

**Abstract.**—This study quantified the temporal and spatial abundance of juveniles of two *Photololigo* species on the continental shelf off Townsville, Australia with the use of light-traps. The two *Photololigo* species (A and B) showed very distinct and separate spatial distribution patterns. *Photololigo* sp. A was found close to the coast and was the smaller and more abundant of the two species. This species was most abundant in surface waters, although larger individuals were generally caught deeper. There was no evidence of vertical movements during the night. The presence of small and large juvenile *Photololigo* sp. A during summer and winter months suggests spawning and recruitment occur throughout the year. In contrast, *Photololigo* sp. B was caught predominantly offshore. All sizes of *Photololigo* sp. B were caught both near the benthos and at the surface in the mid-lagoon, but farther offshore juveniles were deeper and larger. The presence of small juvenile squid of both species throughout the summer suggests that these species spawn for an extended period during the summer. This study demonstrates that light-traps are an effective way of sampling small cephalopods.

## Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef Lagoon

**Natalie A. Moltschaniwskyj**

Department of Marine Biology, James Cook University of North Queensland  
Townsville, Queensland 4811, Australia.

**Peter J. Doherty**

Australian Institute of Marine Science, PMB 3  
Townsville, Queensland 4810, Australia.

The current poor state of knowledge about processes important in squid population dynamics is mainly due to limited information about the juvenile phase (Voss, 1983; Boyle, 1990). Life-history characteristics have largely been derived from information about the adult phase. Our limited information about young squid is demonstrated in attempting to define the life-history phases (Young and Harman, 1988). Jackson and Choat (1992) suggest, given the comparatively short life time of tropical squid (<250 days), that a proportionally long period of the life cycle is spent as small individuals. In the case of *Loligo chinensis*, with a summer life time of 120 days, individuals less than 60 days old (<50-mm mantle length) have not been studied. Hence, for almost half the life history of most squid there is not even the most basic information. Temporal and spatial abundance patterns of juvenile squid will provide a basis for understanding the processes of mortality, growth, and recruitment. However, such information has traditionally been difficult to obtain because of problems in capturing and identifying a sufficient size range of juvenile cephalopods (Vecchione, 1987).

To examine the ecology of juvenile squid it is necessary to use techniques that catch a size range of individuals, hatchlings to juveniles, in good condition. Pelagic squid produce either benthic or pelagic eggs and have a planktonic juvenile phase (Boletzky, 1977). Juvenile squid are alert, mobile organisms that easily avoid capture by towed nets (Vecchione, 1987). The use of a combination of different towed nets to sample an area enables the collection of a wider size range of juvenile squid (Rodhouse et al., 1992). However, it is difficult to obtain replicates needed to provide density estimates from towed nets. In this study we have employed an alternative technique based on light-attraction that is effective in sampling pelagic juvenile fishes. Automated light-traps (Doherty, 1987) can overcome the problems of net avoidance and enable sampling at discrete depths in the water column. The ability to sample concurrently within an area ensures that estimates of variability in abundance are not confounded by time. This technique also collects live material in good condition, which can facilitate taxonomic identification. However, sampling an unknown volume of

water by individual traps requires cautious interpretation of abundance estimates (Choat et al., 1993).

There are four species of loliginid squid currently recognized in the Townsville region: *Sepioteuthis lessoniana*, *Loliolus noctiluca*, *Photololigo* sp. B, and *Photololigo* sp. A.<sup>1</sup> There are currently no morphological descriptions of the two *Photololigo* species, but they can be readily identified by using allozyme electrophoretic techniques (Yeatman and Benzie, in press). Previously both of these species have been referred to as *Photololigo (Loligo) chinensis* (Jackson and Choat, 1992; Yeatman and Benzie, in press), but neither correspond to *P. chinensis* from Thailand.<sup>2</sup> Electrophoretic analysis of a subset of juveniles collected during three months of the program found that all *Photololigo* sp. A were found less than 33 km offshore and 90% of the *Photololigo* sp. B were found 33 km or more offshore.<sup>2</sup> Because these species are morphologically identical as juveniles, we assumed that all individuals found at stations less than 33 km offshore were *Photololigo* sp. A and that *Photololigo* collected more than 33 km offshore were *Photololigo* sp. B. *Photololigo* sp. A (previously known as *Loligo chinensis*) has been the topic of recent growth studies using statolith aging techniques (Jackson and Choat, 1992). This species is a small short-lived neritic squid. Individuals are approximately 60 days old when they appear in the adult population and they can grow to 180 mm in 120 days. Little is known about the early life-history and juvenile distribution patterns of either *Photololigo* species. The objectives of this study were to describe the spatial and temporal distribution patterns of juvenile *Photololigo* species across the continental shelf in the Townsville region of the Great Barrier Reef.

## Materials and methods

### Sampling design

Two major habitat types are found on the continental shelf, off Townsville, Australia. The inshore habitat is a 56 km wide soft bottom coastal lagoon ranging in depth from 15 m to 40 m. The offshore habitat is a complex reef matrix of similar extent, dissected by channels ranging from 40 m to 75 m deep at the shelf break. To assess the cross-shelf distribution of juvenile squid, four automated light-traps (Doherty, 1987) were deployed at fifteen sampling stations spanning the continental shelf and the

western Coral Sea (Fig. 1). Abundance along this transect was assessed over four months, October to January, during two austral summers, 1990/91 and 1991/92. At each station, the abundance of juvenile squid was determined at two depths by deploying two pairs of light-traps. In each pair, one light-trap was suspended immediately below the surface while the other light-trap was set deeper. In 1990/91, all deep light-traps were suspended 20 m below the surface. In 1991/92, the deep light-traps were suspended within 5 m of the bottom to a maximum of 100 m in the Coral Sea.

