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Cross-Shelf Distribution Patterns Of Tropical Juvenile Cephalopod Sampled Using Light Attraction.

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Abstract

This study investigated the association of cephalopod genera with location and depth in the waters of the central Great Barrier Reef. Stations along short (40 km) transects were sampled using light-traps at four locations across the continental shelf and slope: coastal Great Barrier Reef Lagoon, inter-reef passages (Magnetic and Palm), near reef environments ranging from mid to outer-shelf locations and the Coral Sea. A total of 13 cephalopod genera was caught from monthly cruises, conducted from October to January of 1990/91 and 1991/92. *Octopus*, the most abundant juvenile cephalopod was present in relatively high numbers at all shelf locations, with a few caught in the Coral Sea. The myopsid squid *Photololigo* was the most abundant squid in the collections but was rarely caught outside the Great Barrier Reef Lagoon. In contrast, the second most abundant squid, the oceanic *Sthenoteuthis* was uniformly distributed among all the habitats. Cephalopod assemblages at both depths in the Great Barrier Reef Lagoon were significantly different from those of the three other areas. This location supported highest abundances of *Octopus*, *Photololigo* and *Abralia*. Assemblages deeper in the water column were dominated by *Octopus*, and *Abralia* was always found near the benthos in the lagoon. In contrast *Euprymna*, the fourth most abundant genus was collected only at the surface. Reef passages and near-reef sites shared similar assemblages, with the squid component dominated by *Sthenoteuthis*. Very low numbers of cephalopods were caught in the Coral Sea using light attraction. High concentrations of cephalopods detected in the middle of the Great Barrier Reef Lagoon are consistent with present knowledge about oceanographic processes over this shelf.

Introduction

Juvenile cephalopods are a diverse and important component of the nektonic community found in pelagic environments, being both predators and prey within the pelagic food chains and providing important sources of food for commercial fisheries. Despite this importance early life-histories of most cephalopods are poorly described and fundamental information is lacking. Australian waters have a rich diversity of cephalopod species (Lu & Phillips 1985), that extends into tropical waters (Roper & Hochberg 1987). High biological diversity and limited taxonomic base increases the difficulty of describing this fauna and juveniles of these species have received little attention. Historically, sampling has been limited by the effectiveness of towed nets as sampling devices. Juvenile squid are agile and effective swimmers capable of evading towed net designs (Vecchione 1987) and a size range of juveniles can only be obtained by using multiple gear types (Rodhouse *et al.* 1992). Logistically it is difficult to sample more than one location at a time using towed nets and hence synoptic views of spatial distribution usually ignore the temporal component in the data collection. This is no problem when distribution and abundance patterns are static, but juvenile squid distributions are often determined by current systems (eg. *Illex illecebrosus* Dawe & Beck 1985). Furthermore net damage suffered by small soft-bodied specimens hinders identification of specimens (Vecchione 1987). Automated light-traps (Doherty 1987) provide an alternative solution to both of these problems and allow juvenile cephalopods in good condition to be sampled through time at multiple locations (Thorrold 1992).

The aim of this study was (1) to investigate the usefulness of light-traps as tools for sampling a range of juvenile cephalopod genera and (2) to describe the distribution and abundance of the juvenile cephalopod fauna sampled by light attraction. Our sampling was based on regular sampling of a cross-shelf transect from turbid coastal to clear oceanic environment, both close to and far from reefs to include maximum contrast. Here we describe the cross-shelf and vertical patterns to provide the spatio-temporal framework for designing further work into the local dynamics or regional patterns of specific taxa.

Materials and Methods

Sampling was based on repeated replicate trapping within four major cross-shelf locations near Townsville (Fig. 1):

a) Great Barrier Reef (GBR) Lagoon. This is a 56 km wide stretch of open water dividing the mainland from the nearest coral reefs. It is a shallow (15-40 m) gently sloping soft bottom habitat. A number of factors combine to influence the hydrodynamics of the GBR Lagoon: the East Australian Current in the Coral Sea and the outer half of the continental shelf, wind stress on the shallowing water column near the coast, water depth and fresh-water discharge from rivers (Wolanski 1981, King & Wolanski 1992). When winds oppose the poleward influence of the East Australian Current, a coastal trapped layer is formed and velocity shear occurs across the GBR Lagoon (Wolanski & Ridd 1990). The cross-shelf extent of the coastal boundary layer is controlled by wind stress and is unstable over time.

b) Reef Passages. Two broad relatively deep passages (Magnetic and Palm) dissect the reef matrix in the Townsville region of the GBR. Both provide major conduits for semi-diurnal tidal waves that oscillate perpendicular to the coast (Dight *et al.* 1990a). When the East Australian Current meanders close to the shelf-break, upwelling can occur and cold intrusions can be forced along the bottom of the passages, occasionally extending as far inshore as the coastal boundary in the GBR Lagoon (Andrews & Gentien 1982).

c) Coral Reefs. Four reefs (Keeper, Helix, Faraday and Myrmidon) of similar size, but different cross-shelf locations, were selected to represent shallow near-reef environs. All four reefs are located on the southern side of the Magnetic Passage and should have experienced the same dominant water flow.

d) Coral Sea. Waters beyond the shelf break, where depths exceed 1000m, were sampled to determine which cephalopod taxa are associated with oceanic waters and to monitor exchange between coastal and oceanic habitats.

