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, and 60-80 m depths) at each nearshore (1 or 2 nmi) stations and in nine depth strata (neuston, 0-20, 20-40, 40-60, 60-80, 80-100, 100-120, 120-160, and 160-200 m depths) at the offshore (5 and 15 nmi) stations. MOCNESS tows were 12 minutes in duration and neuston tows 24 minutes. Replicate tows were taken day and night.

In the field, larvae were preserved in 10% buffered formalin. After the surveys, zooplankton displacement volumes were measured, and samples were transferred to 50% isopropyl alcohol. All larval fishes were sorted from the whole samples under dissecting microscopes and stored in vials in alcohol until identification.

Larval Identification

Larvae larger than 3.0 mm notochord or standard length (SL) were identified by the criteria of Nishikawa and Rimmer (1987), and those smaller than 3.0 mm SL by reference to the descriptions in Collette et al. (1984) and Fritzsche (1978). *Acanthocybium* larvae were identifiable at all sizes. Other scombrids approximately 2.5-3.0 mm SL were identified only as *Auxis**Euthynnus*, *Katsuwonus*, or *Thunnus* spp. Scombrid larvae smaller than approximately 2.5 mm SL were assigned to the unidentified Scombridae category. *Auxis* larvae were not identified to species or larval type, but two species, *A. thazard* and *A. rochei*, are known to occur in Hawaii. *Thunnus* larvae larger than 3.0 mm SL were identified to species by their pigment characters (Matsumoto et al. 1972; Nishikawa and Rimmer, 1987). These identifications are offered skeptically, because pigment may be more variable in these species than has been described based on identification of larger larvae by osteological (Richards and Potthoff 1974) and electrophoretic characters (Graves et al. 1988). Our specimens of "*T. albacares*" and "*T. obesus*" are smaller than those identified by Richards and Potthoff (1974) and Graves et al. (1988); we are uncertain whether the variability found in those studies is similar for larvae in our study.

Data Analysis

For this study, only the first replicate sample was processed for the December, April, and June cruises, whereas both replicates were processed for the September cruise: Mean values of larval density (number per 1,000 m^3) were determined for the September samples except densities related to specific environmental features or for comparisons among seasons: In the latter case, numbers from the first replicate only are used.

Environmental data collected from the MOCNESS sensors were used during and after sampling. During sampling, real-time depth information was used to target the depth strata sampled.

Conductivity, temperature, and depth data were stored on disc at 4-second intervals. Salinity and sigma-*t* were calculated from standard formulas (Fofonoff and Millard 1983). Cumulative histograms of temperature, salinity, and sigma-*t* of the water sampled were plotted for all hauls sampled with the MOCNESS. Physical environmental data from the Manta net tows were estimated by the data values for the shallowest depth sampled by the MOCNESS in the same sample series (typically 0-1 m) and weighting by the numbers of observations in a standard MOCNESS haul. Although haul duration for the Manta was twice as long as for the MOCNESS, the mouth area and volume sampled were approximately half. Thus, roughly equal volumes were sampled. Subsets of the histograms of T and S also were made for those hauls containing scombrid larvae of different taxa. These estimates were not weighted by larval density but, rather, reflect presence or absence only.

RESULTS

Sampling Variability

Sampling variability between replicate samples was estimated by determining the coefficient of variation in the 104 pairs of samples in the September 1985 cruise for selected taxa that were moderately abundant. The mean values of the coefficient of variation (Table 1) reflect the variation in abundance between replicate samples. Values for scombrids were generally quite high, and these values reflect the patchy nature of larval scombrid distribution.

Seasonality of Occurrence

The abundance of larvae varied seasonally. In September 1985, collections were dominated by *Thunnus* spp. (Fig. 2), representing 227 of 365 scombrid larvae in the first replicate series. More than half were sufficiently large to be identified to species, and 95% were *T. albacares*. Larval *Thunnus* spp. were absent in December 1985 and April 1986 but again dominated the collections in June 1986. These later samples were typically smaller larvae, so only 19.3% were identified to species, and 90% of these were *T. albacares*. *Katsuwonus pelamis* showed a seasonal pattern similar to that of *Thunnus* spp. but at lower densities. *Acanthocybium solandri* larvae were rare in all seasons, with only five larvae taken in September and six in June. *Auxis* spp. were rare in December, moderately abundant in September and June, but dominated the collections in April: *Auxis* spp. represented 416 of the 421 scombrid larvae taken in April.

Distribution Patterns

Larval *Thunnus* spp. were generally most abundant on the leeward side and at the leeward station closest to shore (Fig. 3). They were not taken at depths greater than 64 m and were most abundant in the upper 20 m (mean = 16.0 m, Table 2). They were captured in the neuston at night but rarely in daytime. In September, more larvae were taken at night on the leeward side, where the highest densities occurred at the nearshore station (Fig. 3A). In June, densities were greatest in daytime collections at the nearshore station on both windward and leeward sides of the island (Figs. 3C, D). Consistent diel movements were not evident, except larvae were captured in the neuston at night. At the nearshore leeward stations, larvae appeared to be dispersed throughout the upper 20 m in September and the upper 40 m in June (Figs. 3A, C).

Larval *Katsuwonus pelamis* were present in the same seasonal cruises, but generally in lower densities than larval *Thunnus* spp. Larval *K. pelamis* larvae were never taken at depths greater than 84 m and were rare in the neuston (Fig. 4); however, they had the greatest mean depth of occurrence of any of the scombrid taxa studied (Table 2). There was a trend toward greater densities in offshore waters, evident on both leeward and windward transects.

Larval *Auxis* spp. were moderately abundant but showed variable patterns of distribution. They were typically restricted to water shallower than 60 m; the mean depth of occurrence was intermediate between that of *Thunnus* spp. and *Katsuwonus* (Table 2). No consistent pattern of onshore-offshore distribution was evident (Fig. 5). In April, when abundance was highest, distribution on the leeward side was relatively uniform, no larvae occurred at the offshore station in the daytime. On the windward side, larvae were virtually lacking at the offshore station. The strongest evidence of a diel movement was observed at the nearshore station on the windward side in April. *Auxis* larvae were most abundant in the 0-10 m stratum by day but had a broader vertical distribution at night, with their maximum abundance in the 50-60 m stratum. The lack of such a pattern at other stations and times, however, suggests that something other than diel migrations may account for the changes in depth distribution.

Relationship of Larval Distributions to Physical Features

The distribution of larvae was related to specific physical characteristics of the water column taken by the MOCNESS sensors during each sample. *Thunnus* larvae were found in the warmest water sampled during our study but never in temperatures below 24.2°C (Table 2). In seasons of greatest abundance, the temperature distribution in samples containing *Thunnus* larvae was clearly skewed to warmer water as compared to that for all samples (Fig. 6A). Temperature distributions during December and April, when *Thunnus* larvae were rare or absent, were very low by comparison. Distribution relative to salinity was less restricted, and the range of salinity during December and April overlapped those temperatures at which *Thunnus* are taken in other months (Fig. 6B).

Although mean depth of occurrence was greatest for *Katsuwonus* larvae, the seasonal distribution resulted in a relatively high mean temperature of occurrence (Table 2). Temperature and salinity distributions for the samples containing *Katsuwonus* larvae (Fig. 7) were very similar to those for *Thunnus* larvae (Fig. 6), despite the greater depth distribution.

Larval *Auxis* spp. had the most interesting distribution relative to physical characteristics, largely because of their greater seasonal abundance (Fig. 2). Although mean depth of occurrence was intermediate between *Thunnus* and *Katsuwonus*, mean temperature was much lower, and mean salinity greater (Table 2). In September and June, the water column characteristics where *Auxis* occurred (Fig. 8) were very similar to those for the other taxa analyzed. Samples from April, however, were considerably different; temperatures were significantly lower (Fig. 8A), and salinity was characterized by a bimodal distribution (Fig. 8B).

DISCUSSION

A variety of studies using different types of plankton sampling gear have shown that scombrid larvae occur primarily in the mixed layer and upper portion of the thermocline (Strasburg 1960; Davis et al. 1990). The widespread geographic occurrence of larvae (Nishikawa et al. 1985), however, suggests that spawning is distributed over wide areas and seasons. Availability of appropriate spawning and larval habitat may be an important feature. Aside from depth, the physical characteristics of the habitats occupied by different larvae are relatively restricted, particularly for *Thunnus* spp. (Fig. 6). The temperature range where *Thunnus* larvae were captured agrees with that from other studies (e.g., Davis et al. 1990). The seasonality observed in our study is similar to that in Matsumoto (1966) who found such seasonality may relate to the absence of appropriate temperatures in this subtropical area, since larvae are present year-round in equatorial waters. If the larval habitat can indeed be characterized by specific features of depth, temperature, and salinity, then evaluating the likelihood of larval occurrence in different areas may be possible. *Auxis* spp. occurred in the widest range of temperature and salinity, principally because the high abundance in April (Figs. 2, 8). Although the spawning seasons of *A. thazard* and *A. rochei* are unknown, the marked difference between the physical characteristics of the waters where larvae of this genus occur (September and June versus April, Fig. 8) conceivably may be related to seasonal dominance of one species.

Diel vertical migration was not clearly evident for any of the taxa in this study. This contrasts with other studies, which have observed a general pattern: When larvae are abundant, they occur in shallow water during the day and disperse to deeper water during the night (Richards and Simmons 1971; Davis et al. 1990). We observed this pattern only for *Auxis* larvae at the nearshore windward station in April, but it was not a consistent feature in our samples.

The greater abundance of larval *Thunnus* spp. near islands has been noted by Miller (1979), Leis et al. (1991), and Nishikawa and Ueyanagi (1991). Our nearshore leeward sampling station was near areas where Miller (1979) observed high *Thunnus* larval abundances. While larval *Katsuwonus* and *Auxis* spp. showed no systematic pattern of higher abundance on the leeward and windward sides, larval *Thunnus* spp. were typically more abundant on the leeward side of the island (Fig. 3). Similarly, Lobel and Robinson (1988) observed higher densities of larval *T. albacares* in an eddy off the leeward side of the Island of Hawaii. While we have no evidence for the presence of an eddy during our sampling, the abundance fell off rapidly with increasing distance from shore. The importance of such locally high larval abundance is unknown, but may be related to foraging conditions for early larvae (Hernandez-Leon 1991). This topic requires further investigation.

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Table 1.--Variation in larval densities between replicate samples taken in September 1985 as shown by the mean coefficient of variation (CV). N, number of pairs of samples where at least one contained the taxa of interest.

Taxon	*N*	CV	SD
All ichthyoplankton	104	0.433	0.325
All scombrid larvae	37	1.028	0.487
Thunnus spp.	29	1.112	0.479
T. albacares	23	1.155	0.470
Auxis spp.	16	1.329	0.248
Katsuwonus pelamis	23	1.259	0.307

Table 2.--Distribution of larvae of different species with respect to environmental factors. Values are based upon data from MOCNESS sensors collected at 4-second intervals. Only those samples containing larvae of a given taxon are used in the calculations, taken across all seasons; values are not weighted by number of larvae or by larval density.