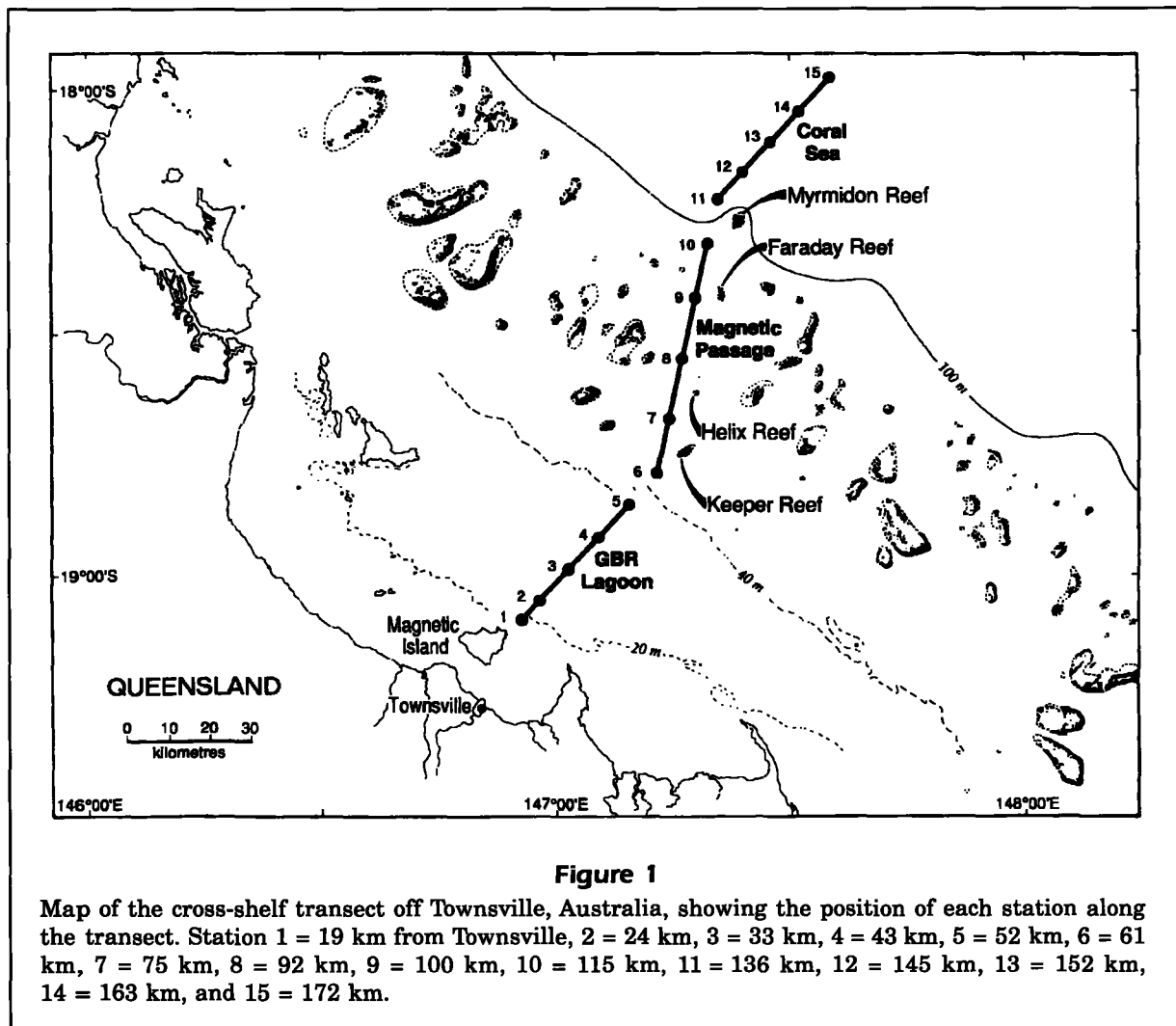
In all deployments, the two pairs of light-traps were released approximately 300 m apart and allowed to drift for one hour. Allowing the traps to drift in the water minimized potential problems with differential water movement among stations. The use of drifting light-traps has been shown to be a more effective way of catching pelagic organisms than anchored light-traps in open water (Thorrold, 1992). After one hour, the four light-traps were retrieved and the entire catch was fixed and preserved in 100% ethanol. Each evening the first light-trap was deployed after 1930 hours (Eastern Standard Time) and the last light-trap retrieved before 0430 hours. Travel time between each station allowed only five cross-shelf stations to be sampled per night. Thus, each night's activity concentrated on one of the two continental shelf habitats or the Coral Sea. Each monthly cruise consisted of nine nights during which time each of the 15 stations was sampled three times. However, sea conditions were not always favorable. Sampling effort at each station is shown in Table 1.

It was not logistically possible to sample all stations in each habitat simultaneously. Therefore, time of night is confounded with station position. Haphazard selection of the first station sampled each night ensured that no station was consistently sampled at the same time on all nights. Cruises were scheduled to include the new moon because this is the lunar phase when light attraction has proved most effective for fishes and various invertebrates (Milicich, 1992). Temperature and salinity profiles of the water column were collected at each station by using a Seabird Conductivity Temperature Device during the 1991/92 summer.

Concurrent with the summer cross-shelf sampling, light-traps were anchored within 100 m of the southeasterly side (weather-side) of four reefs; Keeper, Helix, Faraday, and Myrmidon, to sample near-reef water (Fig. 1). The use of drifting light-traps near the reefs was not possible. During the summer of 1990/91, four light-traps were anchored at each reef; three immediately below the surface

<sup>1</sup> C. C. Lu, Museum of Victoria, Australia, pers. commun. 1990.

<sup>2</sup> J. Yeatman, James Cook Univ., Australia, unpubl. data 1993.



and one at 20 m below the surface. In 1991/92, an extra light-trap was added at 20 m. The anchored light-traps had an automatic timer, enabling the lights to be switched on and off automatically at predetermined periods during the night. Each light-trap on the reef fished for a total of three hours per night; lights came on for one hour at 2200 hours, 2400, and 0300 hours. Light-traps at all reefs were emptied the following day.

Squid were identified in the laboratory and the dorsal mantle length recorded for each individual. Individuals were measured within 14 days of preservation in 100% ethanol. A comparison of measurements of individuals (ranging in size from 5.3 mm to 29.5 mm) before and 14 days after preservation found that shrinkage was on average 0.5 mm.

Abundance patterns of the two *Photololigo* species during the two summers of sampling were examined by using 'planned comparisons,' where specific pregenerated hypotheses were examined (Day and

Quinn, 1989). For each species we were interested in differences in abundance between years, locations, and depths.

To examine seasonality of juvenile *Photololigo* sp. A, the inshore station (19 km) was sampled during the austral winter months of May, June, July, and August 1991. Three sites at this station were sampled with four shallow and four deep (13-m) light-traps. Sites were sampled during the period of the new moon, on five nights in May and three nights in June, July, and August. Densities in summer and winter months were compared by using an unbalanced one-way analysis of variance (ANOVA), with month as the factor analyzed. Values in each light-trap for nights and sites within a month were treated as replicates.

To determine whether vertical migration might influence horizontal distribution patterns we examined the size structure of *Photololigo* sp. A at two depths during the night. On at least one occasion

Table 1

Total sampling effort for *Photololigo* spp. in each month in light-trap hours (and number of nights sampled) at each station during the two summers of sampling.

