

# Distributions of young cephalopods in the tropical waters of Western Australia over two consecutive summers

George D. Jackson, Mark G. Meekan, Simon Wotherspoon, and Christine H. Jackson

Jackson, G. D., Meekan, M. G., Wotherspoon, S., and Jackson, C. H. 2008. Distributions of young cephalopods in the tropical waters of Western Australia over two consecutive summers. – *ICES Journal of Marine Science*, 65: 140–147.

Cephalopod paralarvae and juveniles were sampled with light traps deployed at the surface and deeper in the southern NW Shelf and on Ningaloo Reef off Western Australia during two consecutive summers. One cross shelf transect (Exmouth) was sampled in the late spring and summers of 1997/1998 (summer 1) and 1998/1999 (summer 2), and a second cross shelf transect (Thevenard) and a long-shore transect (Ningaloo) along the Ningaloo Reef were sampled in summer 2. Species captured in the order of abundance were octopods, *Photololigo* sp., *Sepioteuthis lessoniana*, and *Sthenoteuthis oualaniensis*. Most were captured in shallow traps except for *Photololigo* sp., which was common in both shallow and deep traps with larger animals found in deeper water. The presence of *Idiosepius pygmaeus* in deep water off Ningaloo Reef revealed the species to be eurytopic, inhabiting a wider range of habitats than previously known. *Photololigo* sp. and *S. lessoniana* were more abundant inshore, and octopods were especially abundant on mid-depth stations of the Exmouth transect, probably because of the turbulent mixing and increased productivity there. Fewer *S. oualaniensis* were caught during the first summer on the Ningaloo transect ( $n = 5$ ) than during the second summer ( $n = 79$ ).

**Keywords:** cephalopods, light traps, Ningaloo, squid.

Received 8 June 2007; accepted 24 November 2007; advance access publication 15 January 2008.

G. D. Jackson and C. H. Jackson: Institute of Antarctic and Southern Ocean Studies, University of Tasmania, Private Bag 77, Hobart, Tasmania 7001, Australia. M. G. Meekan: Australian Institute of Marine Science, Darwin Office, PO Box 40197, Casuarina MC, Northern Territory 0811, Australia. S. Wotherspoon: School of Maths and Physics, University of Tasmania, Private Bag 37, Hobart, Tasmania 7001, Australia. Correspondence to G. D. Jackson: tel: +61 3 6226 2975; fax: +61 3 6226 2973; e-mail: [george.jackson@utas.edu.au](mailto:george.jackson@utas.edu.au)

## Introduction

The biology of cephalopod paralarvae (Young and Harman, 1988) and juveniles is of interest because of the ecological importance of the taxon in many marine ecosystems. All cephalopods serve as predators within marine food chains but perhaps are even more important as prey for a variety of vertebrate predators, particularly in open-water oceanic ecosystems (Kubodera *et al.*, 2007; Lansdell and Young, 2007). However, the role of the younger stages and paralarvae in marine trophodynamics is still poorly understood. Paralarvae tend to be associated with specific oceanographic features (Rodhouse *et al.*, 1992), and because of their high metabolism, feeding rates, and rapid growth (Jackson and O'Dor, 2001), they can rapidly reflect changes in their immediate ocean environment. Therefore, recruitment success of the younger stages can provide real-time data on oceanographic conditions, and additionally help to predict adult recruitment (Waluda *et al.*, 1999, 2001, 2004).

The overriding influence of environmental variables on both the successful recruitment of paralarvae and the growth rate is now established for *Loligo opalescens* in the California Current. For example, surveys of *L. opalescens* paralarvae off southern California have revealed dramatic increases in species abundance following periods of very low abundance during *El Niño* events (Zeidberg and Hamner, 2002; Ish *et al.*, 2004). Environmental conditions strongly influence both the abundance and the growth of *L. opalescens* under different oceanographic regimes

(Jackson and Domeier, 2003; Reiss *et al.*, 2004). Moreover, density indices of paralarval *L. opalescens* have assisted in predicting adult recruitment (Zeidberg *et al.*, 2006). By focusing research efforts on the paralarvae of pelagic cephalopods, it is feasible, therefore, to obtain information linking the biological community with oceanographic processes. However, such studies require techniques for consistently sampling these early stages of the life cycle.

Despite advances, there continue to be challenges in sampling the young stages of cephalopods (especially post-paralarval juveniles) because of their ability to avoid towed nets and their patchy distribution in the marine environment (Okutani and McGowan, 1969; Recksiek and Kashiwada, 1979; Wormuth and Roper, 1983; Collins *et al.*, 2002). Recently, light traps have been shown to be a successful means of collecting these life history stages and have been used in the waters of the Great Barrier Reef (GBR) to describe distribution patterns (Thorrold, 1992; Moltshaniwskyj and Doherty, 1994, 1995). Although light traps cannot, as yet, provide data on densities of organisms sampled (Meekan *et al.*, 2000), cephalopods are generally known for their attraction to lights and appear to enter traps readily. The technique can therefore provide a useful method of assessing relative patterns of distribution and abundance. The systematic use of light traps in the future may prove to be better than net surveys at sampling paralarvae and juveniles of cephalopods, and may assist in obtaining samples in known spawning areas or in oceanographic regions where plankton is concentrated.