	Auxis spp.	*Katsuwomus pelamis*	*Auxis solandri*	*Thunnus alalunga*	*Thunnus albacares*	*Thunnus* spp.
N	524	126	11	11	230	751
			Depth (m)			
Min	0.000	0.000	0.000	0.000	0.000	0.000
Max	84.000	84.000	40.000	40.000	55.000	64.000
Mean	23.188	28.461	21.838	13.169	16.285	15.971
SD	18.159	18.443	10.277	11.364	13.894	14.031
			***T* (°C)**			
Min	21.880	22.000	25.750	25.440	24.190	24.190
Max	27.200	27.200	26.900	26.580	27.520	27.520
Mean	24.665	25.646	26.152	26.049	26.051	26.166
SD	1.268	0.920	0.366	0.293	0.588	0.560
			***S* °/₀₀**			
Min	32.440	34.740	34.760	34.740	34.740	34.740
Max	35.810	35.810	35.080	35.010	35.810	35.810
Mean	35.017	34.987	34.852	34.857	34.952	34.941
SD	0.138	0.121	0.062	0.097	0.104	0.094
			Sigma-*t*			
Min	21.677	22.585	22.716	22.784	22.524	22.518
Max	24.459	24.433	23.109	23.210	24.215	24.215
Mean	23.468	23.149	22.892	22.928	22.998	22.954
SD	0.454	0.340	0.091	0.127	0.223	0.200

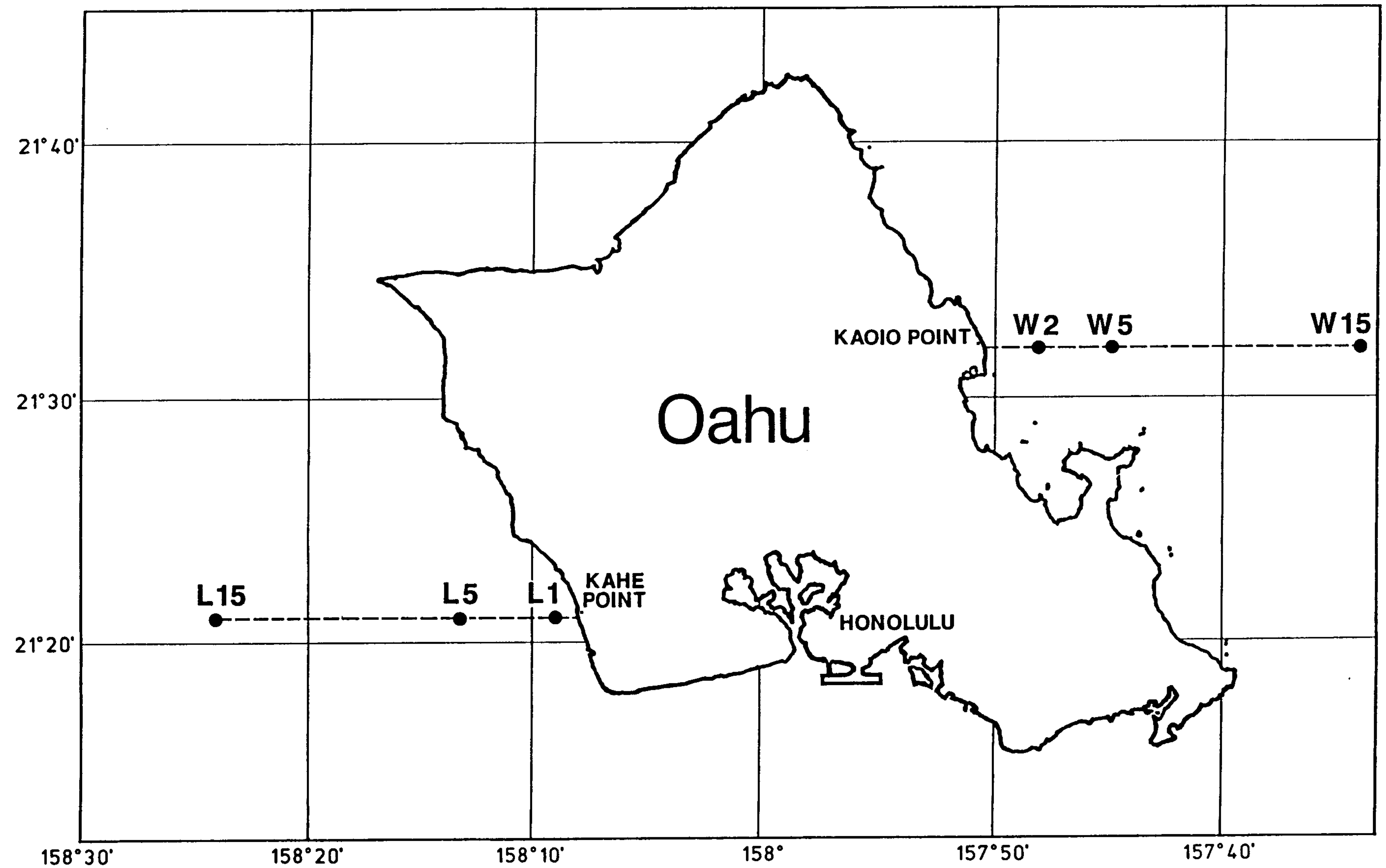

Figure 1.--Map of the study site, Oahu, Hawaii. The station designations stand for leeward (L) and windward (W), and the associated number represents the distance offshore (in nautical miles). The nearshore windward station is twice as far offshore as that on the leeward side, but bottom depths are similar.

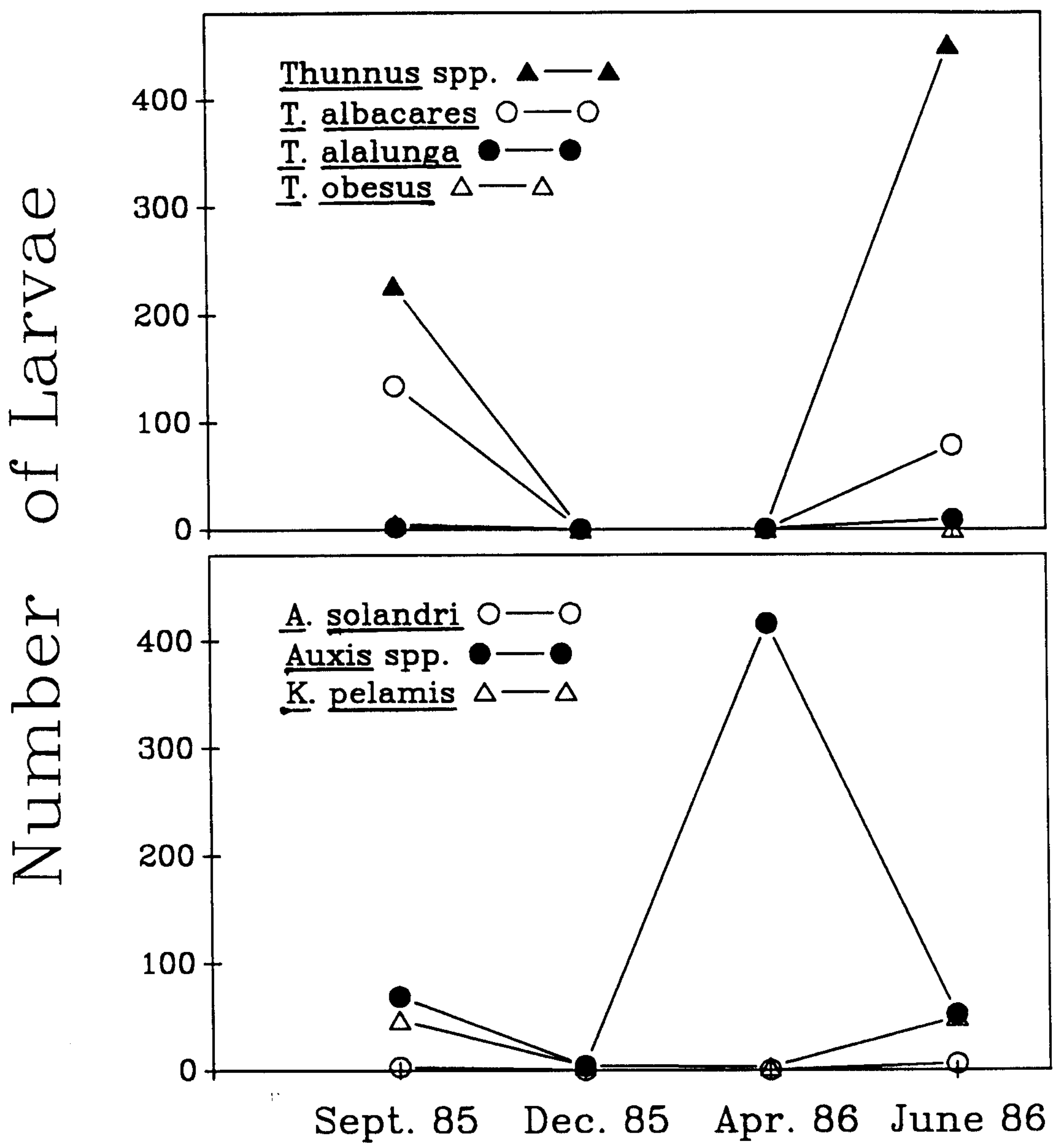

Figure 1.--Map of the study site, Oahu, Hawaii. The station designations stand for leeward (L) and windward (W), and the associated number represents the distance offshore (in nautical miles). The nearshore windward station is twice as far offshore as that on the leeward side, but bottom depths are similar.

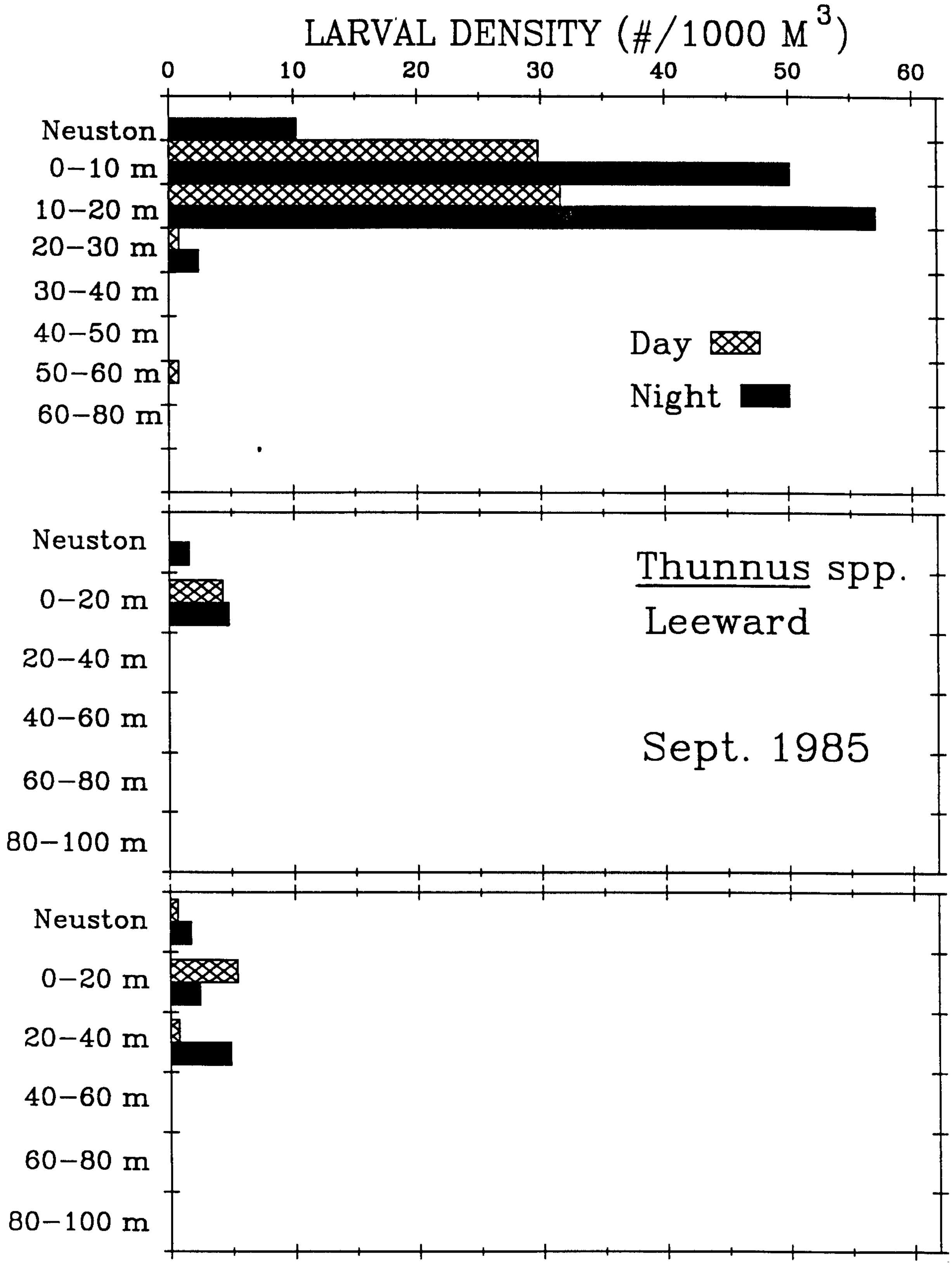

Figure 3.-- Vertical and onshore-offshore distribution of larval *Thunnus* spp. The top panel represents the nearshore station (L1 or W2); the middle panel, station L5 or W5; and the bottom panel, L15 or W15. Samples at the inshore stations were taken only to depths of 80 m, whereas those at the four offshore stations were taken to depths of 200 m. No scombrid larvae were taken at depths greater than 100 m, so the depth strata are not represented on the figures. Cross-hatched bars equal daytime samples; solid bars equal nighttime samples. (A) September 1985, leeward stations.