Year and month	Distance (km) from Townsville															Total no. sampled
	19	24	33	43	52	61	75	92	100	115	136	145	152	163	172	
<b>1990</b>																
Oct	8(2)	15(4)	16(4)	12(3)	16(4)	15(4)	4(1)	4(1)	4(1)	4(1)	12(3)	10(3)	10(3)	10(3)	10(3)	150(40)
Nov	12(3)	12(3)	12(3)	0(0)	16(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	4(1)	4(1)	144(35)
Dec	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	3(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	67(17)
<b>1991</b>																
Jan	12(3)	12(3)	12(2)	12(2)	12(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	4(2)	8(2)	8(2)	136(32)
Oct	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	124(31)
Nov	12(3)	12(3)	11(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	4(1)	4(1)	4(1)	4(1)	4(1)	139(35)
Dec	12(3)	10(3)	11(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	121(31)
<b>1992</b>																
Jan	12(3)	12(3)	12(3)	11(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	123(31)
Total	88(22)	93(24)	90(22)	75(18)	96(22)	87(22)	64(16)	63(16)	64(16)	64(16)	48(12)	46(12)	42(12)	42(11)	42(11)	1004(254)

in each month of the 1991/92 sampling period the 19- and 24-km stations were sampled both early and late in the night. The samples were separated into early (captured before 2400 hrs) and late (captured after 2400 hrs). By combining data from stations, across nights and months, it was possible to compare the size distributions between depths and time of night. A multiway-frequency analysis was used to determine the effect of time of night and depth on the size-frequency distribution.

## Results

### Distribution patterns

Juvenile *Photololigo* individuals were predominantly caught within 52 km of the mainland (Fig. 2). The few individuals found farther offshore were in the Magnetic Passage (five individuals) and on the reefs (six individuals). *Photololigo* species were not found in the Coral Sea. *Photololigo* sp. A was numerically the most abundant of the two species during both summers (Fig. 2); 856 individuals were caught in 181 hours of light-trapping (4.73 individuals caught per hour), compared with 379 *Photololigo* sp. B caught in 348 hours of light-trapping (1.09 individuals per hour). Catch per hour of light-trapping was greatest for *Photololigo* sp. A, especially at the 24-km station. The catch per unit of effort for *Photololigo* sp. B was greater at the 33-km station (Table

2). Overall, *Photololigo* sp. A juveniles were present in higher numbers at the 24-km station in the surface waters (Table 3). This pattern was consistent in both years, but higher numbers were caught in 1991/92 (Table 3), largely because of very high catches in December 1991 (Fig. 2). In comparison, highest numbers of *Photololigo* sp. B were consistently found at the 33-km station and abundance levels tended to decrease farther offshore (Fig. 2). Overall, *Photololigo* sp. B demonstrated no difference in abundance levels between the two years (Table 4). In contrast to *Photololigo* sp. A, juvenile *Photololigo* sp. B was more abundant deeper in the water column (Table 4). Farther offshore, *Photololigo* sp. B juveniles were present in very low numbers and were caught only in the deep light-traps (Fig. 2).

*Photololigo* sp. A ranged in size from 2.6 to 47.9 mm. The size-frequency distributions at the two depths were not significantly different between the 19-km and 24-km stations ( $\chi^2=12.28$ ;  $df=9$ ;  $P=0.1979$ ) (Fig. 3). There was no systematic change in the size-frequency distribution of *Photololigo* sp. A during either summer (Fig. 4). A modal shift in the size-frequency distribution in January 1992 suggested that fewer small individuals were available to be caught. However, catches were very low in this month.

*Photololigo* sp. B ranged in size from 3.6 to 61.6 mm (Fig. 3). From the size-frequency distributions it was clear that larger juveniles were found farther offshore and deeper in the water column (Fig. 3). No

modal shift in the size-frequency distribution during the summers was apparent (Fig. 4). However, catches were low in most months.

The multiway-frequency analysis established that the size-frequency distribution of juvenile *Photololigo* sp. A at both depths changed as a function of time of night (Table 5). Small juveniles dominated in the surface waters, but larger individuals were generally found closer to the benthos (Fig. 5). During the night, the relative abundance of small individuals decreased at both depths. Close to the

benthos an increase in large individuals was evident. There was no discernible pattern of vertical migration; however, combining data across months to increase the number of juveniles in the analysis removed the possibility of detecting vertical migration in any one month.

The number of *Photololigo* sp. A juveniles captured during the winter months was similar to most of the summer monthly catches (Fig. 6); although winter catches never reached levels such as those seen in December 1991 (Table 6). The large number of small juveniles captured over the winter (Fig. 6) indicates that *Photololigo* sp. A spawns and hatches in both seasons. A similar size range was captured at each sampling during the summer months (Fig. 7).

### Physical parameters

Both temperature and salinity decreased nonlinearly across the lagoon; discontinuities in both variables occurred midway across the Lagoon (Fig. 8). Temperature or salinity discontinuities were detected on at least six out of nine nights between the 33-km station and one or both of the neighbouring stations. This suggested that in the lagoon the water mass was heterogenous and may have influenced the distribution patterns of juvenile squid.

Salinity-temperature profiles of the water column at each station indicated thermoclines were present on some nights (Table 7). A thermocline was defined as a temperature change greater than 0.5°C between surface and bottom water; differences as great as 3°C were detected during January. However, these thermoclines were a temporally and spatially unstable feature of the water column, possibly due to variable wind conditions and the shallow body of water being sampled.

### Discussion

Light-traps have provided a technique by which spatio-temporal distribution patterns of two *Pho-*