Sampling this range of locations required that each was sampled in a way appropriate to its physical nature. The greatest difference in sampling strategy was that the three open water locations (GBR Lagoon, reef passages and Coral Sea) were sampled by drifting light-traps, whilst waters near the coral reefs were sampled by anchored light-traps. The important difference is that water around anchored traps can be exchanged by local current patterns leading to larger swept volumes per hour of operation compared to the drifting light-traps that should act as lagranian drifters and fish the same body of water. Table 1 provides a summary of the sampling strategies employed at each location. To determine the vertical distribution of juvenile cephalopods in the water column light-traps were at two depths; at the surface and deep. In 1990/91 the deep light-traps fished at 20 m at all stations. During 1991/92 the deep light-traps were set within three meters of the benthos, except in the open sea where the maximum depth was 100 m.

Table 1.   Sampling program in each location.

Location	# of Stations	Traps	1990/91		1991/92	
			Depth(m)	# of traps	Depth(m)	# of traps
Lagoon	5	Drifting	0	2	0	2
			20	2	Near benthos	2
Passage	5[a] (10[b])	Drifting	0	2	0	2
			20	2	Near benthos	2
Reef	4	Anchored	0	2	0	3
			20	1	20	2
Open Sea	5	Drifting	0	2	0	2
			20	2	100	2

[a] 1990/91
[b] 1991/92 (Palm Passage was not sampled in 1990/91.

All sampling was carried out during ten day periods centred on the new moons of October, November, December and January of 1990/91 and 1991/92. Stations in the GBR Lagoon, passages and Coral Sea were sampled a maximum of three nights each period. Water masses near the reefs were sampled for a maximum of nine nights, during each of those months. At the end of the first summer of sampling, it was clear that cephalopod catches in the Coral Sea were very low and that other locations

warranted more sampling effort. Hence sampling effort was reduced offshore but increased elsewhere, notably by adding Palm Passage (in 1991/92 only). In addition to these changes bad weather resulted in occasional abandonment of stations and/or transects, which reduced effort equally in deep and shallow water (Table 2).

Table 2. Total fishing effort (in light-trap hours) in each location and depth, pooled across the two summers.

Location	Deep	Shallow
Lagoon	220	219
Passage	225	226
Reef	311	613
Open Sea	114	113

Replication at each station was provided by simultaneously deploying two light-traps at each depth several hundreds of meters apart. Each night the light-traps were fishing at the first station by 1930 hrs (Eastern Standard Time). Light-traps were retrieved after one hour of fishing and the catch was processed while the ship was moving to the next station on the transect. The last trap was recovered by 0530 hrs, which meant that it was only possible to sample five stations per night in this manner due to the distances between the stations. As stations in each location were sampled sequentially each night, time of night is confounded with station within a location. Likewise only one location could be sampled in a night, hence location is confounded with night. These effects were minimised, to some degree, by haphazardly selecting the location sampled on a night and the direction along the transect was sampled in each location on a particular night. Replication in the near reef waters consisted of shallow and deep light-traps anchored on the southern reef slope to standardise position with respect to water flow. All anchored light-traps at each reef fished for a total of three hours per night (between the hours of 2100 and 2200 hrs, 2400 and 0100 hrs, and 0300 and 0400 hrs) to reduce the confounding effects of tide and time.

Temperature and salinity profiles adjacent to drifting light-traps were obtained using a Seabird conductivity-temperature device during the cruises in October, November and January 1991/92. These data were used to determine the position of

the boundary layer in the Great Barrier Lagoon on the assumption that there would be a temperature differential across the front. To standardise for monthly changes in these parameters, deviations of temperature and salinity for each station were calculated from the pooled average for each month and the deviations averaged over time.

Specimens were fixed and preserved in 100% ethanol and identification of the cephalopods was undertaken in the laboratory. Given taxonomic problems associated with juvenile cephalopods specimens were identified to the genus level. Dr. C.C. Lu (Victoria Museum, Australia) kindly identified sample specimens for a reference collection that was used for all subsequent identifications. Terminology describing the pre-adult phase of cephalopods has recently been defined (Young & Harman 1989) and we have used the term 'juvenile' to describe the stage between hatching and sub-adult.