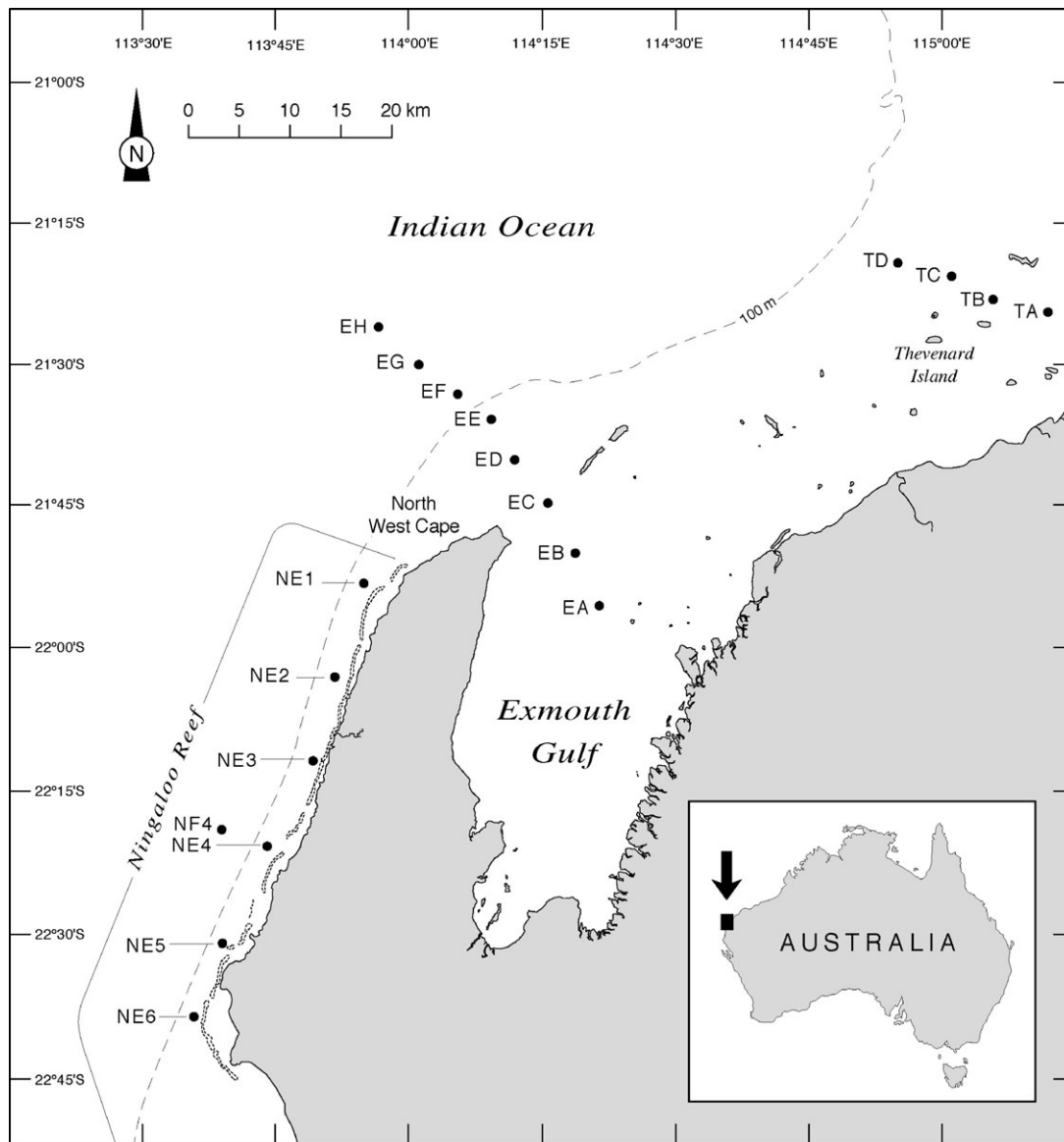
The cephalopods analysed here were sampled as part of a larger study of seasonal differences, cross shelf distributions, and the diets of fish larvae and invertebrates over the southern NW Shelf and Ningaloo Reef region of Western Australia (Meekan *et al.*, 2001, 2003, 2006; Wilson *et al.*, 2003a, b; Sampey *et al.*, 2004). Sampling was during the late spring–summer periods of 1997/1998 and 1998/1999, and provided a relatively large sample of small pelagic cephalopods from the region.

The two consecutive seasons provided a unique opportunity to study the distribution and abundance of cephalopod paralarvae and juveniles under differing physical and biological conditions. Austral summer 1997/1998 was characterized by an *El Niño* event that resulted in cooler water conditions and enhanced productivity attributable to enhanced upwelling. In contrast, the 1998/1999 summer experienced *La Niña* conditions that caused well-developed water column stratification, warmer temperatures, and less productivity (Meekan *et al.*, 2003). The current study tested the efficacy of light traps for sampling paralarvae and

juveniles of cephalopods off the southern NW Shelf region of Western Australia, documented the species present in the water column and their cross shelf distribution, and finally, analysed identifiable differences between species composition and abundance between the two seasons of very different oceanographic conditions.

**Methods**

Cephalopods were collected by light traps during ten oceanographic cruises between October and March of 1997/1998 (summer 1) and 1998/1999 (summer 2). Eight stations were sampled on one cross shelf transect (Exmouth Gulf, EA–EH) during both years. Each year, five cruises sampled the Exmouth transect (cruises 1–5 in summer 1, cruises 6–10 in summer 2). Two additional transects were included during summer 2. A cross shelf transect (Thevenard) was sampled ~80 km north of the Exmouth Gulf transect, and consisted of four stations (TA–TD) all within the 100-m depth contour. A further transect was



**Figure 1.** Map showing the region where transects were located for deployment of the light traps in this study. The Exmouth transect stations are designated by “E”, Thevenard stations by “T”, and Ningaloo stations by “N”.

sampled along the front of Ningaloo Reef and consisted of six stations inside (NE1–NE6) and one (NF4) outside the 100 m isobath (Figure 1).

Two light trap designs were used in the study, a large three-chamber trap, and a smaller single-chamber trap (see Figure 1 of Meekan *et al.*, 2001). Both traps mapped spatial distribution of captured fish and invertebrates equally well (Meekan *et al.*, 2001; Wilson *et al.*, 2003a). At each station, light traps were deployed in shallow and deep modes. During the 1997/1998 sampling season, two large and two small traps were deployed at the sea surface, with the trap entrance slits situated ~1 m below the surface. Simultaneously, two large traps were also deployed in deep water (3 m off the bottom or at 75 m in deep water). During the 1998/1999 season, only small traps were used, a pair being deployed in both shallow and deep modes at each station. Trap deployment began in the evening after dark (around 20:00) and ceased before sunrise around 04:30. At each station, traps were released and allowed to drift freely with the current for ~1 h. Either four inshore or four offshore stations were sampled each night, and the order of sampling was alternated each night (i.e. if the sampling ran from inshore to offshore one night, the direction of sampling was reversed the following night). On retrieval of the traps, the collected organisms were removed and preserved immediately in 100% ethanol. Cephalopods were sorted from the catches in the laboratory. Standardized catch rates were calculated by fitting a Poisson generalized linear model to the catch data, using a log effort offset (McCullagh and Nelder, 1989) to adjust for the differential effort. This assumes that catch was proportional to fishing effort. The fitted model was then used to predict catch rates for a standardized effort of 1000 trap h.