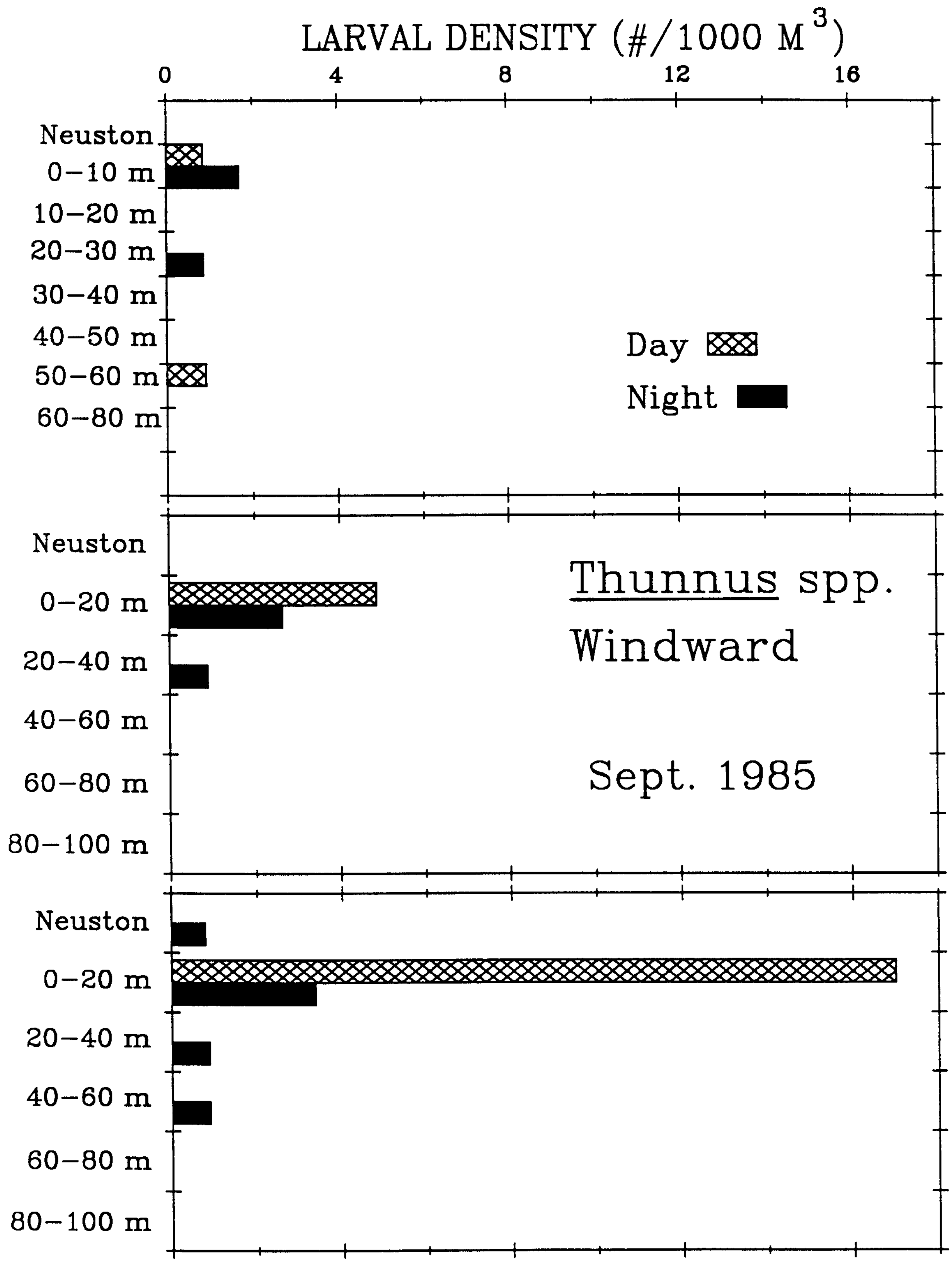

Figure 3B.--Continued. (B) September 1985, windward stations.

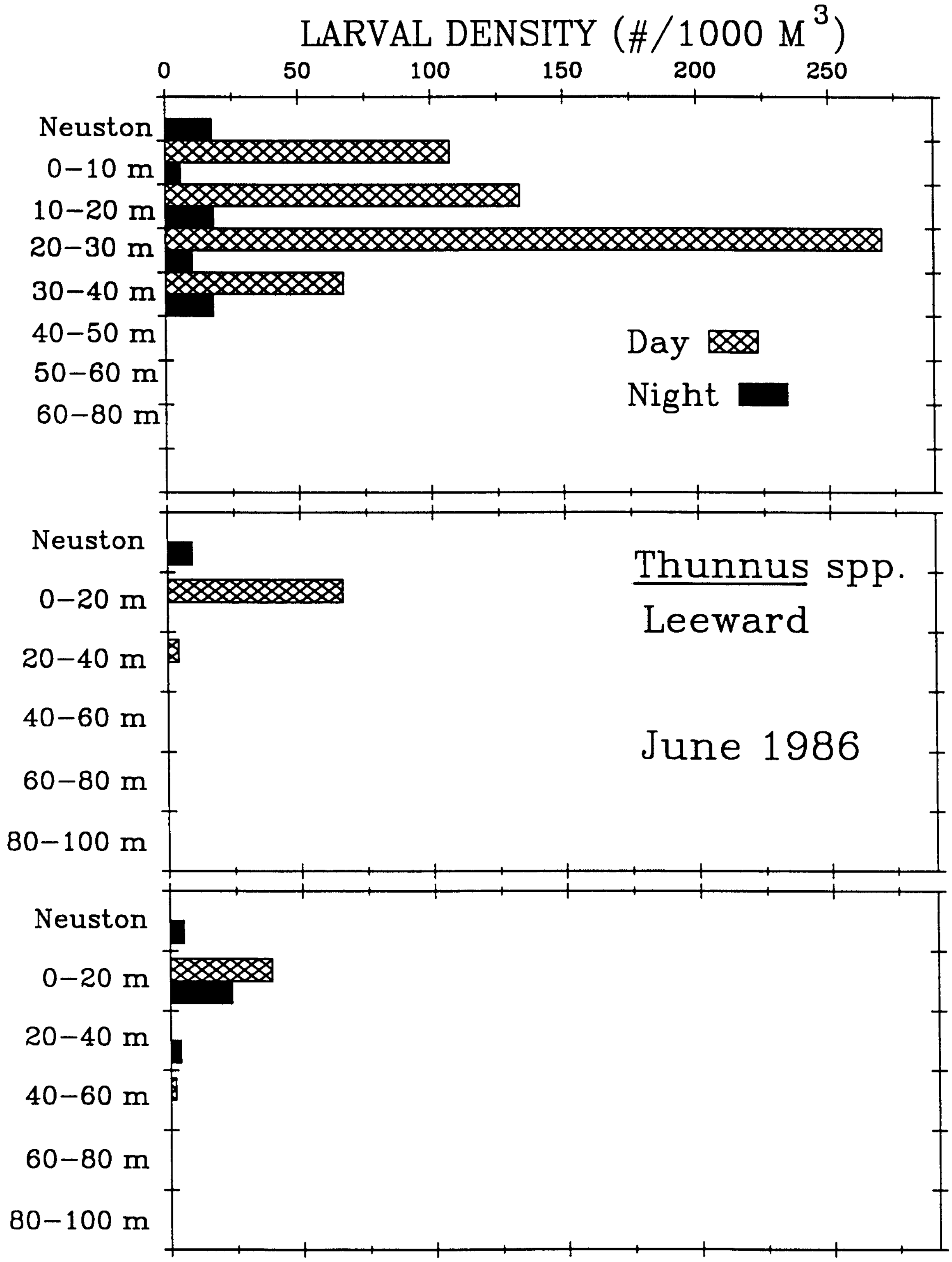

Figure 3C.--Continued. (C) June 1986, leeward stations.

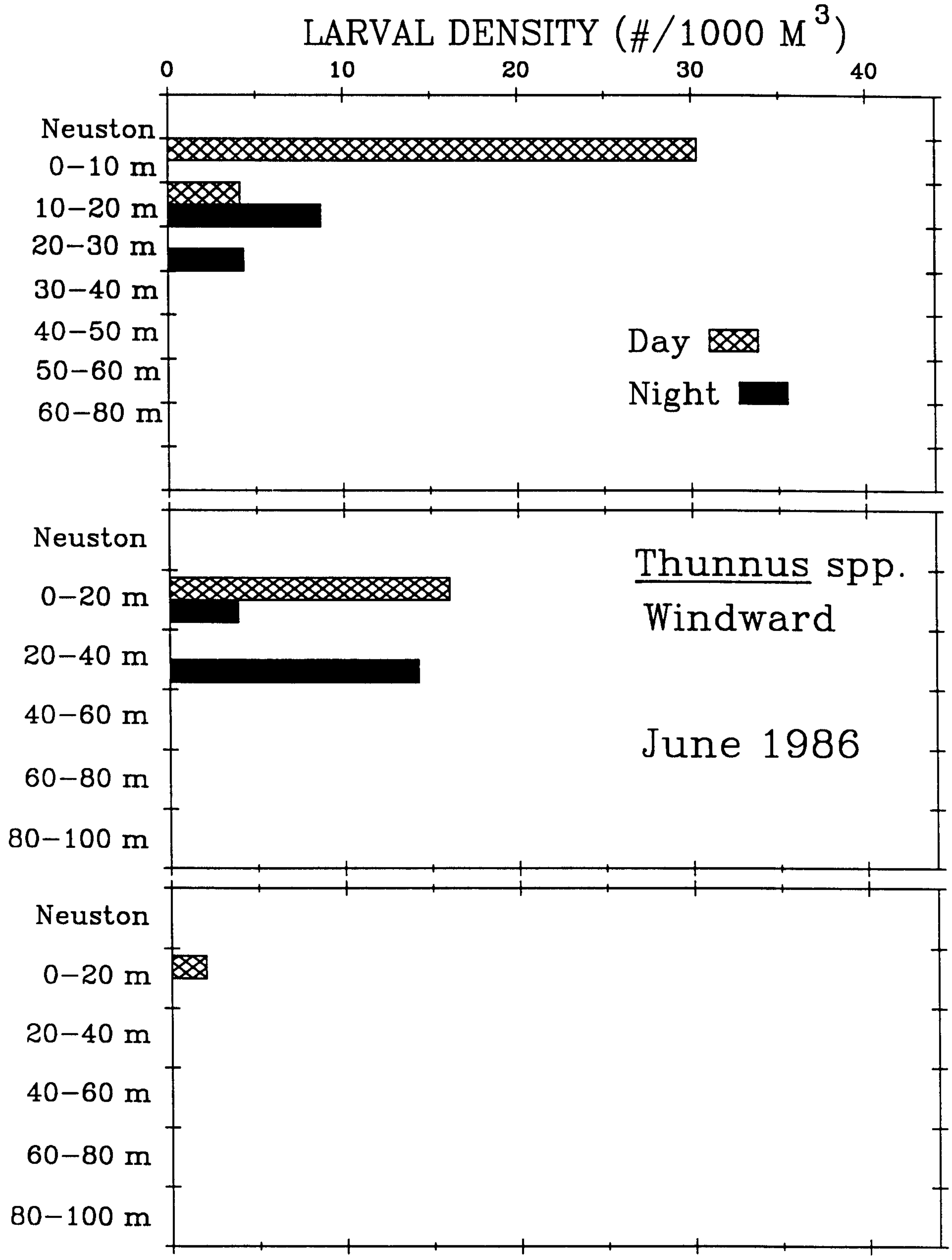

Figure 3D.--Continued. (D) June 1986, windward stations.