Multivariate techniques were used to analyse the relationships between the cephalopod genera and locations. These techniques are useful to examine relative abundances of a suite of species. Multivariate analysis of variance (MANOVA) determined the effect of location, depth and their interaction on the density of the cephalopod assemblages. The data were examined for multivariate normality and homogeneity of variances (Multivariate Levene's Test). The data were $log10+1$ transformed before analysis. The MANOVA was followed by a canonical discriminant analysis (CDA) to determine which cephalopod genera were associated with different locations and depths.

Results

A total of 3862 juvenile cephalopods representing 13 genera, including sepioids, myopsids, oegopsids and octopods, were caught using light-traps during the two summers of sampling. The two most abundant genera were *Octopus* and *Photololigo* (Table 3). Most of the genera were very rarely caught, especially *Sepia*, *Pyroteuthis*, *Abraliopsis*, *Argonauta* and *Pterygioteuthis*.

The diversity of juvenile cephalopods was similar in the GBR Lagoon, the passages and the coral reefs. In the Coral Sea, very few juvenile cephalopods were captured and the diversity was very low. *Sthenoteuthis* and *Octopus* were both caught but in very low numbers. Numbers of juvenile cephalopods varied as a function of an interaction between location and depth (Table 4). Highest catches of juveniles were taken in the GBR Lagoon, especially from deep light-traps (Fig. 2). Catches from the reefs and passages were lower than those in the GBR Lagoon, but the relative proportion of cephalopods between depths remained the same with highest catches deeper in the water column (Fig. 2).

Table 4.   Analysis of variance table, examining the catch of juvenile cephalopods as a function of depth and location. Data for both summers of sampling have been combined.

Source	df	Sums of Squares	Mean Square Estimates	F-value	Probability
Location	3	51.729	17.243	173.89	0.0001
Depth	1	1.703	1.703	17.17	0.0001
Location*Depth	3	1.237	0.412	4.16	0.0060
Error	2030	201.592	0.0992		

Catches among stations in the GBR Lagoon were significantly different (Table 5). Low numbers of cephalopods were caught on the edges of the GBR Lagoon, with elevated abundances at two stations (24 and 33 km) in the middle (Fig. 3). Clear temperature and salinity gradients are evident across the GBR Lagoon (Fig. 4). Surface water temperature and salinity at the two stations closest to the coast were

consistently higher than the average values for the GBR Lagoon. Further offshore surface water parameters were lower than the average.

Table 5. Analysis of variance table, examining number of juvenile cephalopods caught at the four different stations within the GBR Lagoon. Data for both summers are combined.

Source	df	Sums of Squares	Mean Square Estimates	F-value	Probability
Distance	4	10.713	2.678	12.24	0.0001
Error	434	94.940	0.219		

Octopus, the most abundant of all the cephalopod juveniles, was present at all locations, although rare in the Coral Sea. Juvenile *Octopus* were considerably more abundant in deep traps within each location and highest catches were taken in the GBR Lagoon (Table 3). Due to its numerical abundance, this genus greatly influenced the aggregate patterns shown in Figs. 2 and 3. Among the squid, *Photololigo* was also very abundant in the GBR Lagoon, but low numbers were caught around the reefs and in the passages. In contrast to *Octopus*, *Photololigo* was more common in surface waters (Table 3). The other nine genera were caught in relatively low numbers. *Sthenoteuthis*, the second most abundant squid, was ubiquitous throughout the areas sampled and was the only species caught with any consistency in the Coral Sea. The sepioid *Euprymna*, the fourth most abundant genera, was predominantly caught in the surface light-traps in the GBR Lagoon, passages and reefs.

Multivariate analyses were carried out using the most abundant genera: *Octopus*, *Photololigo*, *Sthenoteuthis*, *Euprymna*, *Sepioteuthis* and *Abralia*. It was evident that the distribution of juvenile cephalopods was depth and location specific as indicated by the significant location-depth interaction (Pillai's Trace 0.466 F=24.4786 df 42, 12198 Pr=0.0001). Most of the differences in juvenile cephalopod composition occurred between the GBR Lagoon and the other three locations (Fig. 4a). In particular the GBR Lagoon was clearly discriminated due to high numbers of *Octopus* and *Photololigo*. Without this dominance, the other locations appeared to be very similar (Fig 4a). An examination of the variation described by the second and third

axes clearly showed the differences between the depths (Fig. 4b). In particular, the GBR Lagoon exhibited different assemblages of cephalopods at the two depths. This major difference was largely due to *Abralia* (Table 3). This genus was only caught in relatively high numbers during the 1991/92 summer when light-traps were deployed close to the benthos. *Abralia* and *Octopus* were very dominant in samples caught in the deep traps in the GBR Lagoon, passages and reefs. *Octopus* was also caught more commonly in deep light-traps whereas the sepioid *Euprymna* was caught predominantly in the surface light-traps (Table 3). *Photololigo*, *Sepioteuthis* and *Sthenoteuthis* were more common in surface light-traps, but these genera were also relatively abundant in catches from deep light-traps (Table 3). The depth distribution of *Sepioteuthis* was dependent upon the location; they were present in deep samples at the reefs and surface traps in the GBR Lagoon.