## Results

In all, 1889 cephalopods were collected over the two summers (Table 1). Four taxa of squid could be identified to species, two to genus, and two only to family (Sepiolidae and Octopodidae). Octopods were the most abundant cephalopod captured by the traps, accounting for more than half the catches. The octopods were predominantly benthic species, and although there were some pelagic forms, we did not differentiate them and used the

single category in all analyses. *Photololigo* were the next most abundant cephalopod, followed by *Sepioteuthis lessoniana* and *Sthenoteuthis oualaniensis*. All other taxa were captured in low numbers or as single animals (e.g. *Brachioteuthis*).

Length frequency analysis of the three most abundant squid species from the Exmouth transect (Figure 2) over the two summers showed that the traps generally sampled small squid. Data for *S. oualaniensis* were excluded for summer 1 because only five animals were caught. Dorsal mantle length (DML) of *Photololigo* ranged from 3.2 to 74.1 mm, though only a few large specimens were captured, the majority having a DML of <40 mm. There was no marked difference in DML distribution between the two summers. *Sepioteuthis lessoniana* paralarvae collected by the traps were relatively small, with all specimens <15 mm DML. All *S. oualaniensis* (except for two individuals) were <25 mm DML, with animals <10 mm DML abundant. Of the 81 individuals of *S. oualaniensis* captured over the two summers, 27 were rhynchoteuthion paralarvae of DML 5.0–7.2 mm. However, the smallest non-rhynchoteuthion paralarvae captured were 4.6, 5.0, and 5.2 mm.

Fitting a Poisson model to the data weighting by effort revealed strong evidence of a change in catch rate across the two summers on the Exmouth transect, but this was not consistent among taxa (Figure 3). Octopods, *S. oualaniensis*, and *Photololigo* all showed an increase in catch rates in summer 2 compared with summer 1. However, the trend was reversed for *S. lessoniana*, significantly greater catch rates being obtained in the first summer compared with the second summer.

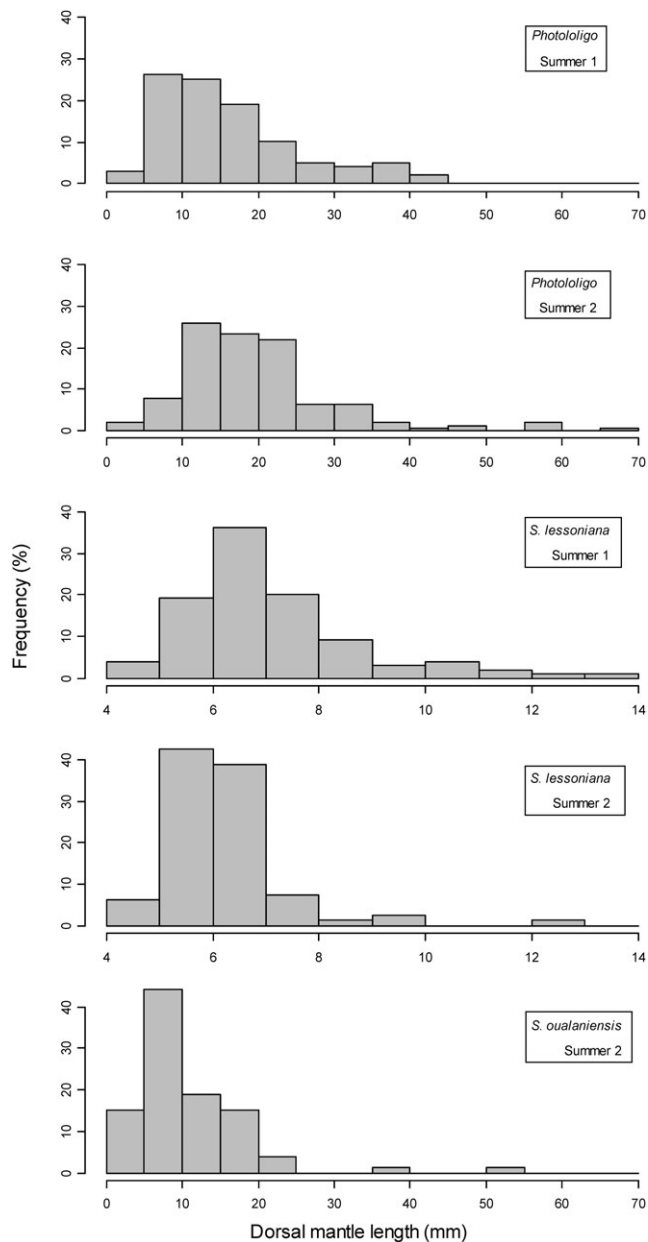
## Cross shelf distributions

### Exmouth

Except for one specimen captured at station EH in summer 1, all the *Photololigo* were collected at inshore stations (EA–EE). Catch rates in summer 2 were much higher inshore at station EA than at other inshore stations, but catch rates in summer 1 at the same station were comparatively low. There was no consistent trend in the rate of capture of *Photololigo* with depth (Figure 4). *Sepioteuthis lessoniana* was also restricted to inshore stations EA–EE. There were better catch rates of this species in the shallow traps, very few being caught in the deep traps during summer 1 and none during summer 2. In both summers,