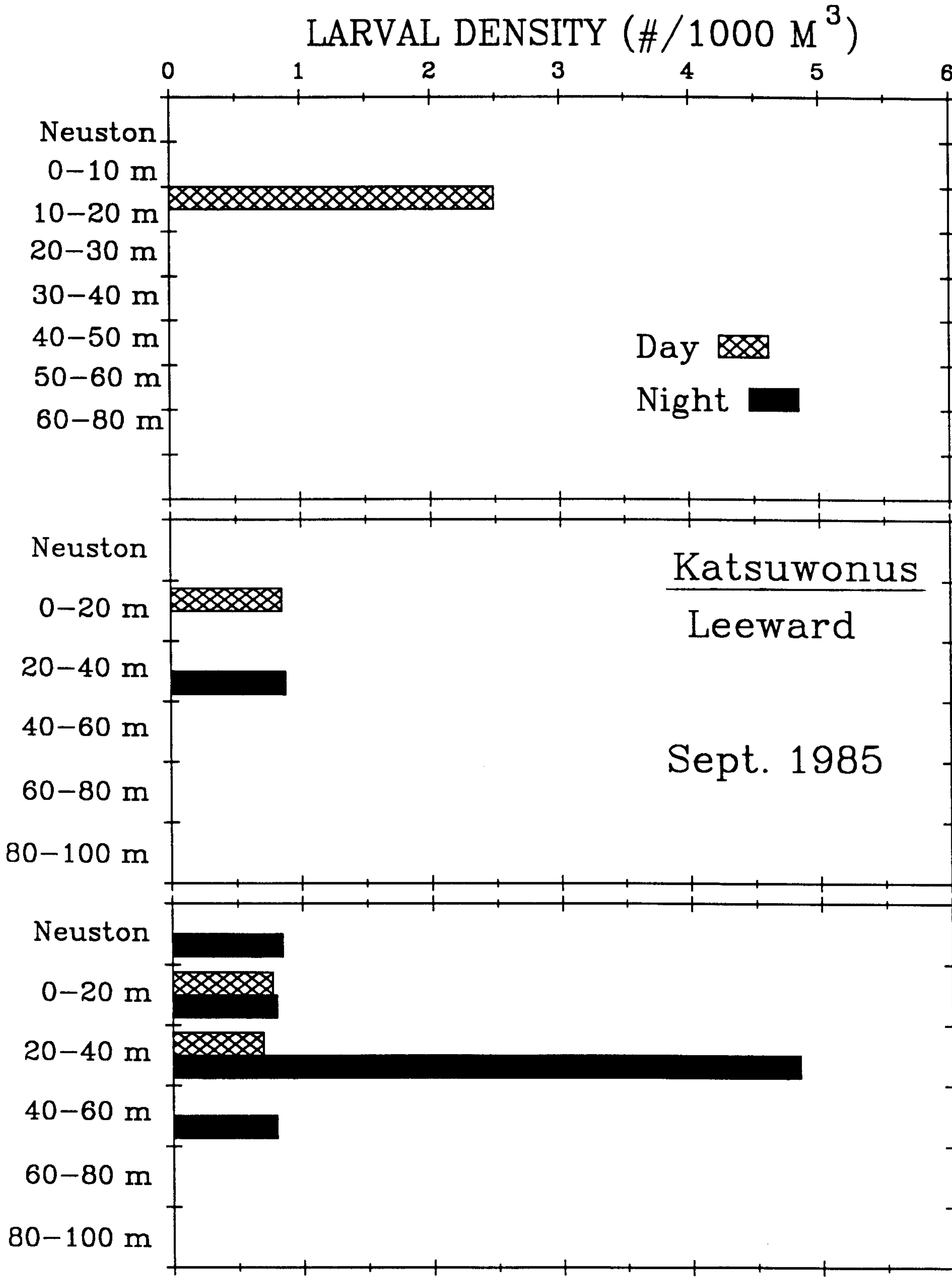

Figure 4.--Vertical and onshore-offshore distribution of larval *Katsuwonus pelamis*. The top panel represents the nearshore station (L1 or W2); the middle panel station L5 or W5; and the bottom panel, L15 or W15. Samples at the inshore stations were taken only to depths of 80 m, whereas those at the four offshore stations were taken to depths of 200 m. No scombrid larvae were taken at depths greater than 100 m, so the depth strata are not represented on the figures. Cross-hatched bars equal daytime samples; solid bars equal nighttime samples. (A) September 1985, leeward stations.

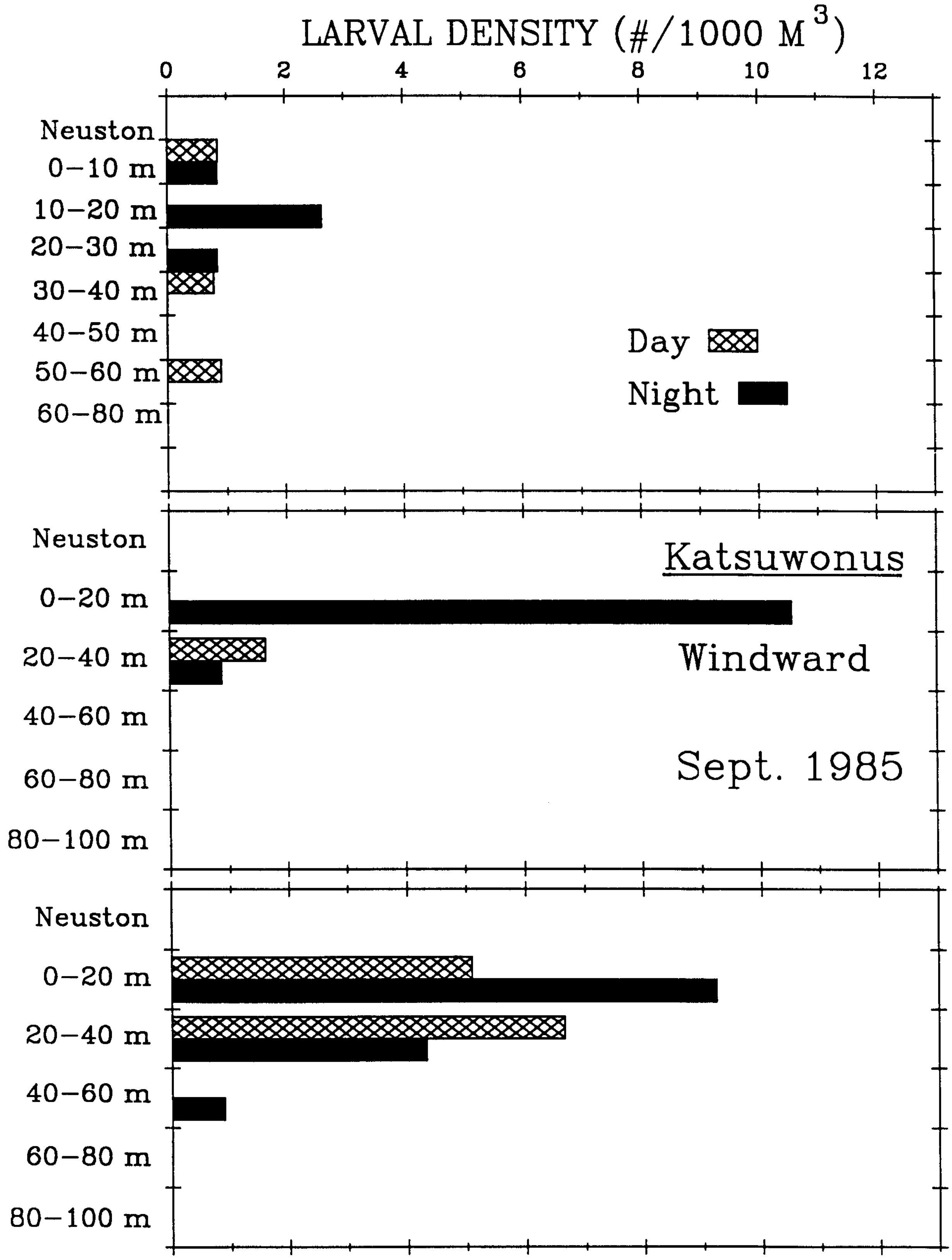

Figure 4B.--Continued. (B) September 1985, windward stations.

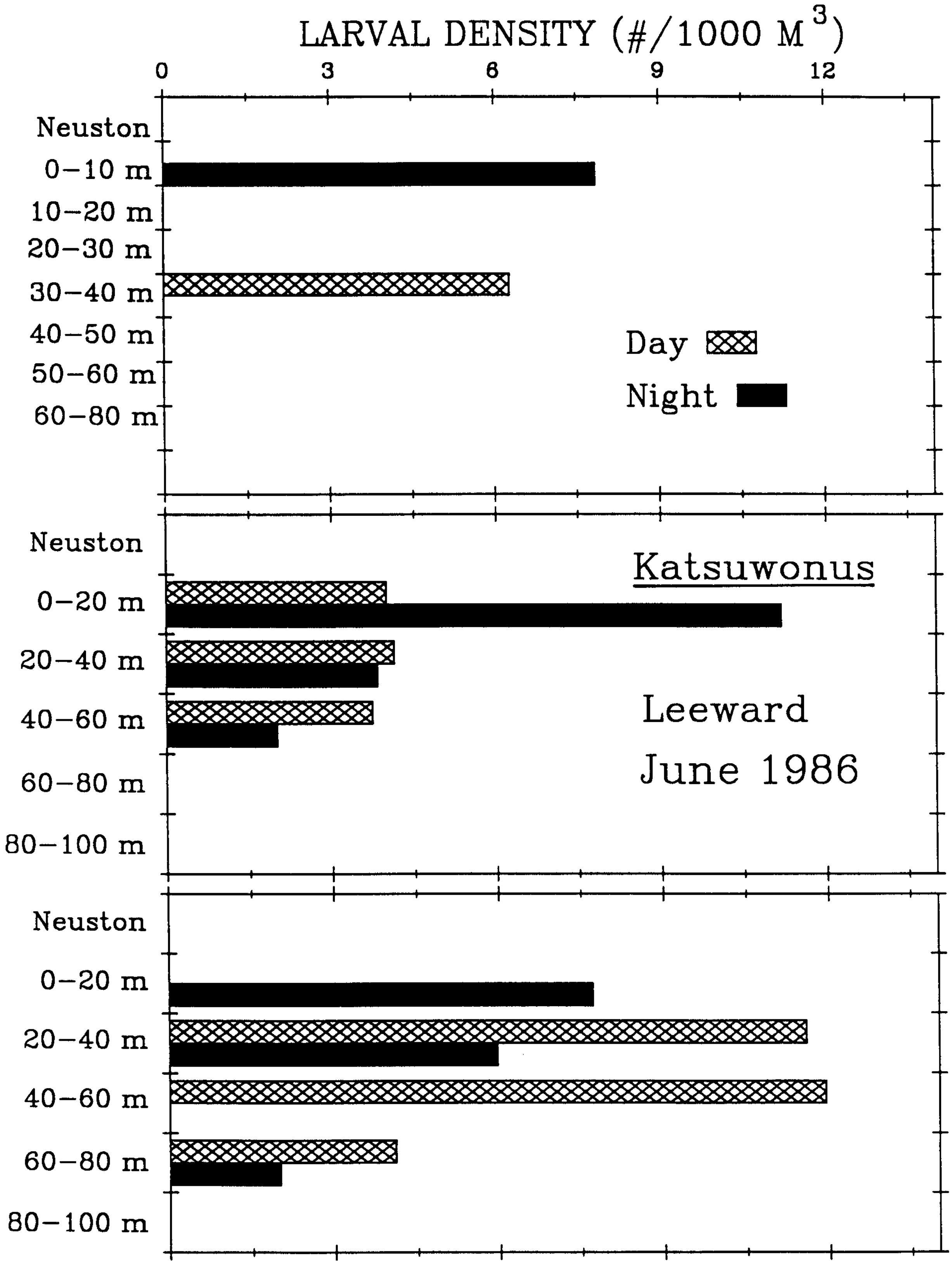

Figure 4C.--Continued. (C) June 1986, leeward stations.