Discussion

This study demonstrates that submersible light-traps can be useful alternative sampling devices to assess the relative abundance of some cephalopod species. Twelve genera of juvenile cephalopods were caught using active attraction instead of passive collection. Although no independent assessment is available to show that we sampled all the available diversity, clearly a wide range of taxa show responses to light that can be exploited to determine their relative abundance levels. Both *Octopus* and *Photololigo* were caught in high enough numbers to allow the examination of temporal and spatial distributions in more detail (Moltschaniwskyj & Doherty 1994). The live state of all material collected by this method also demonstrates the usefulness of light-traps to provide material for physiological and behavioural investigations not previously possible.

By deploying light-traps in drifting and anchored modes, we were able to sample a wide a range of habitats from coastal to oceanic conditions, near and far from reefs. However, there must be caution when interpreting light-trap catch rates. With little known yet about the sampling efficiency of light-traps, comparisons of catch rates can only provide an index of relative abundance. While this is adequate for many questions about recruitment and juvenile supply, such comparisons depend on unchanging efficiency. This is less of a problem when sampling the same place over time (eg. Milicich *et al.* 1992), but it can become a problem when sampling a wide range of environments as in this study. This assessment has not been tested for cephalopods, but the following arguments suggest that the patterns shown here were not caused by differential catching efficiency of the light-traps.

By including pelagic and near-reef habitats this study deployed light-traps in water conditions ranging from shallow coastal turbid water to deep oceanic transparent water . Therefore biases in light-trap efficiency due to water clarity will result in better performance in clearer water. Thus any species demonstrating rising abundance away from the mainland could provide an ambiguous case. None of the species sampled in this study showed this pattern and highest catches were from lagoonal

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stations close to the coast. While these may be biased estimates of true abundance it is likely that the inshore samples have underestimated densities, therefore resulting in a greater difference between inshore and offshore patterns than identified in our study. On this basis we do not believe that variable light-trap efficiency among different water masses contributed to the qualitative patterns of abundance observed.

As different modes of deployment were necessary to sample habitats near and far from reefs caution is needed when comparing catch rates from drifting and anchored traps. Thorrold (1992) showed that drifting traps catch higher numbers of fish in open water than anchored ones implying that current speed past the light-traps affected capture efficiency. If this was true, real abundances may have been under-estimated in near-reef habitats when sampling was deliberately spread over three sampling periods each night to include periods of tidal flow and slack. The extent to which this was offset by the longer period of sampling by light-traps each night in the near-reef habitat and the exposure to greater volumes of water is unknown and is unlikely to be simple. However, we have emphasised relative abundance levels of cephalopod genera rather than absolute comparisons. At this level light-traps captured similar cephalopod genera on the reefs and in the adjacent passages and few differences were detected the relative abundance of cephalopod genera.

The greatest differences detected by this study were those related to cross-shelf location and depth. The Coral Sea yielded surprisingly sparse catches of cephalopods with only the oceanic genus *Sthenoteuthis* being caught with any consistency. Apart from this one genus that was ubiquitous to all locations and obviously able to tolerate a wide range of conditions, the Coral Sea appears not to provide suitable nursery conditions for any shelf taxa. This may be due to the oligotrophic status of the East Australian Current that dominates this habitat or the selective disadvantage imposed by rigid southward advection in this strong boundary current. Most genera sampled by this study complete their early life history on the continental shelf where there was no evidence that the coral reef habitat or passages contained any unique assemblages.

Using towed nets, Dunning (1985) was able to obtain reasonable numbers of juvenile ommastrephid squid in deep oceanic water off the east Australian coast, but far to the south. It appeared that the two techniques, towed nets and light-traps were catching different sized individuals. Ommastrephids caught in towed nets ranged in size from 0.8 mm to 4.4 mm (Dunning 1985) compared with 2.4 mm to 59.0 mm caught using the light-traps (unpub. data). This difference in sizes may be due to the abilities of the two techniques to target different ontogenetic stages. Or the two studies were sampling different locations and the larger ommastrephid juveniles are undergoing a shift into shallower water as they grow. Other studies have demonstrated that the light-traps do show size selectivity, capturing larger fish larvae and juveniles than towed plankton nets (Choat et al. 1993, Thorrold 1993)