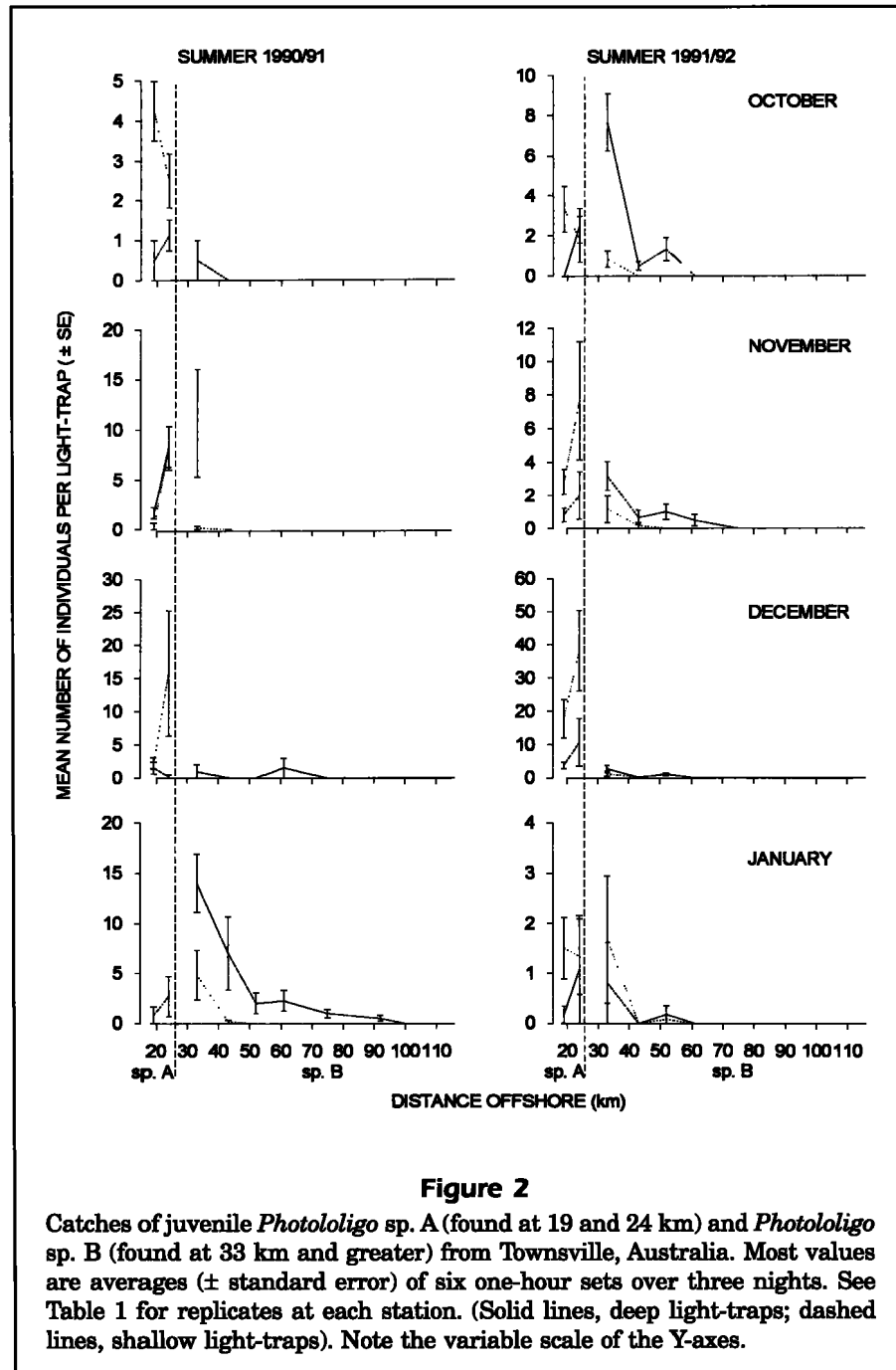


Figure 2

Catches of juvenile *Photololigo* sp. A (found at 19 and 24 km) and *Photololigo* sp. B (found at 33 km and greater) from Townsville, Australia. Most values are averages ( $\pm$  standard error) of six one-hour sets over three nights. See Table 1 for replicates at each station. (Solid lines, deep light-traps; dashed lines, shallow light-traps). Note the variable scale of the Y-axes.

*tololigo* species can be described. Identification of *Photololigo* species using allozyme electrophoresis suggests that the two species are separated geographically across the Great Barrier Reef Lagoon (Yeatman and Benzie, in press). This separation occurs in a region of the coastal lagoon where temperature-salinity data indicate heterogeneity. High numbers of juvenile *Photololigo* sp. A at stations close to the mainland suggests that spawning grounds for this species may be close to the coast, a feature typical for loliginid squid (Mangold, 1987). Furthermore, the presence of small and large individuals during summer and winter months indicates that spawning, hatching, and recruitment are not seasonal events. This characteristic may be more common for tropical species that tend to have shorter lifespans than temperate species (Jackson and Choat, 1992). Large numbers of small juveniles collected during the winter may be a function of slower growth during the winter (Jackson and Choat, 1992). Little is known about *Photololigo* sp. B adults; however, the presence of juveniles in this region suggests that an adult population does occur in the Townsville region and that spawning occurs throughout the summer. The identification of juvenile *Photololigo* was confirmed on a subsample of specimens captured during the summer. Conclusions drawn from this study are based upon the assumption that the offshore distribution pattern of the two species was consistent in all other months of sampling.

Juvenile squid are not easily sampled with towed nets (Vecchione, 1979; Vecchione and Gaston, 1985; Holme, 1974). They have highly developed sensory and locomotor systems (Boletzky, 1974) and it is likely that these animals are often undersampled because of net avoidance. Choat et al. (1993) have shown that plankton nets select for small larval fish, but larger

fish are captured from the same water column by using light attraction. Thorrold (1992), as well as this study, showed that light-traps are a useful technique for capturing juvenile squid. However, like most sampling techniques, the light-traps have biases. One problem is that light-traps sample an unknown volume of water. Nonetheless, they have

**Table 2**

Catch per hour of light-trapping for each *Photololigo* species across the Great Barrier Reef Lagoon for eight months of summer sampling. *Photololigo* sp. A at stations 19 km and 24 km and *Photololigo* sp. B farther offshore.

Month	Species A		Species B				Total
	19km	24km	33km	43km	52km	61km	
<b>1990</b>							
Oct	2.38	1.81	0.25	0	0	0	0.62
Nov	0.75	8.25	5.42	—	0	0	2.88
Dec	1.88	8.00	0.50	0	0	0.75	2.63
<b>1991</b>							
Jan	0.42	1.33	9.42	3.58	1.00	1.13	2.91
Oct	1.67	2.17	4.25	0.25	0.67	0	1.50
Nov	1.83	4.83	2.17	0.42	0.50	0.25	1.67
Dec	10.67	24.42	1.92	0.17	0.50	0	6.28
<b>1992</b>							
Jan	0.83	1.75	1.67	0.17	0.08	0	0.75
Total	2.59	6.31	3.30	0.72	0.36	0.17	2.33