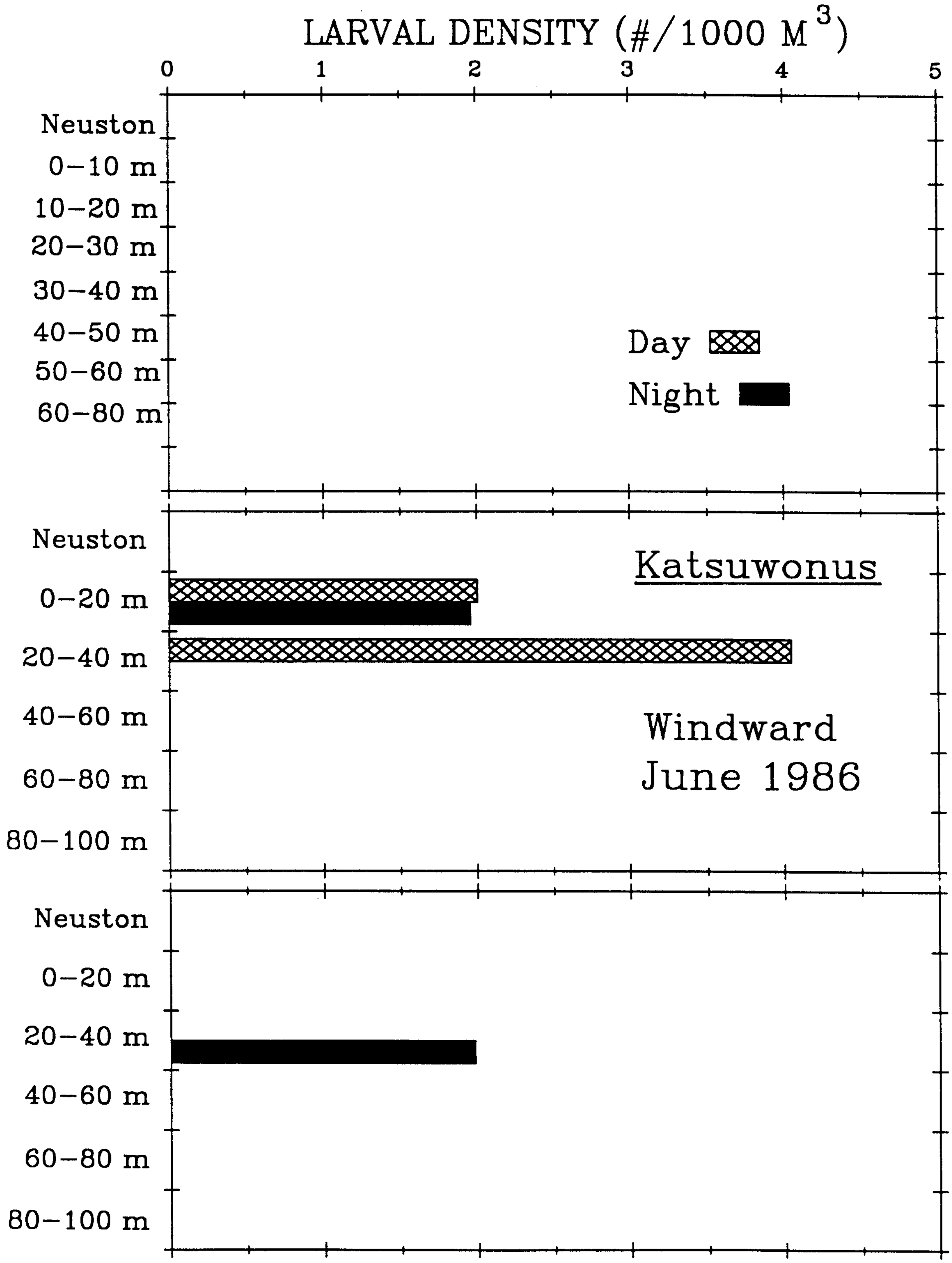

Figure 4D.--Continued. (D) June 1986, windward stations.

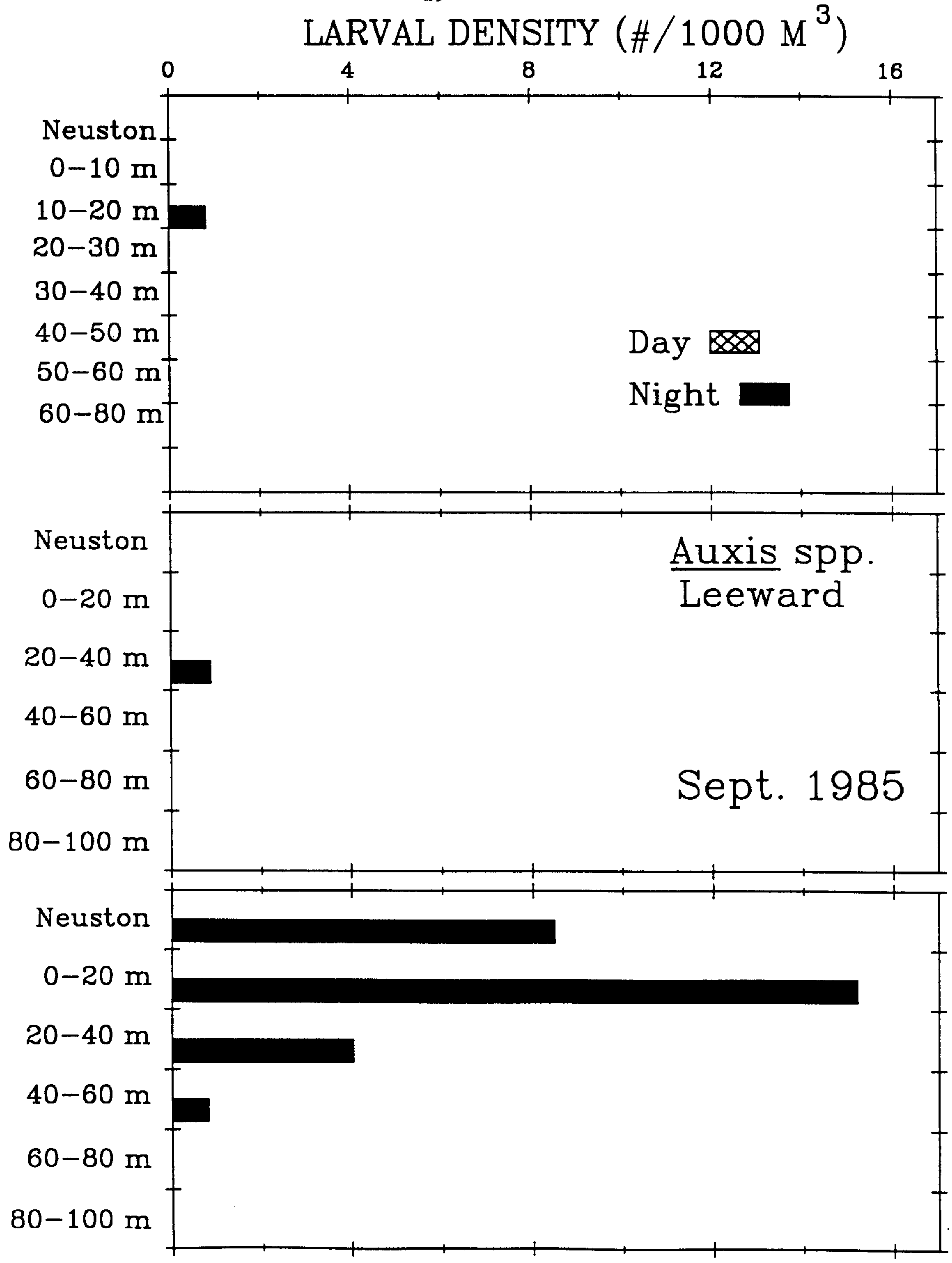

Figure 5.--Vertical and onshore-offshore distribution of larval *Auxis* spp. The top panel represents the nearshore station (L1 or W2); the middle panel, station L5 or W5; and the bottom panel, L15 or W15. Samples at the inshore stations were taken only to depths of 80 m, whereas those at the four offshore stations were taken to depths of 200 m. No scombrid larvae were taken at depths greater than 100 m, so the depth strata are not represented on the figures. Cross-hatched bars equal daytime samples; solid bars equal nighttime samples. (A) September 1985, leeward stations.

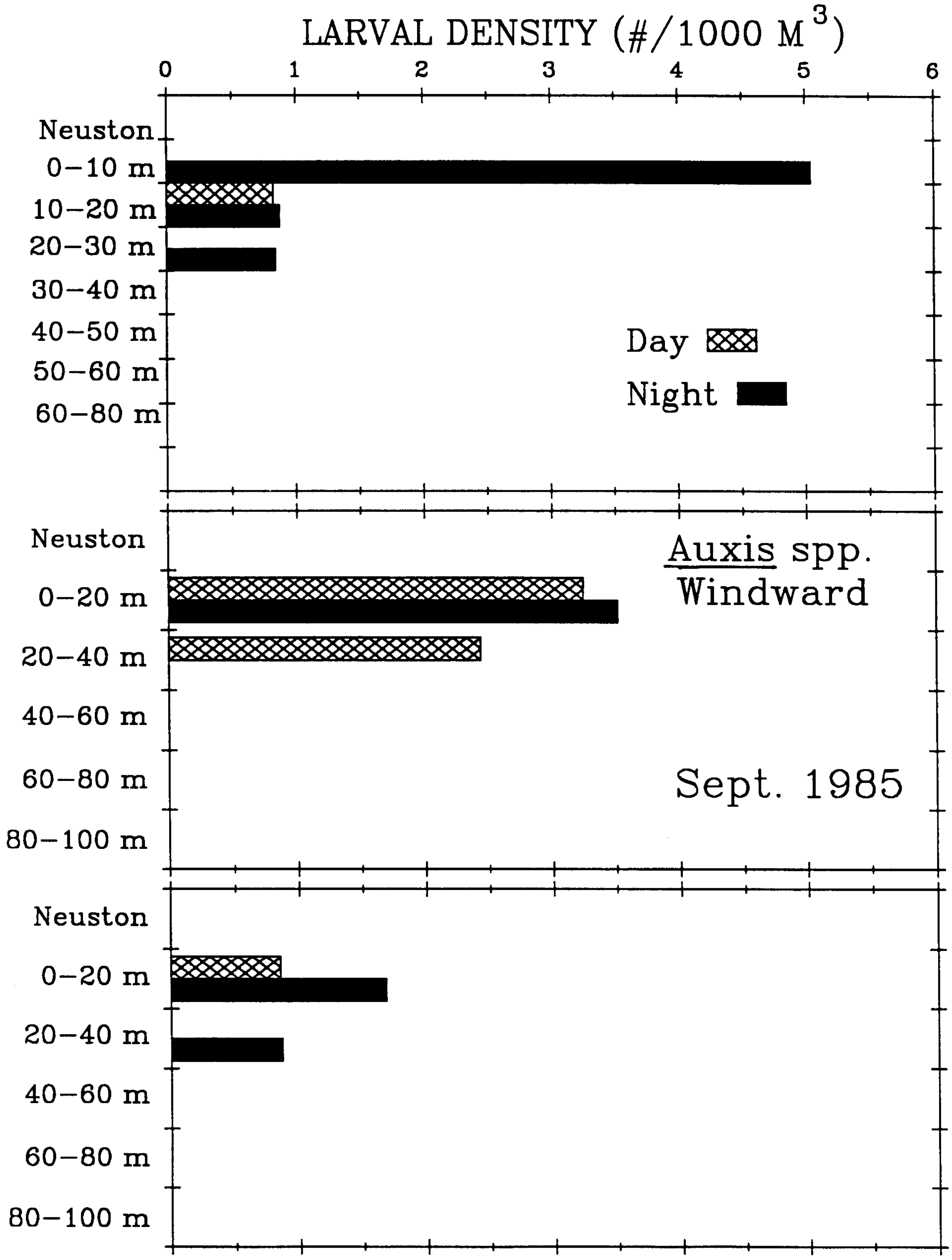

Figure 5B.--Continued. (B) September 1985, windward stations.