Although the highest diversity occurred in near reef waters, the GBR Lagoon was not that much different and yielded the highest catch rates for the six most abundant genera. High numbers of juvenile cephalopods in a region of the GBR Lagoon 24 to 33 km offshore suggest that juveniles in this area either have higher probabilities of surviving or are aggregating, actively or passively, in this area. High numbers of juvenile cephalopods have also been caught in this area with towed nets (Jackson 1986). There is a frontal system in this region of the GBR Lagoon, produced by the interaction of a coastal boundary water mass and the East Australian current (Wolanski 1981, Wolanski & Ridd 1990). Differences in the surface water temperatures and salinities across the GBR Lagoon indicate that this interaction of the two water masses is occurring midway across the GBR Lagoon. High secondary productivity (Sammarco & Crenshaw 1984, Thorrold & McKinnon 1992) and high densities of juvenile and larval fish (Thorrold in press) suggest this area is important biologically and hydrodynamically. Given that juvenile squid are able to exogenously feed within hours of hatching (Boucher-Rodoni et al. 1987), the higher secondary production of the GBR Lagoon would provide suitable feeding grounds for rapidly growing predators. Boundary regions have been identified as areas in which juvenile cephalopods are an important component of the nektonic community (Reid et al. 1991, Rodhouse et al. 1992). The interactions of cephalopods in this community are

not recognised and these areas may determine growth and survivorship of juvenile squid.

The presence of a juvenile cephalopod assemblage characteristic of specific locations and depths has interesting implications on the dispersal of the juveniles to and away from adult populations. The location and depth occupied by juveniles will modify the extent and rate of dispersal, thereby determining growth rates and recruitment patterns (O'Dor & Coelho 1993). During the summer the longshore current is predominantly southward, however, closer to the coast in shallower water (<40 m) water moment is more restricted than on the outer shelf (Williams *et al.* 1984). Dispersal rates and extent will also be affected by the depth in the water column, closer to the benthos dispersal will be more restricted than at the surface (Williams *et al.* 1984, Dight *et al.* 1990b). Given the complex nature of hydrology interacting with topography it is difficult to speculate on the source of juveniles. Generally the trend is for movement southward and inshore according to modelling of the dispersion of passive particles (Dight *et al.* 1990a). So it is likely that adult populations to the north and offshore may be responsible for the juvenile cephalopods caught in the GBR Lagoon. Since water movement is restricted across the shelf the dispersal of juvenile cephalopods across the shelf will be limited (Williams *et al.* 1984, Dight *et al.* 1990). Therefore, the observed cross-shelf patterns of abundance of different genera, may be a function of species specific spawning areas across the shelf. Such distinct cross-shelf patterns of species have been described for larval flathead (Andrews 1982) and juvenile *Photololigo* (Moltschaniwskyj and Doherty 1994).

This is the first study that has used automated light-traps for a quantitative examination of juvenile cephalopod assemblages. It indicates that cephalopods may be an important component of a nektonic community that has been described in the GBR Lagoon (Sammarco & Crenshaw 1984). The use of light-traps to describe spatial and temporal abundance of pelagic organisms is still relatively new (Doherty 1987). Ecological investigations of the juvenile phase of both pelagic and benthic cephalopods require the capture of juveniles over a variety of locations and in different water conditions. Catches of cephalopods were often very low making

generalisations about spatial patterns difficult to make. However, a sampling program concentrating on regions of importance, such as the GBR Lagoon, is now possible in the future. Light-traps are a successful and useful technique to capture juvenile cephalopods that have eluded other methods used in this region (Jackson 1986). Furthermore identification of areas where high densities of zooplankton, teleosts and cephalopods occur provides an exciting opportunity to investigate community interactions involving juvenile cephalopods, particularly from the perspective of squid-predator-prey interactions.