**Table 3**

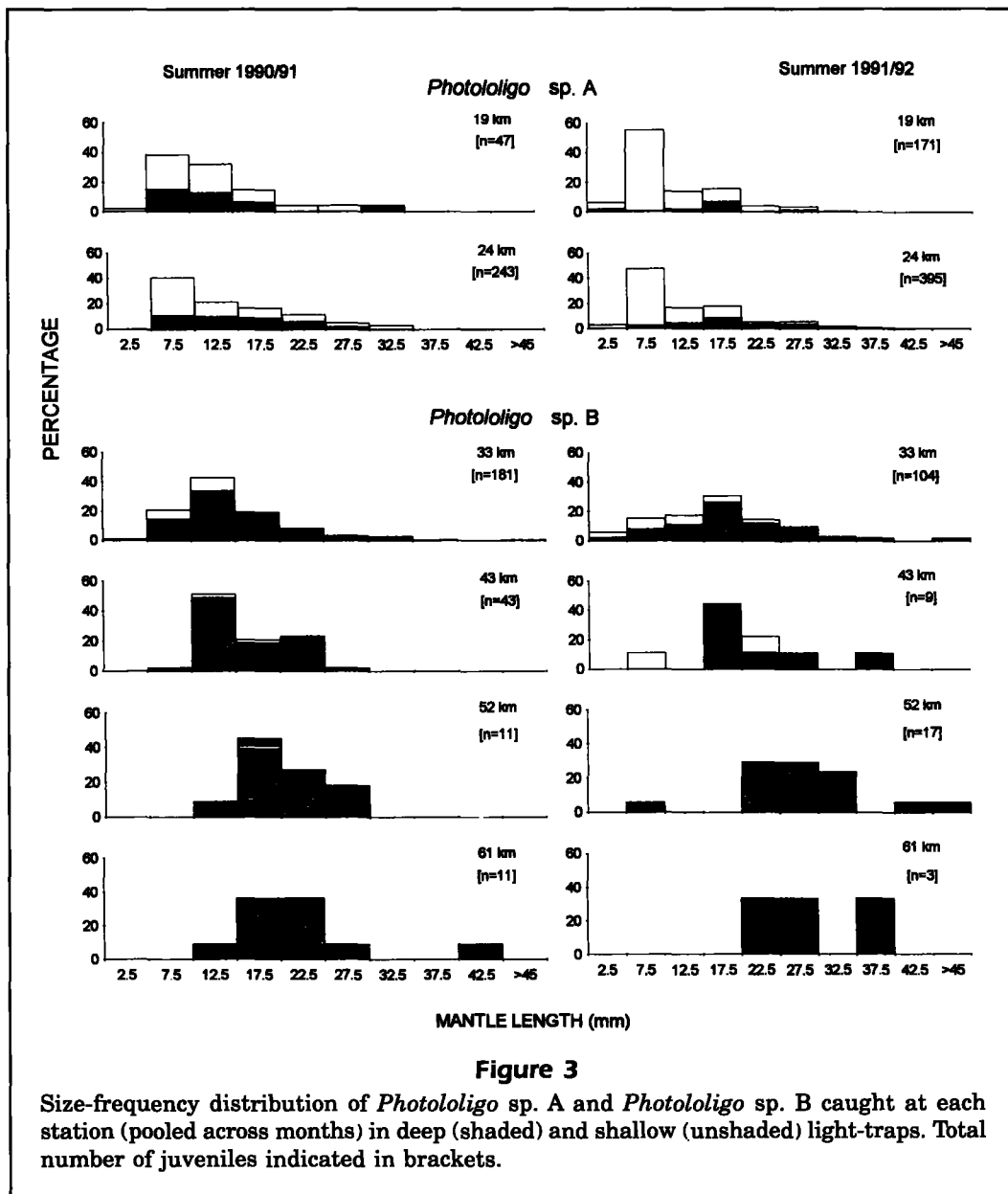
Planned comparisons of juvenile *Photololigo* sp. A densities between depths, years, and sites.

Contrast	df	Contrast sums of squares	Mean squares	F-value	P>F
Depths	1	9.8165	9.8165	12.20	0.0006
Years	1	3.7565	3.7565	4.67	0.0320
Sites	1	8.6892	8.6892	10.80	0.0012
Residual	177	142.3838	0.8044		

**Table 4**

Planned comparisons of juvenile *Photololigo* sp. B densities between depths and years.

Contrast	df	Contrast sums of squares	Mean squares	F-value	P>F
Depths	1	17.0607	17.0607	37.85	0.0001
Years	1	0.0438	0.0438	0.10	0.7554
Residual	335	148.7448	0.4507		



**Figure 3**

Size-frequency distribution of *Photololigo* sp. A and *Photololigo* sp. B caught at each station (pooled across months) in deep (shaded) and shallow (unshaded) light-traps. Total number of juveniles indicated in brackets.