**Table 1.** Catches of young cephalopods by light traps on different transects in each of the two summers.

Taxon	Exmouth summer 1	Exmouth summer 2	Thevenard	Ningaloo	Total
Sepioidea					
Sepiolid	2	6	2	4	14
Idiosepiidae					
<i>Idiosepius pygmaeus</i>	1	2	1	13	17
Loliginidae					
<i>Photololigo</i>	102	156	220	103	581
<i>Sepioteuthis lessoniana</i>	103	81	9	1	194
Brachioteuthidae					
<i>Brachioteuthis</i> sp.	–	1	–	–	1
Ommastrephidae					
<i>Nototodarus hawaiiensis</i>	–	3	–	3	6
<i>Sthenoteuthis oualaniensis</i>	5	79	1	6	91
Octopods	147	447	72	319	985
Total	360	775	305	449	1 889

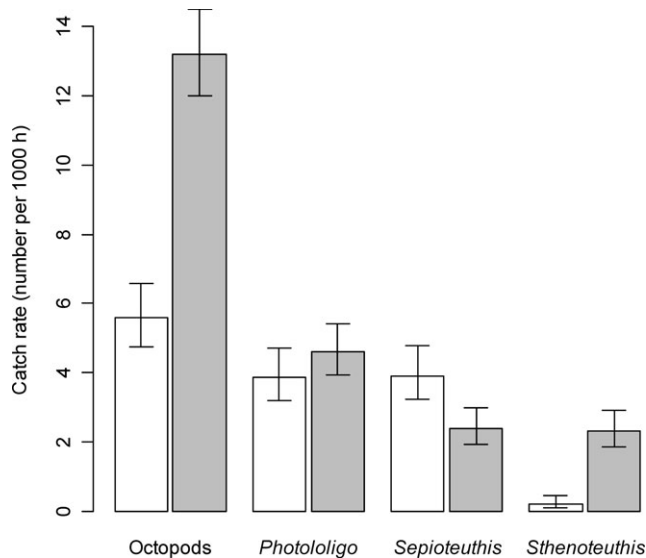


**Figure 2.** Length frequency distributions of *Photololigo* and *S. lessoniana* in the 1997/98 and 1998/99 summers, and *S. oualaniensis* in summer 2 collected by light traps at stations on the Exmouth transect.

catches were best at station EB (Figure 4). In summer 1, only four *S. oualaniensis* were taken at the most offshore station (EH), and one at EC. However, during summer 2, 79 of these squid were collected, and they were present at all stations, except the most inshore station, EA. Catches were best at station ED, and almost all were caught by the shallow traps (Figure 4).

The best catch rates of octopods during both summers were at station ED. In summer 2, catches were widespread along the transect, but in summer 1, very few or no individuals were caught at some stations. There was also a consistent trend of better catch rates by shallow traps than by deep ones (Figure 4).

*Photololigo* was the only species caught in appreciable numbers in both shallow and deep traps, so we investigated whether the size



**Figure 3.** Mean light trap catch rates for octopods and the three most abundant squid species compared between summers. The paired bars for each species represent summer 1 (left white bar) and summer 2 (right shaded bar). Error bars are approximate 95% confidence intervals for the catch rates. Note that *Sepioteuthis* refers to *S. lessoniana*, and *Sthenoteuthis* refers to *S. oualaniensis*.

of animals varied between shallow and deep water. Most *Photololigo* captured on the Exmouth transect were collected during the last two cruises each summer. Fitting log DML against cruise and depth resulted in a highly significant difference in size with depth on this transect ( $p < 0.001$ ). The median size (DML) of the shallow-caught squid was just 73% of the DML of the deep-caught squid (95% CI: 63.5–84%). Therefore, we conclude that there was a consistent trend of increasing body size in squid caught deeper (Figure 5).

*Thevenard*

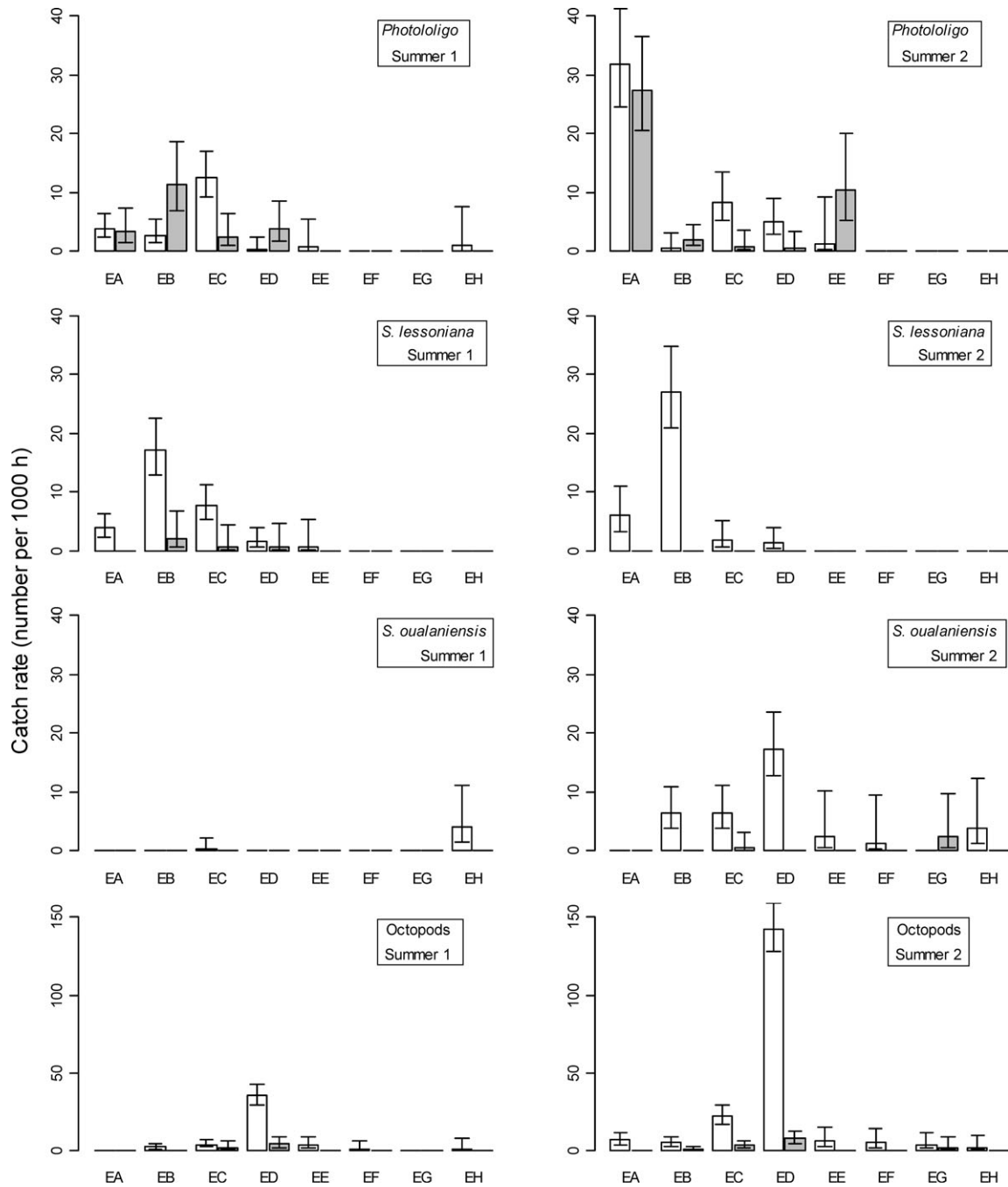
This transect was only sampled during five cruises during summer 2, and only appreciable numbers of *Photololigo* and octopods were captured. *Photololigo* was found at all four stations, and catch rates peaked at station TB, in the shallow traps. Considerably more squid were captured in the shallow than in the deep traps, except at station TD, where there were similar (but low) catches at both depths (Figure 6).