Acknowledgments

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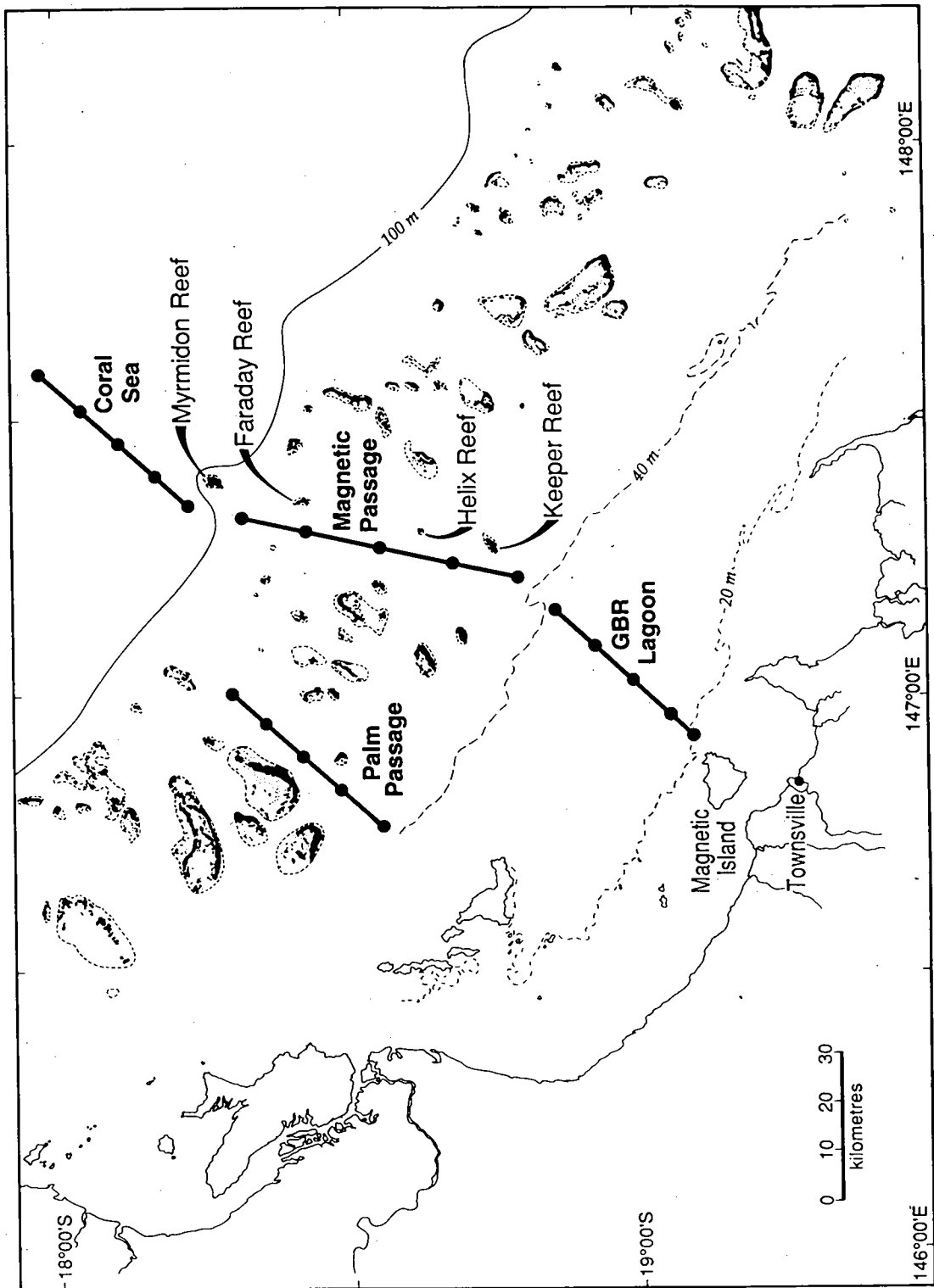
Figure 1.   A map of the continental shelf and slope of the coast of Townsville, Queensland, Australia. The locations and stations sampled are indicated.
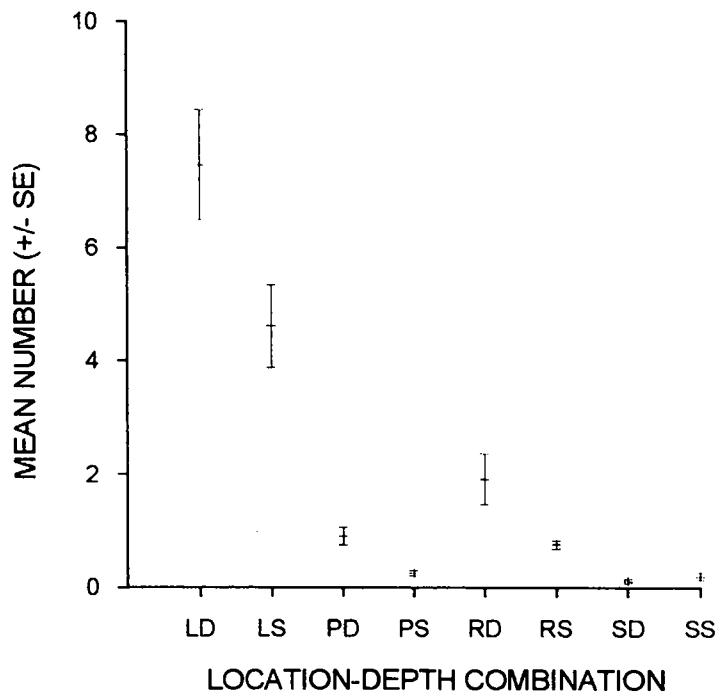
Figure 2.   A comparison of the average number of cephalopods captured per hour of light-trapping between the four locations sampled in the GBR. Values are the average per light-trap hour ± standard error. LS - GBR Lagoon shallow, LD - GBR Lagoon deep, PS - passage shallow, PD - passage deep, RS - reef shallow, RD - reef deep, SS - open sea shallow, SD - open sea deep.