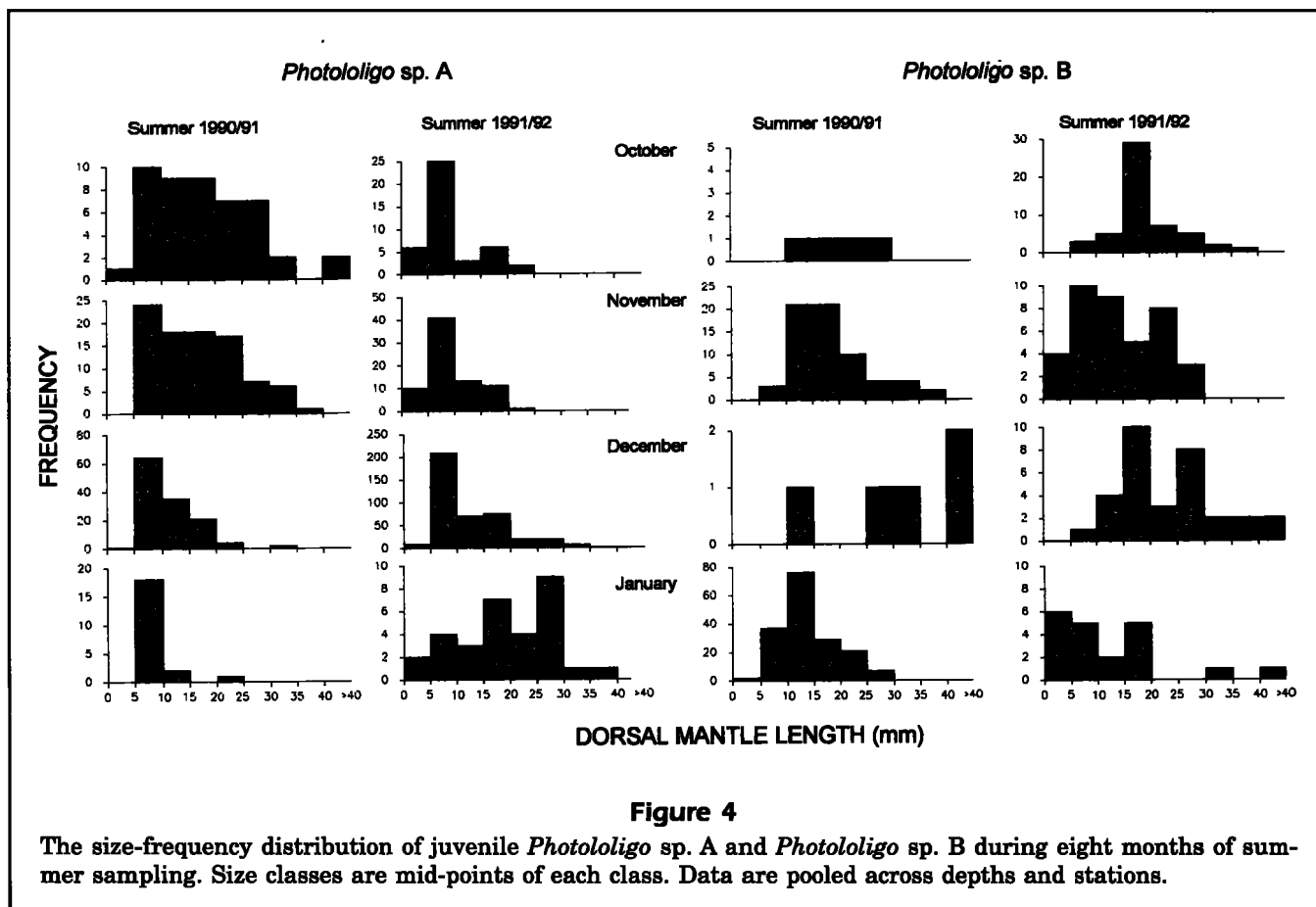
**Table 5**

Results of the multiway frequency analysis to examine changes in the size distribution of *Photololigo* sp. A between time of night and depth.

Source	df	$\chi^2$	P
Depth	1	92.8	0.00
Time	1	25.57	0.00
Depth $\times$ Time	1	0.19	0.66

been validated as useful devices for monitoring relative abundance patterns in larval supply of pelagic juvenile fish at fixed locations (Milicich et al., 1992).

Great care needs to be exercised when interpreting catch rates from different locations because changes in water transparency can bias light-trap efficiency. Similarly, it is not possible to quantitatively compare catches from drifting and anchored light-traps (Thorrold, 1992). This is because the former act as lagrangian drifters and sample photopositive organisms from within a constant light pool. In contrast, the moored light-traps experience a variable water flow that may greatly increase the volume of water swept in an hour of sampling. Despite more intensive sampling on the reefs, catches of *Photololigo* were low and we conclude that spawning does not occur near the reefs and that juvenile *Photololigo* individuals are concentrated in the lagoon. In the



present study, a gradient of turbidity across the shelf makes it possible that inshore catches would underestimate abundance if corrected for diminishing light-pools. However, if the error was significant, it would only exaggerate, not diminish, our observation that juvenile squid were more abundant within the coastal lagoon.

High catches of juvenile squid in the coastal lagoon were at locations where discontinuities were often observed in surface temperature and salinity. Hydrodynamic modelling of this region suggests that the coastal lagoon is often subject to velocity shear (King and Wolanski, 1992). Water in the lagoon typically flows southward under the influence of the poleward East Australian Current, which pushes water onto the outer shelf and through the reef matrix, especially through channels like the Magnetic Passage. Under typical south-easterly wind conditions the shallow body of water trapped against the coast moves in the opposite direction, northwards. The result is a velocity shear between the two water masses and a

**Table 6**  
Analysis of variance examining differences between densities of *Photololigo* sp. A at the 19 km station between summer months of 1990/91 and 1991/92 and winter months of 1991.

Source	df	Contrast sums of squares	Mean squares	F-value	P>F
Month	11	1118.200	101.654	9.55	0.0001
Residual	214	2277.910	10.644		

zone of low residual displacement. Modelling studies suggest that the cross-shelf location of this feature, referred to as a separation front (King and Wolanski, 1992), will shift seawards as the wind strength increases and vice versa. This mobility of the frontal region is consistent with the daily and monthly variability of salinity and temperature at the surface indicated by our physical monitoring during the second summer.

This low-shear zone is identified as a significant place for aggregation of planktonic organisms. Cross-shelf studies have shown highest abundances of larval reef fishes in a similar location near the



center of the Great Barrier Reef Lagoon (Thorrold, in press). These catches included individuals taken from reefs farther offshore, as well as piscivorous larvae of various scombrids from inshore (Thorrold, 1993). It is not clear whether aggregation of these stages is passive, due to hydrodynamics, or the result of attraction to the coastal boundary area by enhanced secondary productivity in this frontal zone

(Thorrold and McKinnon, 1992). This discontinuity may be a mechanism separating the two *Photololigo* species geographically. The separation of juvenile cephalopod species in the Gulf Stream east of New England is thought to be closely related to meso-scale hydrological features (Vecchione and Roper, 1986). The importance of hydrological features in aggregating juvenile squid has been identified in a

number of species (Rodhouse and Clarke, 1985; Brunetti and Ivanovic, 1992; Rodhouse et al., 1992). This suggests that these areas are ecologically important for juvenile squid.

The second way in which shelf-scale hydrodynamics affects the stability of the water column is the intrusion of upwelled waters from the shelf-break driven onto the shelf by variations in the speed and position of the East Australian Current. These cold intrusions can be tracked into the Great Barrier Reef Lagoon (King and Wolanski, 1992) and the strong thermal stratification observed in January 1992 was consistent with an intrusion at this time. A cold bottom layer at 33 km was evident on one night in November, but the inner stations were not stratified. The presence of juvenile *Photololigo* at most stations in all months, despite a range of physical conditions, suggests juvenile *Photololigo* can tolerate substantial environmental variation. This tolerance is consistent with a nonseasonal reproductive strategy, which is

essential for a species that lives for only four months.