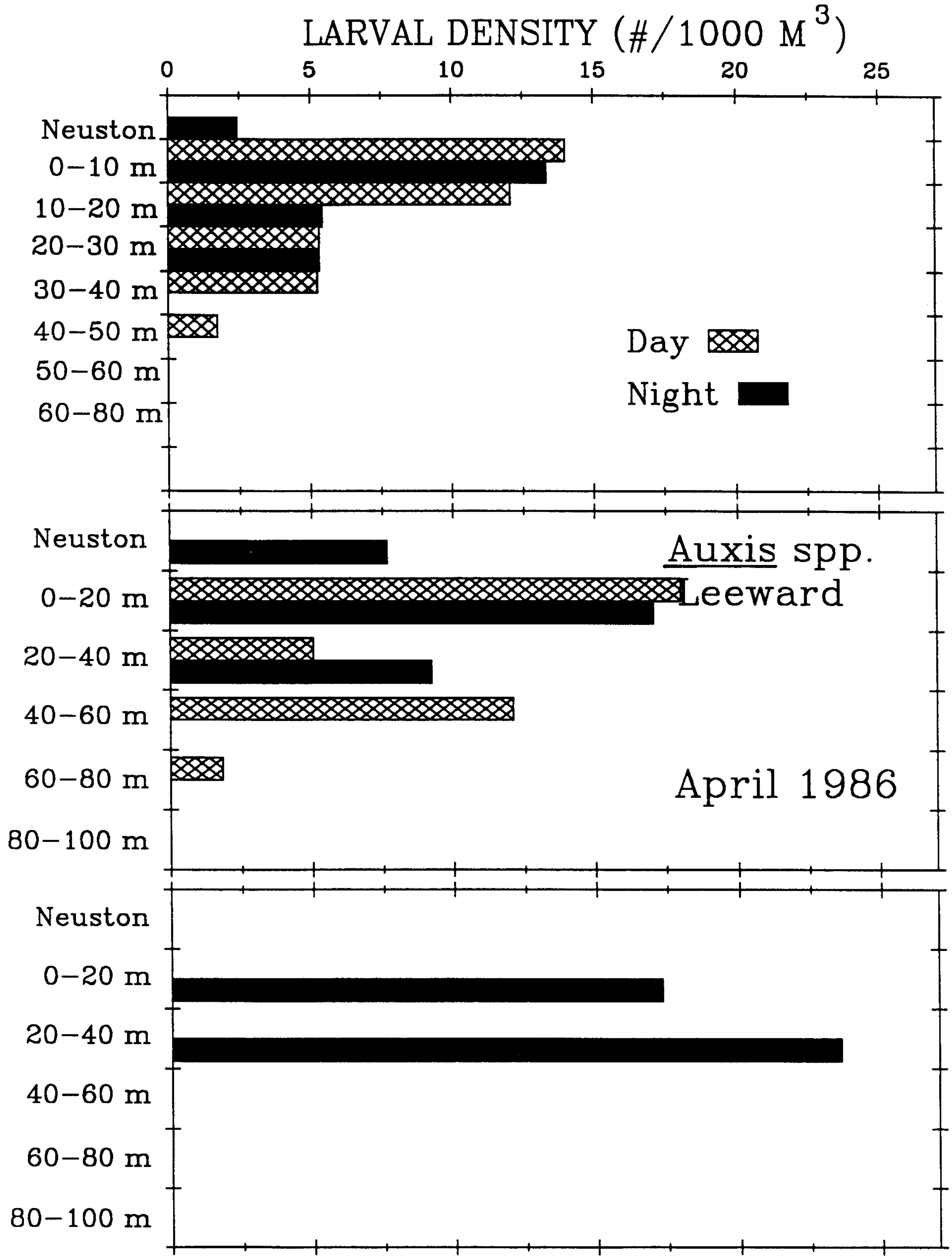

Figure 5C.--Continued. (C) April 1986, leeward stations.

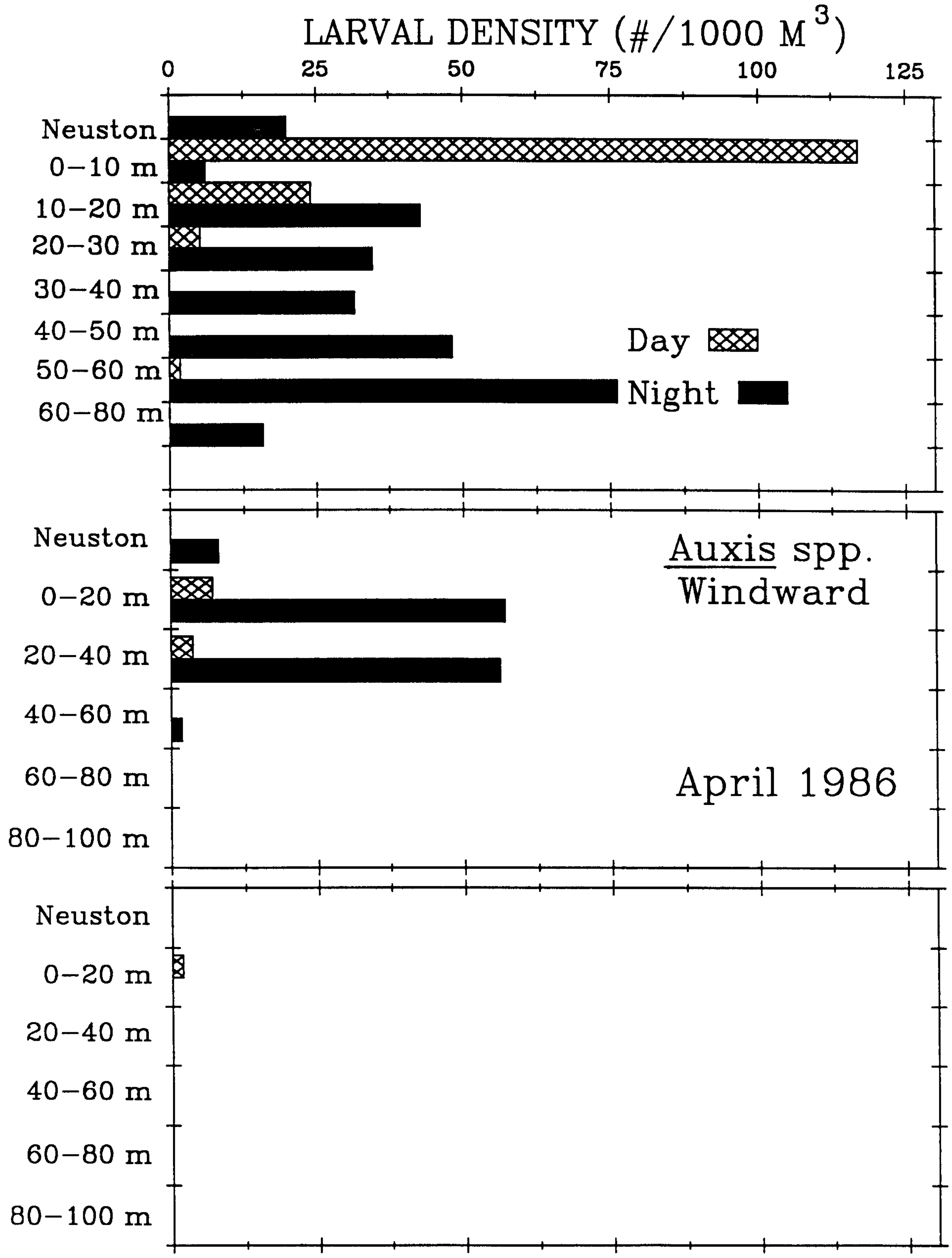

Figure 5D.--Continued. (D) April 1986, windward stations.

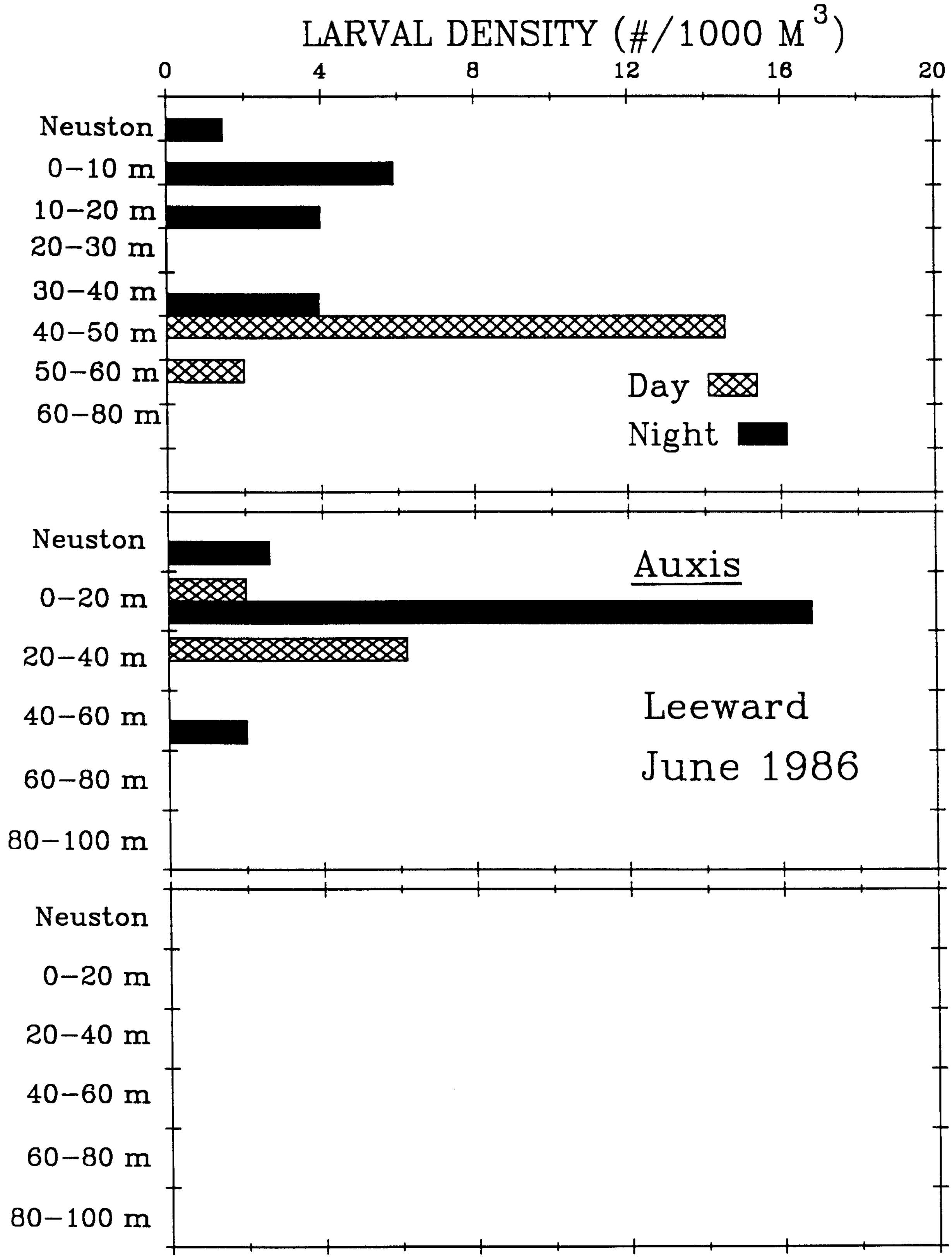

Figure 5E.--Continued. (E) June 1986, leeward stations.