Octopods were captured in greater abundance at the outer station TD, with moderate catches at mid-stations TB and TC, and small catches at inshore station TA. Catch rates were considerably greater in shallow traps, few octopods being taken in the deep traps at any station (Figure 6).

*Ningaloo*

Similar to Thevenard, the Ningaloo transect was only sampled during summer 2, and only *Photololigo* and octopods were captured in appreciable numbers. *Photololigo* was captured at all stations except offshore at NF4 and in the deep traps at NE6. Catch rates were best in deep traps at NE2, and again, there were no consistent patterns in catches with depth (Figure 7).

Octopods were captured at all stations off Ningaloo, but catch rates were very low at the offshore station NF4. There was no clear spatial pattern in abundance, best catches being made at NE1 in the north and at NE5 in the south. Catch rates at these two stations



**Figure 4.** Mean light trap catch rates of *Photololigo*, *S. lessoniana*, *S. oualaniensis*, and octopods on the Exmouth transect during summer 1 and summer 2. The left white bars and right shaded bars for each station represent shallow and deep traps, respectively. Error bars are approximate 95% confidence intervals for the catch rates.

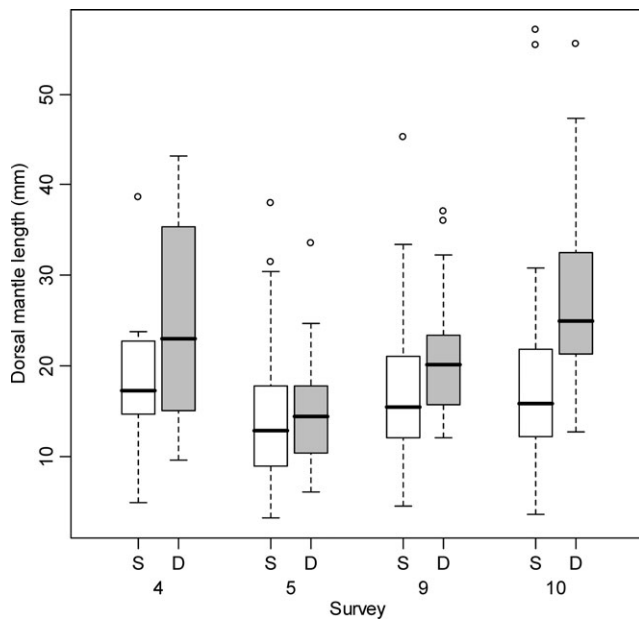
were the highest cephalopod catches of all stations from all transects, with catch rates at NE1 exceeding 500 individuals per 1000 h. Consistent with the other transects, catches of octopods were consistently greater in the shallow than in the deep traps (Figure 7).

Most *Idiosepius pygmaeus* were caught on the Ningaloo transect (13 out of 17; Table 1). Most of these were also caught at the northernmost two stations (NE1, NE2), and all individuals caught on the Ningaloo and Exmouth transects were collected by deep traps. The single specimen captured on the Thevenard transect was caught in a shallow trap.

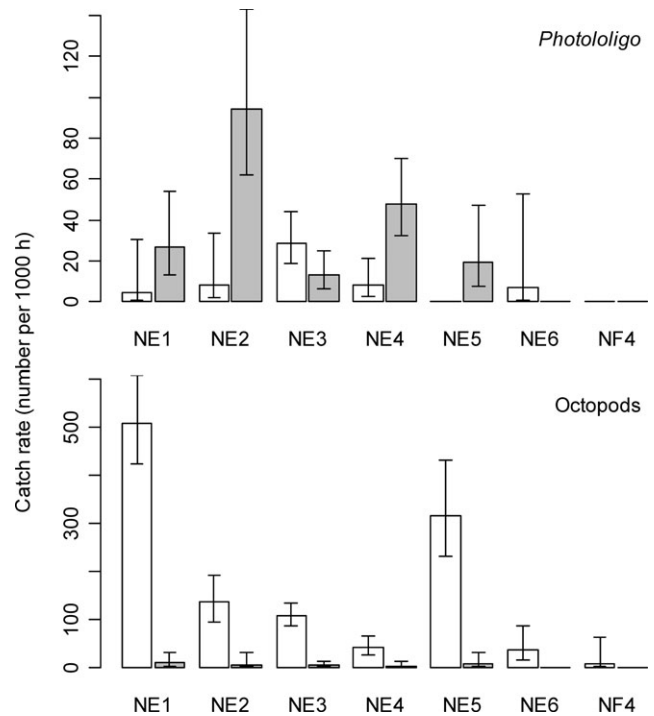
### Discussion

Obtaining ecological information on young stages of tropical cephalopods is of importance to ecosystem studies because of their crucial role as both predators and prey within the micronekton community. Understanding the dynamics of the micronekton continues to be an area where more research is needed. However, research into this important component of the marine community has been limited by the difficulties in sampling paralarvae and especially juveniles of important cephalopod species adequately. An advantage of using light traps is that they are far less size-