During the night there was little evidence of a pronounced vertical migration such as the mass aggregations of juvenile *Loligo* spp. on the benthos (Vecchione and Gaston, 1985) or the general movement to the surface by juvenile *L. pealei* (Vecchione, 1981). The absence of vertical movement during the night suggests that the observed ontogenetic shift of *Photololigo* sp. B farther offshore and deeper is real and not a product of location confounded with time of night when sampling occurred. However, as was noticed in the catch-per-unit-of-effort values, both species are caught in relatively low numbers; hence, conclusions based on small differences that are not significantly different are limited. There was a problem with low numbers in all spatial and temporal trends described. However, this was a preliminary study with just two hours of sampling at each station per night. More intensive sampling in bound-

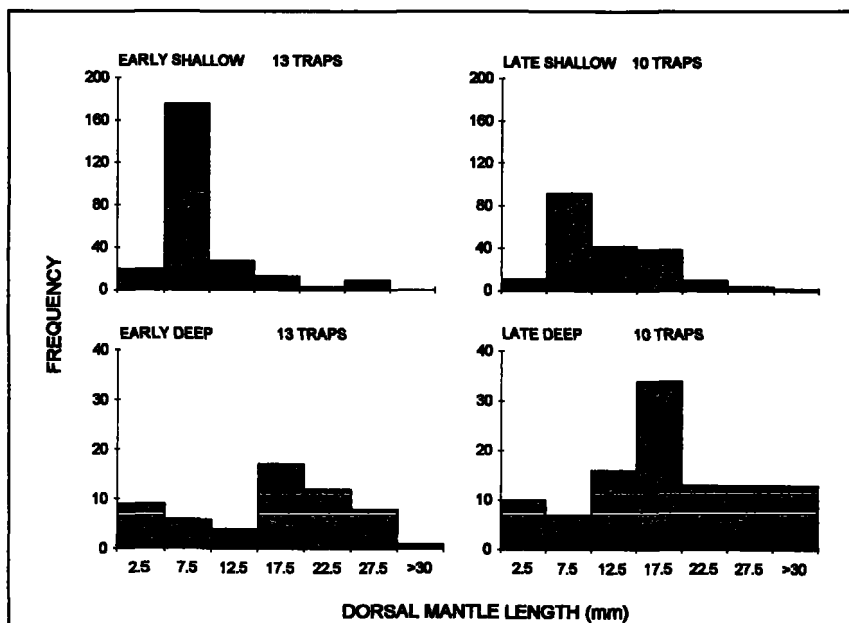


Figure 5

Size-frequency distributions of juvenile *Photololigo* sp. A from the two inshore stations at two sampling depths (pooled across the summer months 1991/92), captured early (before 2400 hr) and late (after 2400 hr) in the night.

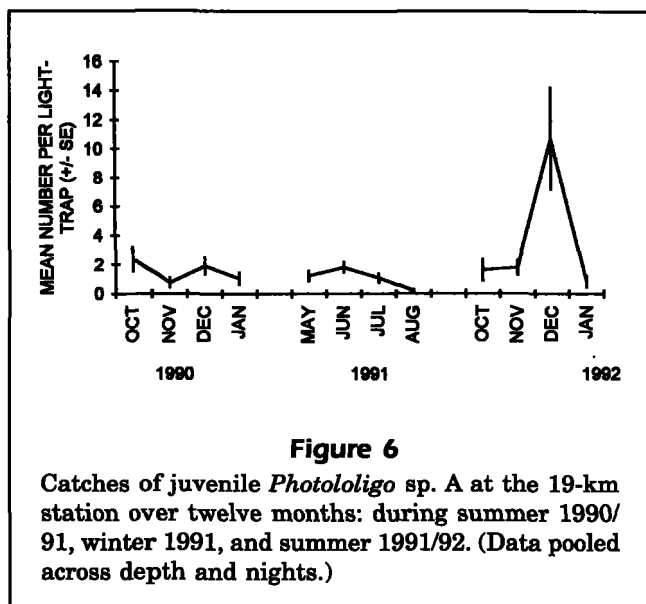


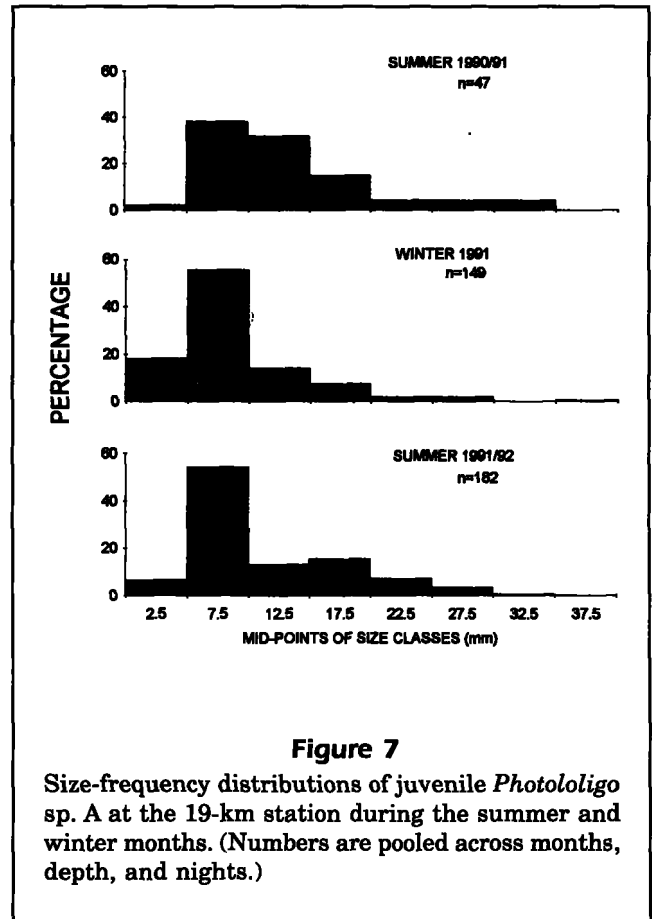
Figure 6

Catches of juvenile *Photololigo* sp. A at the 19-km station over twelve months: during summer 1990/91, winter 1991, and summer 1991/92. (Data pooled across depth and nights.)

**Table 7**

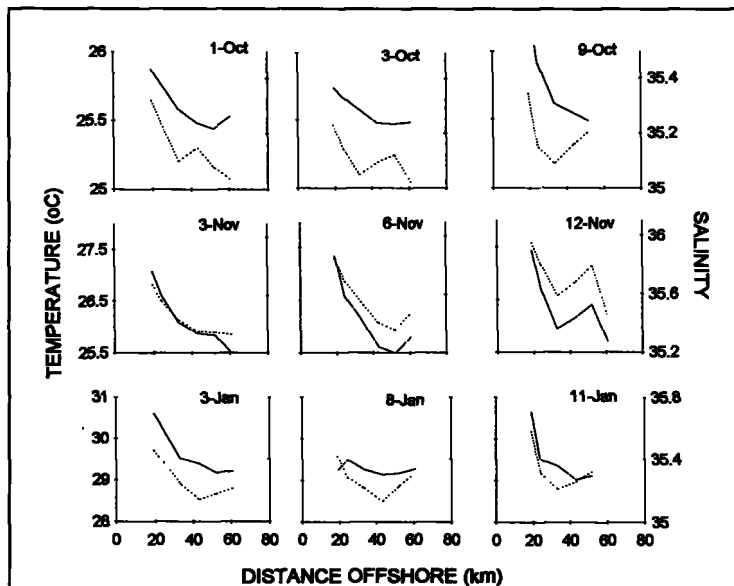
Depth of the thermocline (m) at each station on each night of sampling during the three months of the 1991/92 summer.