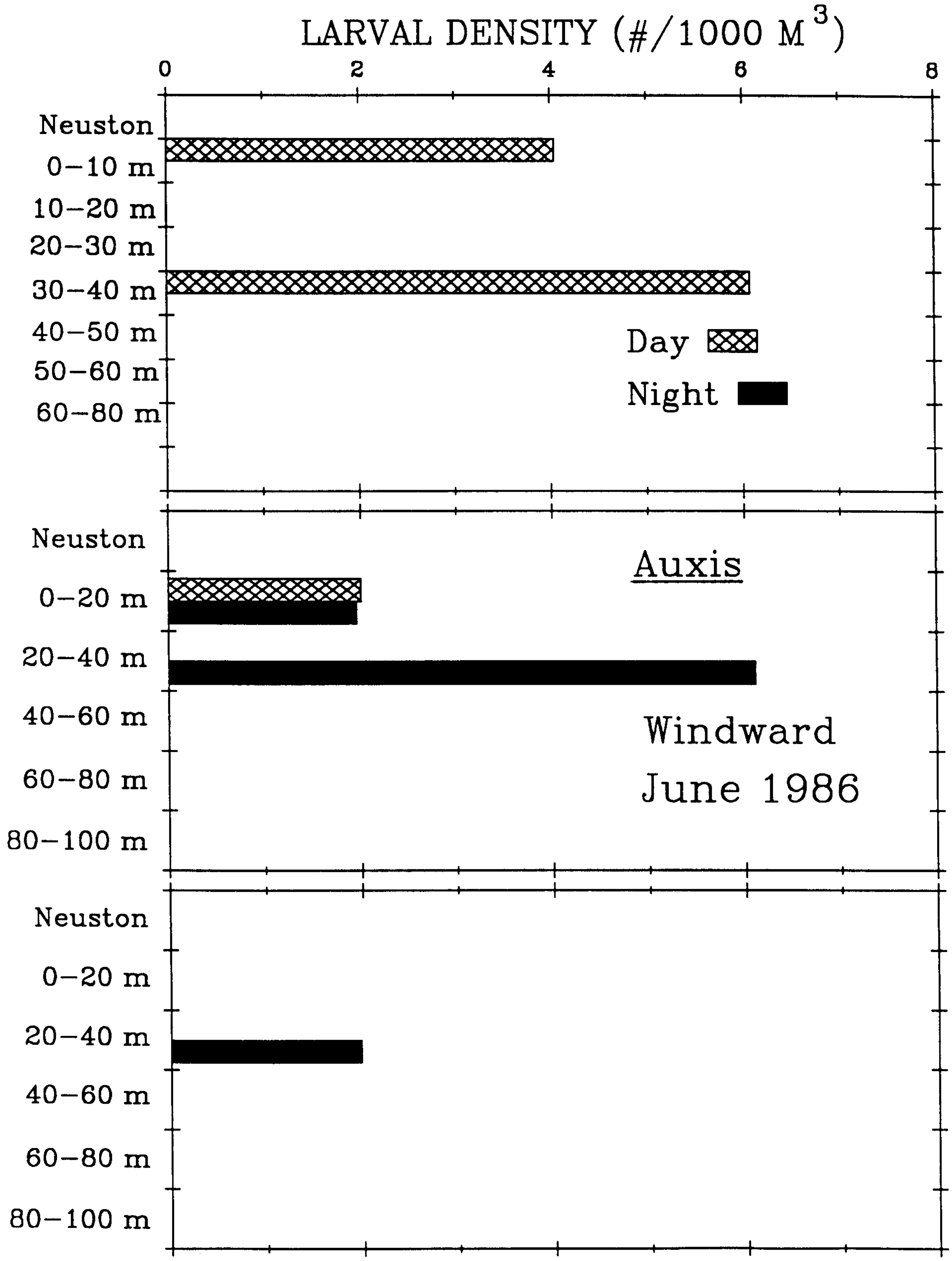

Figure 5F.--Continued. (F) June 1986, windward stations.

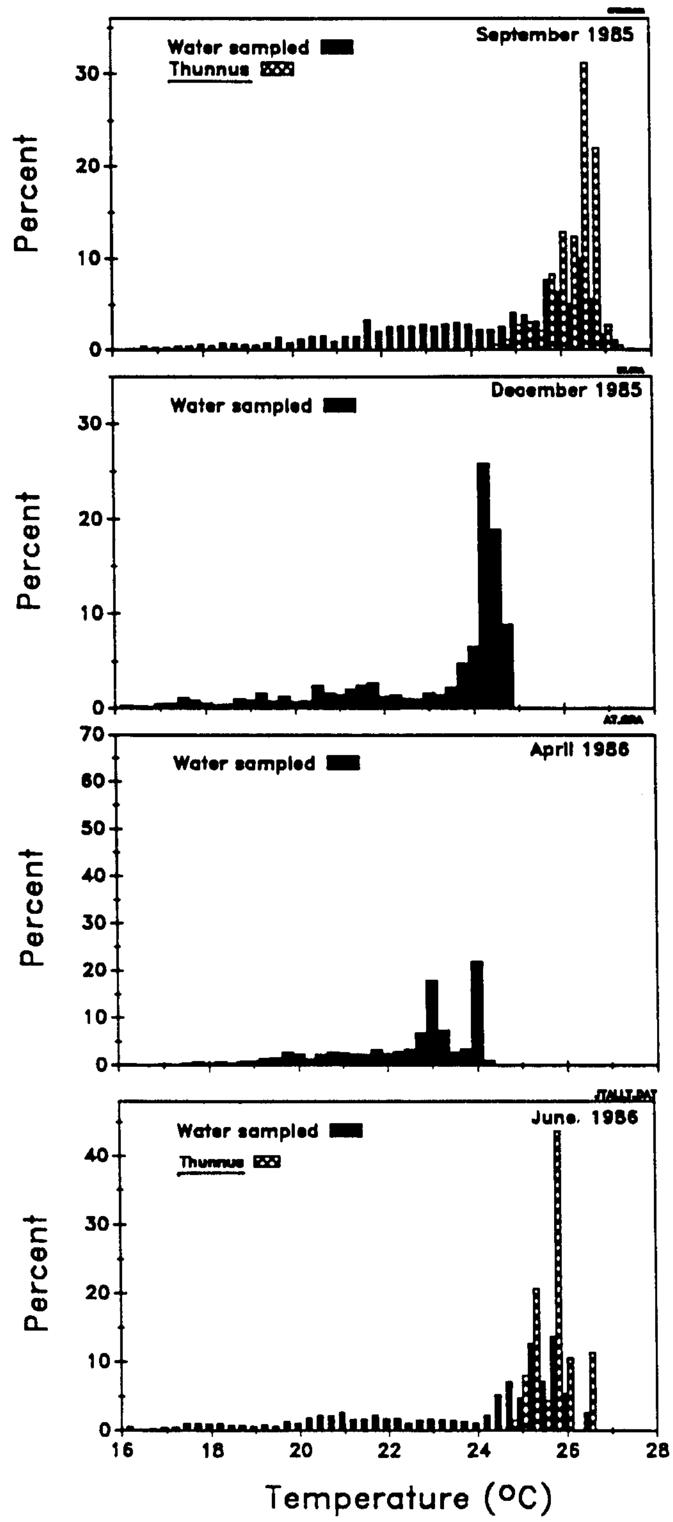

Figure 6.--Temperature and salinity observations during seasonal sampling showing the characteristics of the water where larval *Thunnus* spp. were captured, contrasted to the characteristics of all water sampled. Solid bars equal all water sampled in each seasonal cruise; cross-hatched bars equal the water containing larval *Thunnus* spp. (A) Temperature.

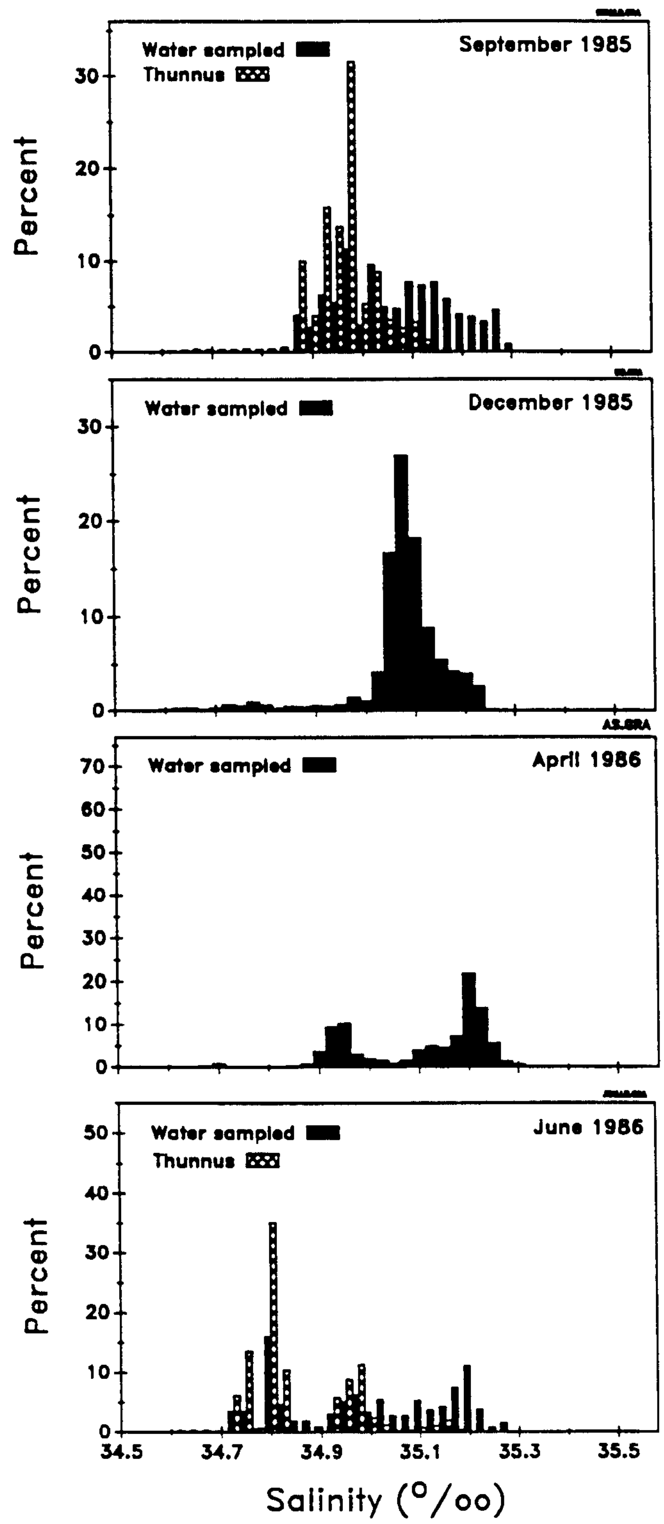

Figure 6B.--Continued. (B) Salinity.