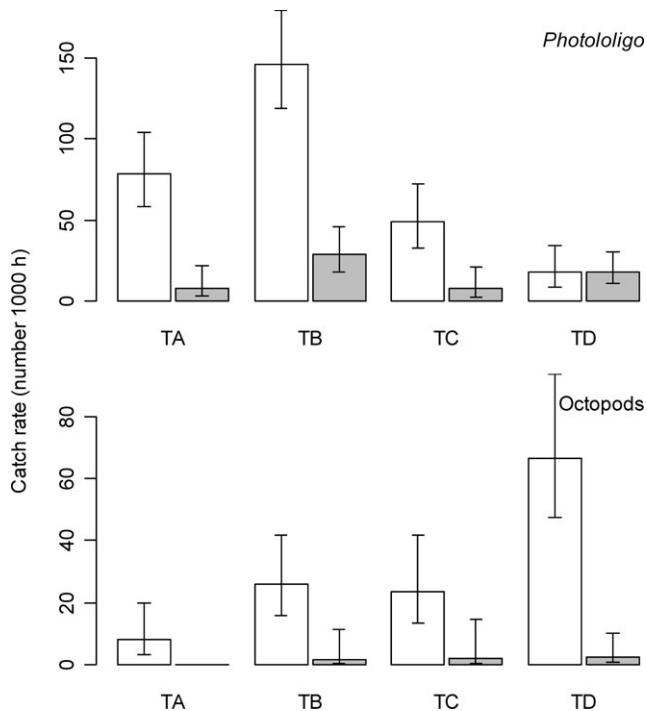




**Figure 5.** The DML for *Photololigo* from the Exmouth transect for the last two surveys of each year, 4 and 5 in summer 1, and 9 and 10 in summer 2, for both shallow (S, white boxes) and deep (D, shaded boxes) deployed light traps. The dark horizontal line represents the median, and the upper and lower boxes the 75<sup>th</sup> and 25<sup>th</sup> percentiles, respectively. The dashed lines represent the range without outliers, and the circles indicate the outliers.



**Figure 7.** Mean light trap catch rates for *Photololigo* and octopods for the Ningaloo transect in summer 2. The left and right bars for each station represent shallow (white bars) and deep (shaded bars) traps, respectively. Note that the scale of the y-axes differs between the two panels. Error bars are approximate 95% confidence intervals for the catch rates.



**Figure 6.** Mean light trap catch rates for *Photololigo* and octopods for the Thevenard transect in summer 2. The left and right bars for each station represent shallow (white bars) and deep (shaded bars) traps, respectively. Note that the scale of the y-axes differs between the two panels. Error bars are approximate 95% confidence intervals for the catch rates.

selective than plankton nets, allowing the collection of individuals over a greater range of sizes and ages and including the post-hatchling and juvenile phases (especially of *Photololigo*). These life history phases have well-developed sensory systems in comparison with very young larvae, and are active swimmers, so like late-stage larval fish are capable of avoiding towed nets (Choat *et al.*, 1993).

Light traps are particularly useful for sampling octopods and loliginid squid (Thorrold, 1992; Moltschaniwskyj and Doherty, 1994). These taxa dominated the paralarval cephalopod community sampled by our study. Interestingly, the abundant taxa in our catches were similar to those collected by light traps off the tropical Australian east coast in GBR waters, where Moltschaniwskyj and Doherty (1995) found an abundance of octopods and *Photololigo*, and also recorded good catches of both *Sepioteuthis* and *Sthenoteuthis*.

Assuming that our catch rates are representative of abundance patterns, our study suggests that octopods and *Photololigo* may be the most abundant cephalopods in the NW Shelf region. *Photololigo* is also very abundant in the GBR lagoon (e.g. Jackson, 1993) where juveniles are a major component of light trap catches (Moltschaniwskyj and Doherty, 1994, 1995). There are likely to be at least two species of *Photololigo* on the NW Shelf that are extremely difficult, if currently not impossible, to separate morphologically as paralarvae. In trawl samples of adults at Port Hedland to the north of our study area, Yeatman and Benzie (1994) detected an inshore and offshore species of *Photololigo* using allozyme electrophoresis. Adults of the offshore species were restricted to waters deeper than 100 m, whereas the

second species was most abundant in shallower waters. There was no evidence from the work of Yeatman and Benzie (1994) that adults of the offshore species inhabited shallow waters or spawned there. Our study captured only one *Photololigo* in water deeper than 100 m, so we expect the remainder of the animals of that species collected by our traps to have been the inshore species. Cross shelf separation in two species of *Photololigo* has also been recorded in northeast Australian waters by Yeatman and Benzie (1994). Moreover, Moltschaniwskyj and Doherty (1994) used allozyme electrophoresis on juveniles captured in light traps, and showed that the juveniles of the two *Photololigo* species in North Queensland also showed cross shelf separation, as did the adults.

*Photololigo* was the only taxon that did not display consistent patterns in abundance with depth, whereas *S. lessoniana*, *S. oualaniensis*, and octopods were mostly collected by traps deployed at the surface. Similar to these latter taxa, nearly all reef and pelagic fish captured by the light traps were also collected in surface waters, although baitfish were captured in the deep traps (Meekan et al., 2006). The deeper distribution of baitfish may be due to predator avoidance and their ability to feed on zooplankton at low light intensity, whereas reef fish accumulate at the surface where light levels allow them to capture prey (Meekan et al., 2006). As cephalopods are also visual predators, similar behavioural requirements might also account for their greater abundance in surface waters.