Sampling period and situation	Depth of thermocline		
	Day 1	Day 2	Day 3
<b>October 1991</b>			
19 km	14	11	Absent
24 km	13	14	Absent
33 km	10	13	Absent
43 km	10	Absent	Absent
52 km	25	Absent	Absent
61 km	31	Absent	—
<b>November 1991</b>			
19 km	Absent	Absent	Absent
24 km	Absent	Absent	Absent
33 km	Absent	Absent	20
43 km	Absent	Absent	22
52 km	Absent	Absent	25
61 km	Absent	Absent	29
<b>January 1992</b>			
19 km	7	7	9
24 km	9	9	9
33 km	11	13	12
43 km	15	15	18
52 km	28	24	27
61 km	31	47	—



**Figure 7**

Size-frequency distributions of juvenile *Photololigo* sp. A at the 19-km station during the summer and winter months. (Numbers are pooled across months, depth, and nights.)



**Figure 8**

Surface temperature (dashed) and salinity (solid) profiles across the Great Barrier Reef Lagoon for each night of sampling in October and November 1991 and in January 1992. The Conductivity Temperature Device failed during the December cruise.

ary waters, both vertical and horizontal, is needed to understand how juvenile squid react to the physical environment. This study has shown that light-traps are useful devices for catching juvenile squid, providing a basis for a more intensive study of the early life-history of squid.

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## Literature cited

- Boletzky, S. v.**  
 1974. The 'larvae' of Cephalopoda: a review. *Thalassia Jugoslavica* 10:45-76.  
 1977. Post-hatching behaviour and mode of life in cephalopods. *Symp. Zool. Soc. Lond.* 38:557-567.
- Boyle, P. R.**  
 1990. Cephalopod biology in the fisheries context. *Fish. Res.* 8:303-321.
- Brunetti, N. E., and M. L. Ivanovic.**  
 1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. *ICES J. mar. Sci.* 49:175-183.
- Choat, J. H., P. J. Doherty, B. A. Kerrigan, and J. M. Leis.**  
 1993. A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. *Fish. Bull.* 91:195-209
- Day, R. W., and G. P. Quinn.**  
 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59:433-463
- Doherty, P. J.**  
 1987. Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. *Bull. Mar. Sci.* 41:423-431.
- Holme, N. A.**  
 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *J. mar. biol. Assoc. U.K.* 54:481-503.
- Jackson, G. D., and J. H. Choat.**  
 1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. *Can. J. Fish. Aquat. Sci.* 49:218-228.
- King, B., and E. Wolanski.**  
 1992. Coastal dynamics along a rugged coastline. In D. Prandle (ed.), *Dynamics and exchanges in estuaries and the coastal zone*, p. 577-598. *Coastal and Estuarine Studies* 74, Springer-Verlag.
- Mangold, K.**  
 1987. Reproduction. In P. R. Boyle (ed.), *Cephalopod life cycles. Vol 2: Comparative reviews*, p. 157-200. Academic Press, NY.
- Milicich, M. J.**  
 1992. Light-traps: a novel technique for monitoring larval supply and replenishment of coral reef fish populations. Unpubl. Ph.D. thesis, Griffith University, 127 p.
- Milicich, M. J., M. G. Meekan, and P. J. Doherty.**  
 1992. Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). *Mar. Ecol. Prog. Ser.* 86:153-166.
- Rodhouse, P. G., and M. R. Clarke.**  
 1985. Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. *Vie Milieu* 35:223-230.
- Rodhouse, P. G., C. Symon, and E. M. C. Hatfield.**  
 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 89:183-195.
- Thorrold, S. R.**  
 1992. Evaluating the performance of light traps for sampling small fish and squid in open waters of the central Great Barrier Reef lagoon. *Mar. Ecol. Prog. Ser.* 89:277-285.  
 1993. Post-larval and juvenile scombrids captured in light traps: preliminary results from the central Great Barrier Reef lagoon. *Bull. Mar. Sci.* 52:631-641.  
 In press. Coupling of pre-settlement reef fish distribution and hydrography in the central Great Barrier Reef lagoon. *Proc. Seventh International Coral Reef Symposium, 1992.*
- Thorrold, S. R., and A. D. McKinnon.**  
 1992. Biological significance of the coastal boundary layer off Townsville, North Queensland. In D. A. Hancock (ed.), *Larval biology. Australian Society for Fish Biology Workshop, Hobart 1991.* Bureau of Rural Resources Proceedings 15:104-109.
- Vecchione, M.**  
 1979. Larval development of *Illex Steenstrup*, 1880, in the northwestern Atlantic, with comments on *Illex* larval distribution. *Proc. Biol. Soc. Wash.* 91:1060-1075.  
 1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda; Myopsida). *J. Shellfish Res.* 1:171-180.  
 1987. Juvenile ecology. In P. R. Boyle (ed.), *Cephalopod life cycles. Vol 2: Comparative reviews*, p. 61-84. Academic Press, NY.
- Vecchione, M., and G. R. Gaston.**  
 1985. In-situ observations on the small-scale distribution of juvenile squids (Cephalopoda: Loliginidae) on the northwest Florida shelf. *Vie Milieu* 35:231-235.
- Vecchione, M., and C. F. E. Roper.**  
 1986. Occurrence of larval *Illex illecebrosus* and other young cephalopods in the slope water/Gulf Stream interface. *Proc. Biol. Soc. Wash.* 99:703-708.
- Voss, G. L.**  
 1983. A review of cephalopod fisheries biology. *Mem. Natl. Mus. Victoria* 44:229-241.
- Yeatman, J., and J. A. H. Benzie.**  
 In press. Genetic structure and distribution of *Photololigo* in Australia. *Mar. Biol.*
- Young, R. E., and R. F. Harman.**  
 1988. "Larva," "paralarva," and "subadult" in cephalopod terminology. *Malacologia* 29:201-207.