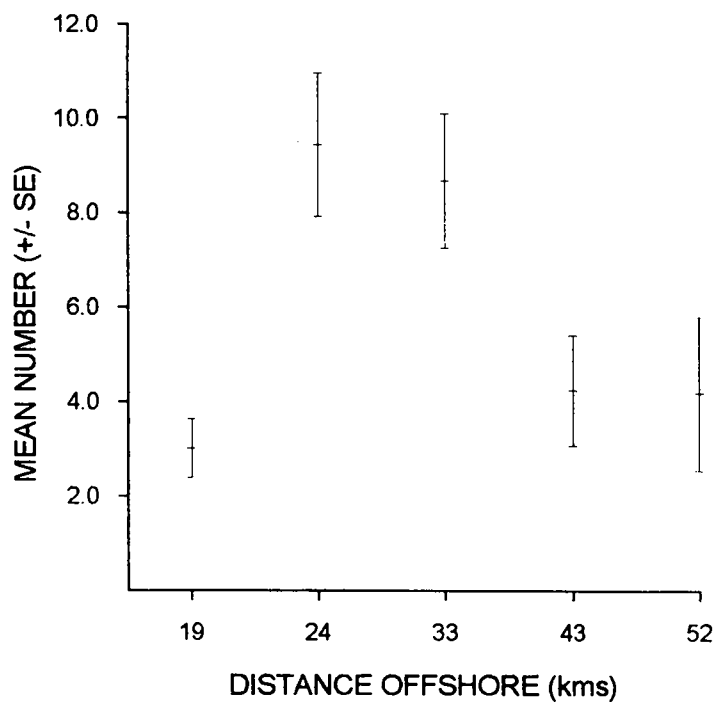
Figure 3.   The distribution of cephalopods sampled using light-traps across the GBR Lagoon.
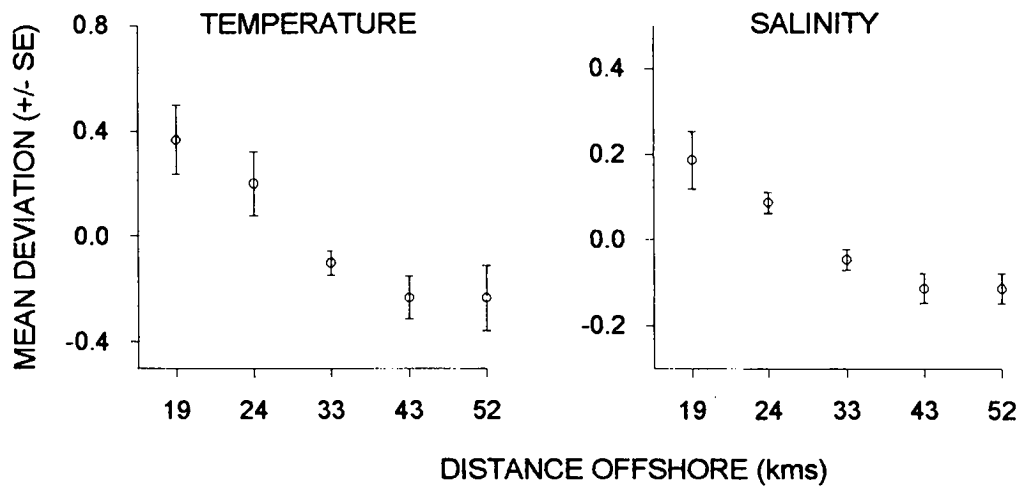
Figure 4.   For each station in the GBR Lagoon the average deviation from the mean temperature and salinity for each month has been calculated. Standard errors for the average deviation over three months are shown.
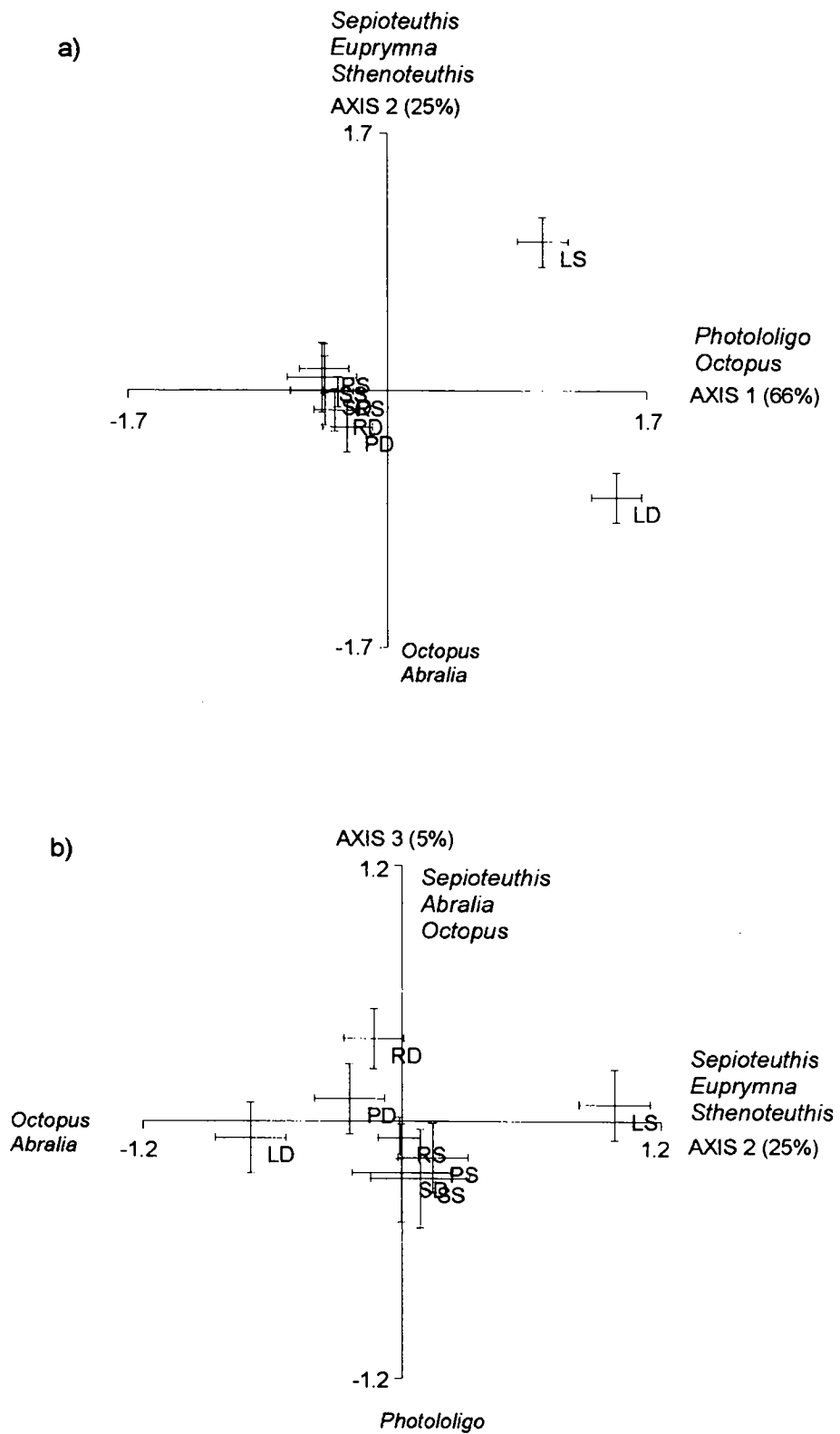
Figure 5.   Canonical discriminant analysis results, showing the relationship of each area-depth combination on the first two discriminant axes. Values plotted are means and standard errors of canonical scores for each location-depth combination. Location symbols as in Figure 2.