Smaller *Photololigo* were collected by traps deployed in shallow water, whereas larger animals were collected in deep deployments. Such ontogenetic changes in depth distribution, with smaller (younger) animals preferring shallow water, appear to be typical of many species, and have been recorded in other loliginids, such as *Loligo pealei* (Vecchione, 1981) and *Lolliguncula brevis* (Vecchione, 1991). This may show the need for young squid to access smaller prey which are likely more abundant at the surface. Zeidberg and Hamner (2002) also found that young *L. opalescens* migrate vertically, with greatest concentrations at 30 m by day but at 15 m by night.

The capture of *I. pygmaeus* in traps deployed in deep water contrasts with previous observations of this species in tropical eastern Australian waters, where it has been found swimming near the surface (Jackson, 1989, 1992). Moreover, the species was not recorded in light traps deployed at the surface and at depth in tropical shelf waters off Queensland by Moltschaniwskyj and Doherty (1995), although Jackson (1992) did report good catches of the species in light traps deployed at the surface in the northern GBR lagoon around Lizard Island. Our study suggests that this species has a broader habitat range than previously recognized, and it may well be capable of inhabiting environments from estuarine mangroves (Jackson, 1989) to deep offshore water. It may also undergo seasonal or ontogenetic migration, because it regularly disappears from nearshore waters during the warm period of the year (Jackson, 1992). Therefore, warm shallow summer temperatures may drive *I. pygmaeus* into deeper habitats.

The comparatively large catches of octopods at stations EC and ED are similar to the patterns found for fish larvae during this sampling programme, 80% of the fish larvae being captured by traps deployed at these stations (Meekan et al., 2006). These stations were at the boundary between well-mixed inshore and stratified offshore waters, and are a region of turbulent mixing of upwelled water transported onshore by flood tides. This upwelling is enhanced by the constriction of current flow between NW

Cape and South Muiron Island, in combination with the shallowing of the shelf (Meekan et al., 2006). The last authors suggested that the abundance of fish larvae at these stations may reflect either passive accumulation in frontal zones between mixed and stratified waters, or alternatively the movement of larvae to take advantage of improved food availability, because copepod abundance peaked at these stations during both summers. As octopods are also visual predators capable of active swimming (Villanueva et al., 1996), they may accumulate at these stations for similar reasons.

Both *Photololigo* and *S. lessoniana* are typically inshore dwellers and our patterns of catches reflect this tendency, most specimens being collected inshore. Although concentrations of copepods were generally greater inshore than offshore (Meekan et al., 2006), the abundance of *Photololigo* extended farther offshore during summer 2 than during summer 1. This pattern occurred despite lower copepod abundance at outer stations of the transect during summer 2 than during summer 1 (Meekan et al., 2006), suggesting that distributions of prey are unlikely to be the sole factor driving cross shelf distribution of this species.

Our study did not reveal marked differences in distributions or abundance of paralarval cephalopods between the 2 years, except for the abundance of *S. oualaniensis*. This is despite differing oceanographic conditions resulting from the shift from *El Niño* conditions in summer 1 to *La Niña* conditions in summer 2, and the associated differences in productivity, fish larval growth, and abundance (Meekan et al., 2003). We also undertook statolith age analysis of *Photololigo* from our collections, but did not find any clear differences in paralarval growth over the two seasons. It is likely that a longer time-series would be needed to understand the dynamic changes in cephalopod paralarvae better. Although *S. oualaniensis* is predominantly a tropical oceanic species, paralarvae and juveniles have been collected on continental shelf and slope waters (Dunning, 1998). The markedly greater abundance during summer 2 than during summer 1 may be related to a greater intrusion of warmer oceanic water onto the shelf during the second summer.

Pelagic cephalopods respond quickly to environmental change because of their short life cycles. Tropical nearshore squid appear to have life histories that are completed in <200 d (Jackson, 2004). The influences of both oceanographic and biological factors are therefore likely to be even more magnified for the juvenile stages. We were able in this study to discern both spatial and temporal differences in the relative abundance of juvenile cephalopods. Understanding the population dynamics of these young stages is critical because of their importance in marine ecosystem dynamics. Future targeted studies deploying light traps over longer time periods may well provide a useful means of sampling these young stages that are difficult to sample with other techniques.

## Acknowledgements

We thank the crew of the Lady Basten and many AIMS staff and volunteers for help with field and laboratory work, and two anonymous reviewers for valued input to the draft manuscript.

## References

- Choat, J. H., Doherty, P. J., Kerrigan, B. A., and Leis, J. M. 1993. A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. *Fishery Bulletin US*, 91: 195–209.