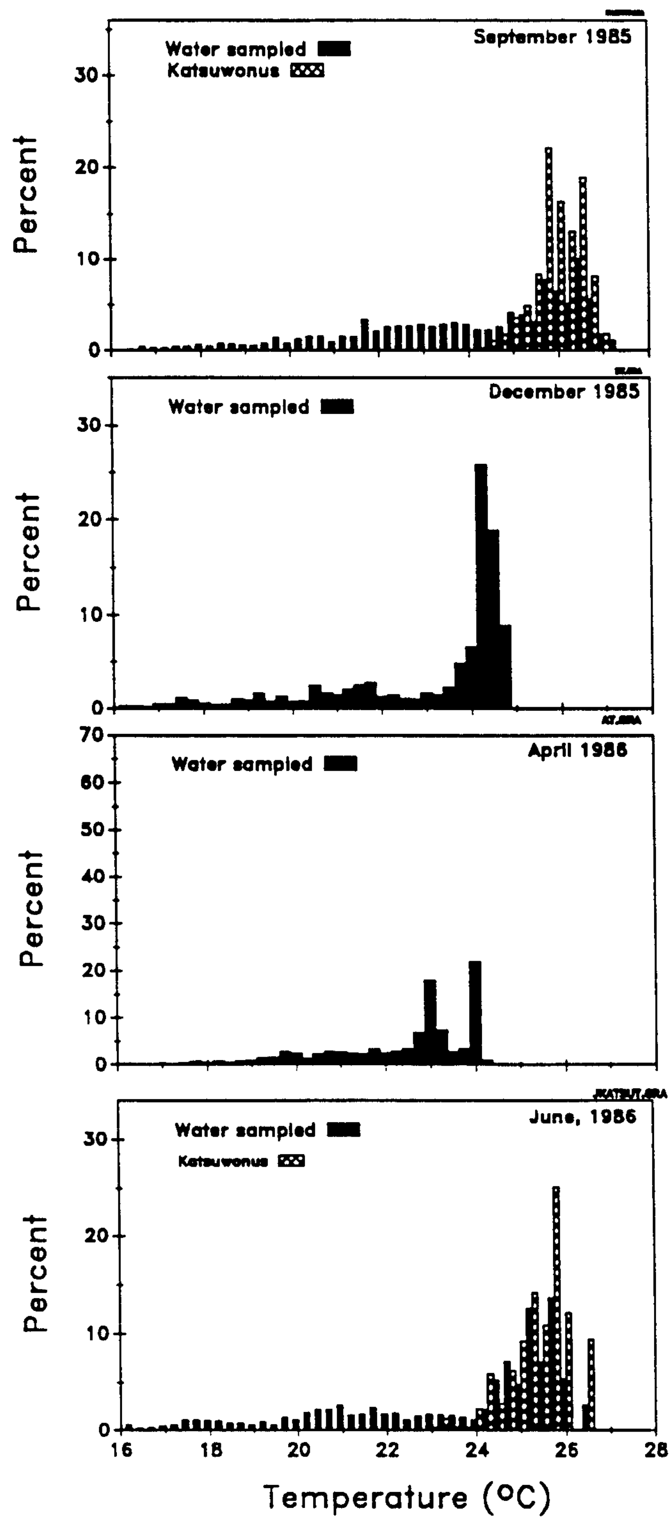

Figure 7.--Temperature and salinity observations during seasonal sampling showing the characteristics of the water where *Katsuwonus pelamis* larvae were captured, contrasted to the characteristics of all water sampled. Solid bars equal all water sampled in each seasonal cruise; cross-hatched bars equal water containing *Katsuwonus pelamis* larvae. (A) Temperature.

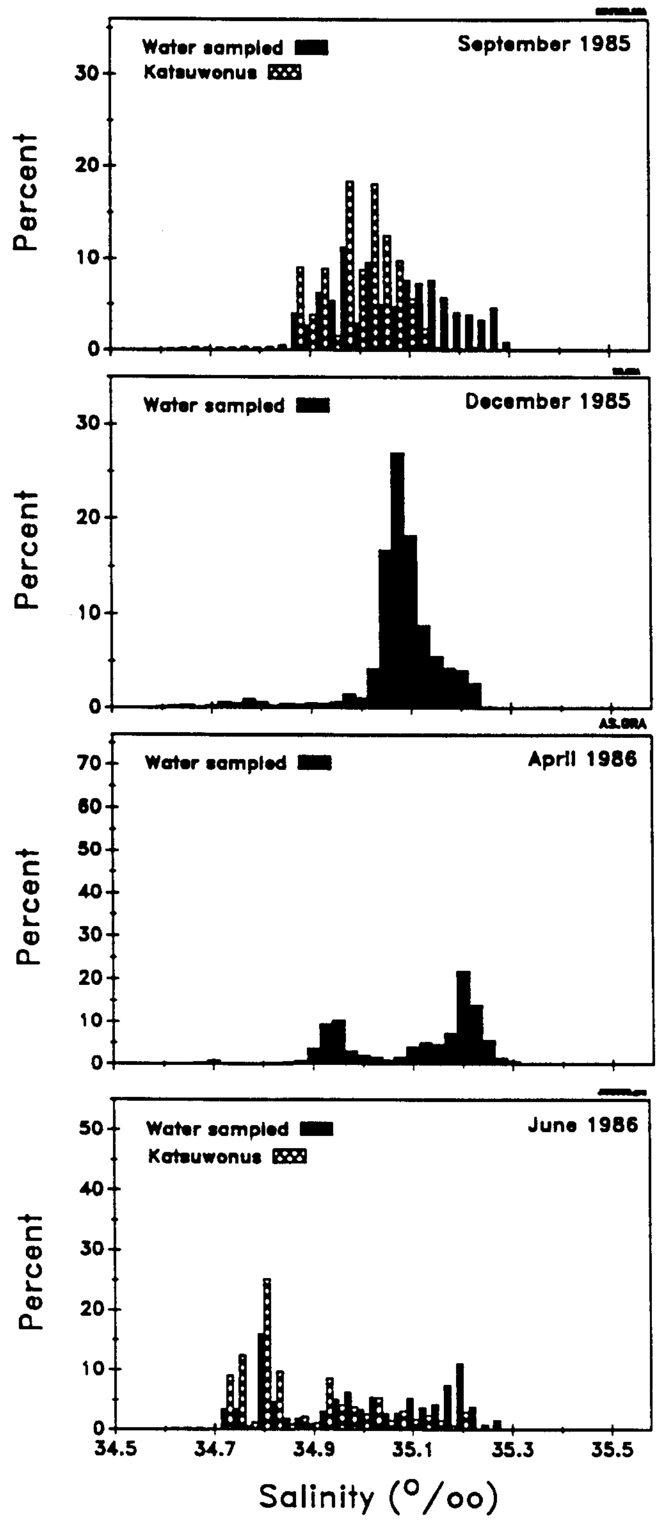

Figure 7B.--Continued. (B) Salinity.

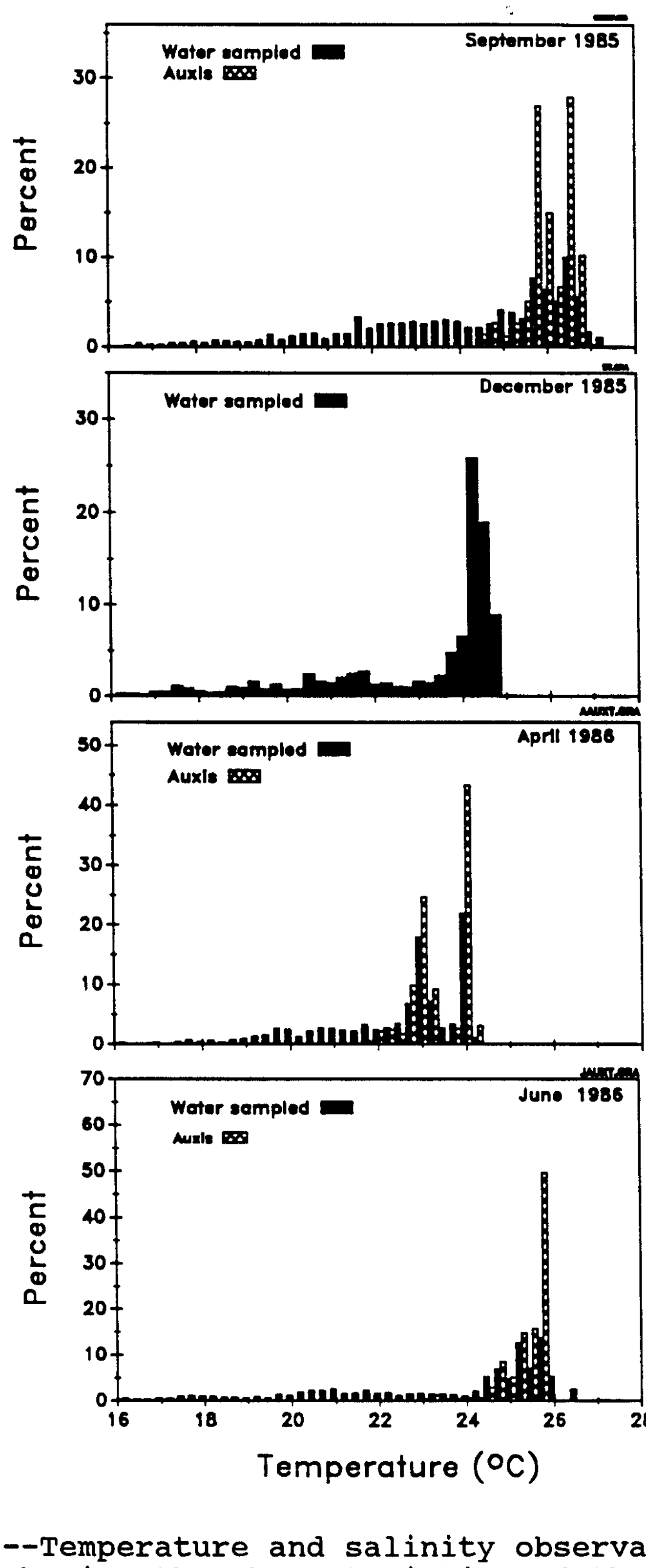

Figure 8.--Temperature and salinity observations during seasonal sampling showing the characteristics of the water where *Auxis* spp. larvae were captured contrasted to the characteristics of all water sampled. Solid bars equal all water sampled in each seasonal cruise; cross-hatched bars equal water containing larval *Auxis* spp. (A) Temperature.

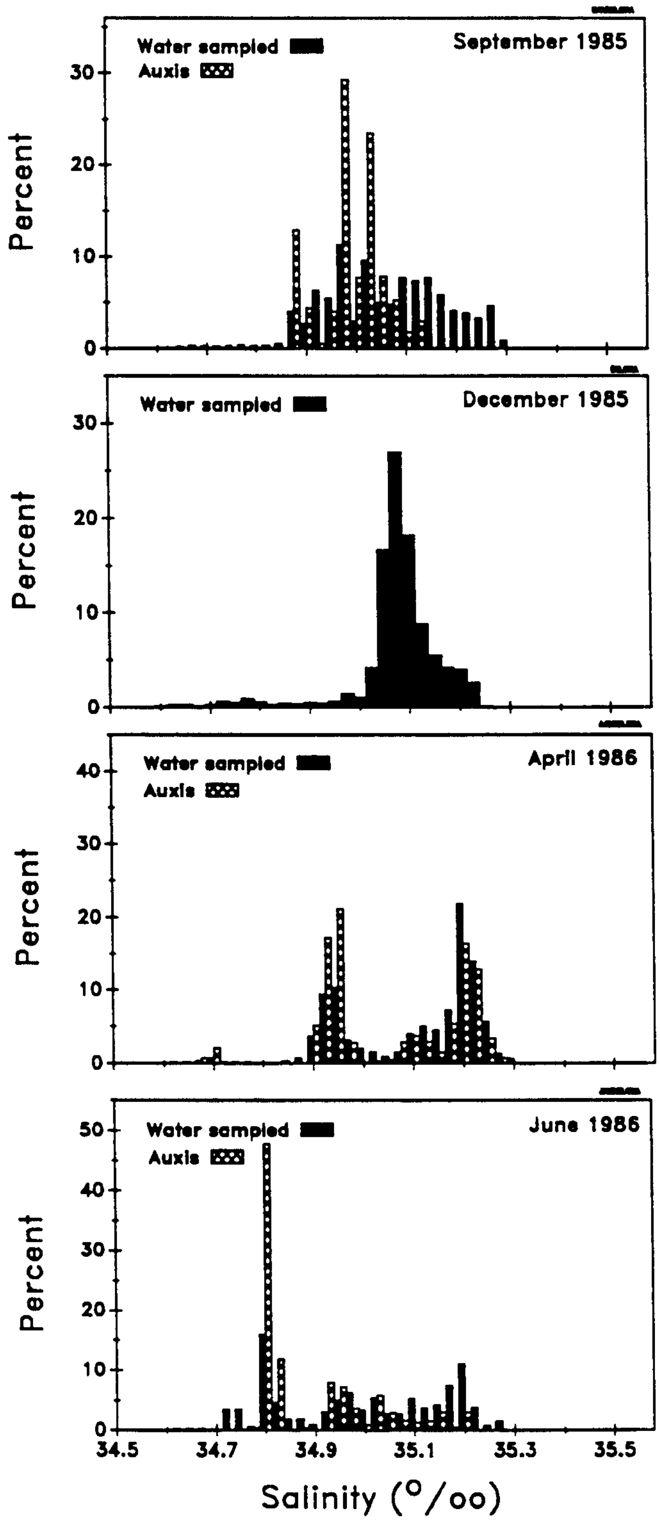

Figure 8B.--Continued. (B) Salinity.