Table 3. The number of cephalopods caught per light-trap hour at each depth location combination. Data have been combined across years. Catch less than 0.01 individuals per light-trap hour are indicated by *. - indicates that no cephalopods were present.

GENERA	TOTAL NUMBER	LAGOON		REEF		PASSAGES		SEA	
		SHALLOW	DEEP	SHALLOW	DEEP	SHALLOW	DEEP	SHALLOW	DEEP
Octopus	2066	0.57	4.57	0.51	1.49	0.05	0.64	0.02	0.07
Sepiola	27	0.01	0.01	*	0.05	*	0.02	-	-
Euprymna	117	0.18	*	0.09	0.03	0.04	-	0.03	-
Photololigo	1314	3.16	2.69	*	0.01	-	0.10	-	-
Sepioteuthis	83	0.18	-	0.03	0.07	0.02	-	-	-
Abralia	57	-	0.12	*	0.07	*	0.02	-	-
Abraliopsis	2	-	-	-	0.01	-	-	-	-
Pyroteuthis	1	-	-	-	-	-	-	*	-
Pterygioteuthis	1	-	*	-	-	-	-	-	-
Sthenoteuthis	182	0.17	0.02	0.09	0.11	0.10	0.05	0.10	0.02
Onkyia	6	*	-	*	*	-	-	*	-
Sepia	1	-	-	*	-	-	-	-	-
Argonauta	5	-	-	*	-	-	-	-	-
TOTAL	3862	936	1630	458	573	50	187	18	10