- Collins, M. A., Yau, C., Boyle, P. B., Friese, D., and Piatkowski, U. 2002. Distribution of cephalopods from plankton surveys around the British Isles. *Bulletin of Marine Science*, 7: 239–254.
- Dunning, M. C. 1998. Zoogeography of arrow squids (Cephalopoda: Ommastrephidae) in the Coral and Tasman Seas, Southwest Pacific. *Smithsonian Contributions to Zoology*, 586: 435–454.
- Ish, T., Dick, E. J., Switzer, P. V., and Mangel, M. 2004. Environment, krill and squid in the Monterey Bay: from fisheries to life histories and back again. *Deep-Sea Research II*, 51: 849–862.
- Jackson, G. D. 1989. The use of statolith microstructures to analyze life-history events in the small tropical cephalopod *Idiosepius pygmaeus*. *Fishery Bulletin US*, 87: 265–272.
- Jackson, G. D. 1992. Seasonal abundance of the small tropical sepioid *Idiosepius pygmaeus* (Cephalopoda: Idiosepiidae) at two localities off Townsville, North Queensland, Australia. *Veliger*, 35: 396–401.
- Jackson, G. D. 1993. Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pygmaeus*. *Fishery Bulletin US*, 91: 260–270.
- Jackson, G. D. 2004. Advances in defining the life histories of myopsid squid. *Marine and Freshwater Research*, 55: 357–365.
- Jackson, G. D., and Domeier, M. L. 2003. The effects of an extraordinary *El Niño/La Niña* event on the size and growth of the squid *Loligo opalescens* off southern California. *Marine Biology*, 142: 925–935.
- Jackson, G. D., and O’Dor, R. K. 2001. Time, space and the ecophysiology of squid growth, life in the fast lane. *Vie et Milieu*, 51: 205–215.
- Kubodera, T., Watanabe, H., and Ichii, T. 2007. Feeding habits of the blue shark, *Prionace glauca*, and salmon shark, *Lamna ditropis*, in the transition region of the Western North Pacific. *Reviews in Fish Biology and Fisheries*, 17: 111–124.
- Lansdell, M., and Young, J. 2007. Pelagic cephalopods from eastern Australia: species composition, horizontal and vertical distribution determined from the diets of pelagic fishes. *Reviews in Fish Biology and Fisheries*, 17: 125–138.
- McCullagh, P., and Nelder, J. A. 1989. *Generalized Linear Models*. Chapman and Hall, London. 511 pp.
- Meekan, M. G., Carleton, J. H., McKinnon, A. D., Flynn, K., and Furnas, M. 2003. What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Marine Ecology Progress Series*, 256: 193–204.
- Meekan, M. G., Carleton, J. H., Steinberg, C. R., McKinnon, A. D., Brinkman, R., Doherty, P. J., Halford, A., *et al.* 2006. Turbulent mixing and mesoscale distributions of late-stage fish larvae on the NW shelf of Western Australia. *Fisheries Oceanography*, 15: 44–59.
- Meekan, M. G., Doherty, P. J., and White, L. 2000. Recapture experiments show the low sampling efficiency of light traps. *Bulletin of Marine Science*, 67: 875–885.
- Meekan, M. G., Wilson, S. G., Halford, A., and Retzel, A. 2001. A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology*, 139: 373–381.
- Moltschaniwskyj, N. A., and Doherty, P. J. 1994. Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef lagoon. *Fishery Bulletin US*, 92: 302–312.
- Moltschaniwskyj, N. A., and Doherty, P. J. 1995. Cross-shelf distribution patterns of tropical juvenile cephalopods sampled with light-traps. *Marine and Freshwater Research*, 46: 707–714.
- Okutani, T., and McGowan, J. A. 1969. Systematics, distribution, and abundance of the epipelagic squid (Cephalopoda, Decapoda) larvae of the California Current. *Bulletin of the Scripps Institute of Oceanography*, 14: 1–90.
- Recksiek, C. W., and Kashiwada, J. 1979. Distribution of larval squid. *Loligo opalescens*, in various nearshore locations. *CalCOFI Reports*, 20: 31–34.
- Reiss, C. S., Maxwell, M. R., Hunter, J. K., and Henry, A. 2004. Investigating environmental effects on population dynamics of *Loligo opalescens* in the southern California Bight. *CalCOFI Reports*, 45: 87–97.
- Rodhouse, P. G., Symon, C., and Hatfield, E. M. C. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series*, 89: 183–195.
- Sampey, A., Meekan, M. G., Carleton, J. H., McKinnon, A. D., and McCormick, M. I. 2004. Temporal patterns in distributions of tropical fish larvae on the North-West Shelf of Australia. *Marine and Freshwater Research*, 55: 473–487.
- 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. *Marine Ecology Progress Series*, 89: 277–285.
- Vecchione, M. 1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda; Myopsida). *Journal of Shellfish Research*, 1: 171–180.
- Vecchione, M. 1991. Observations on the paralarval ecology of a euryhaline squid *Lolliguncula brevis* (Cephalopoda: Loliginidae). *Fishery Bulletin US*, 89: 515–521.
- Villanueva, R., Nozais, C., and von Boletzky, S. 1996. Swimming behaviour and food searching in planktonic *Octopus vulgaris* Cuvier from hatching to settlement. *Journal of Experimental Marine Biology and Ecology*, 208: 169–184.
- Waluda, C. M., Rodhouse, P. G., Poldestrá, G. P., Trathan, P. N., and Pierce, G. J. 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommaastrephidae) and influences on recruitment variability. *Marine Biology*, 139: 671–679.
- Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommaastrephidae) fishery in the South Atlantic. *Marine Ecology Progress Series*, 183: 159–167.
- Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. 2004. Synchronicity in southern hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. *Fisheries Oceanography*, 13: 255–266.
- Wilson, S. G., Carleton, J. H., and Meekan, M. G. 2003a. Spatial and temporal patterns in the distribution and abundance of macrozooplankton on the southern North West Shelf, Western Australia. *Estuarine, Coastal and Shelf Science*, 56: 897–908.
- Wilson, S. G., Meekan, M. G., Carleton, J. H., Stewart, T. C., and Knott, B. 2003b. Distribution, abundance and reproductive biology of *Pseudeuphausia latifrons* and other euphausiids on the southern North West Shelf, Western Australia. *Marine Biology*, 142: 369–379.
- Wormuth, J. H., and Roper, C. F. E. 1983. Quantitative sampling of oceanic cephalopods by nets: problems and recommendations. *Biological Oceanography*, 2: 357–377.
- Yeatman, J., and Benzie, J. A. H. 1994. Genetic structure and distribution of *Photololigo* spp. in Australia. *Marine Biology*, 118: 79–87.
- Young, R. E., and Harman, R. F. 1988. “Larva”, “paralarva” and “sub-adult” in cephalopod terminology. *Malacologia*, 29: 201–207.
- Zeidberg, L. D., and Hamner, W. M. 2002. Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997–1998 *El Niño*. *Marine Biology*, 141: 111–122.
- Zeidberg, L. D., Hamner, W. M., Nezlín, N. P., and Henro, A. 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003. *Fishery Bulletin US*, 104: 46–59.