Journal of the Royal Society of Western Australia, 93: 43–50, 2010

Zooplankton from the inshore waters of Christmas Island (Indian Ocean) with reference to larvae of the red land crab, *Gecarcoidea natalis*

C Davies[1,2] & L E Beckley[1]

[1] School of Environmental Science, Murdoch University, 90 South Street, Murdoch, WA 6150

[2] CSIRO Marine & Atmospheric Research, PO Box 120, Cleveland, Qld 4163

Manuscript received September 2009; accepted December 2009

Abstract

The red land crab, *Gecarcoidea natalis,* which is endemic to Christmas Island in the Indian Ocean, has an obligate marine larval phase. Surface plankton tows, using a 500 μm mesh net, were completed monthly at three sites on the north coast of Christmas Island to determine the composition, abundance and seasonal variation of the macro-zooplankton and detect the presence of red crab zoea larvae. The highest plankton concentrations were found at the end of the south-east monsoon period and, at all other times of the year, plankton settled volumes were very low, typically <0.1 ml/m^3 of water sampled. Despite rearing red crab zoea obtained from spawning females, it was not possible to definitively identify them from among the wide diversity of brachyuran zoea found in the plankton samples.

Keywords: Macro-zooplankton, Brachyuran zoea, red land crab, Christmas Island.

Introduction

Christmas Island is a seamount in the Indian Ocean (10 °S 105 °E), 390 km south-west of Java, Indonesia. The island has four well-defined promontories (Figure 1) and the 73 km perimeter is characterised by steep limestone cliffs fringed by a narrow coral reef (10-50 m in width). These reefs drop off steeply and water depth increases rapidly reaching 5000 m within a few kilometres of the island.

The tropical climate is defined by a steady, dry, south-east monsoon from May-November and an erratic, wet, north-west monsoon from December-April (Clark 1994). The waters around Christmas Island are influenced by the South Equatorial Current which is fed from the east via the Indonesian Throughflow and a weaker anticyclonic gyre from north-west Australia (Wyrtki 1962; Quadfasel *et al*. 1996; Wijffels *et al.* 2002). This South Equatorial Current is strongest at the end of the south-east monsoon and weakens during the north-west monsoon when the eastward flowing South Java Current develops (Wyrtki 1962).

Marine research at Christmas Island has generally been limited to biodiversity surveys of sponges, reef building corals, molluscs, decapod crustacea, echinoderms and fishes (Berry 1988; Allen & Steene 1988; Allen 2000). There have been no studies on the plankton around Christmas Island although, during the Indian Ocean Expedition, zooplankton abundance was measured from tropical to temperate waters along a transect corresponding to longitude 110 °E (Tranter & Kerr 1967).

Of the 20 species of land and intertidal crabs that have been recorded on Christmas Island, the endemic red land crab, *Gecarcoidia natalis,* is the most abundant (Clark 1994). The current population of red crabs has been estimated at approximately 47 million (Parks Australia North 2005).

Each year, at the beginning of the north-west monsoon, millions of red crabs migrate to the ocean to spawn (Hicks *et al.* 1984). Consistent rainfall at the onset of the north-west monsoon usually results in one major spawning event while inconsistent rainfall can result in sporadic or postponed migrations and a breeding season lasting in excess of three months (Hicks 1985). The red crabs spawn in the early hours of the morning on the high tide over a period of 2–3 days between the last quarter of the moon and the new moon (Hicks 1985). Such synchronised lunar spawning has also been documented in Bermuda for a land crab of the same family, *Gecarcinus lateralis* (Wolcott & Wolcott 1982).

Red crab larvae take about 27 days to develop into megalopae which settle along the shore line for two days before returning to the land (Hicks 1985). Large-scale survival and emergence of post-larval red crabs onto the island is sporadic, usually once or twice in ten years (Clark 1994). The larval phase of the red crab is undescribed but other brachyuran crabs are known to have 2–13 zoeal stages. One gecarcinid crab from the tropical and subtropical Atlantic coast of the Americas, *Cardisoma guanhumi,* has been described with five zoeal stages and one megalopal stage (Boltovsky 1999). Studies on megalopae settlement of other brachyuran crabs have shown recruitment to be dependent on oceanographic processes, wind driven currents and tidal movements (Johnson *et al*. 1984; Garvine *et al*. 1997; Flores *et al.* 2002; Perry *et al.* 2003; Lee *et al.* 2005).

This project was designed to determine baseline data on composition, abundance and temporal variation of the macro-zooplankton in the inshore waters around

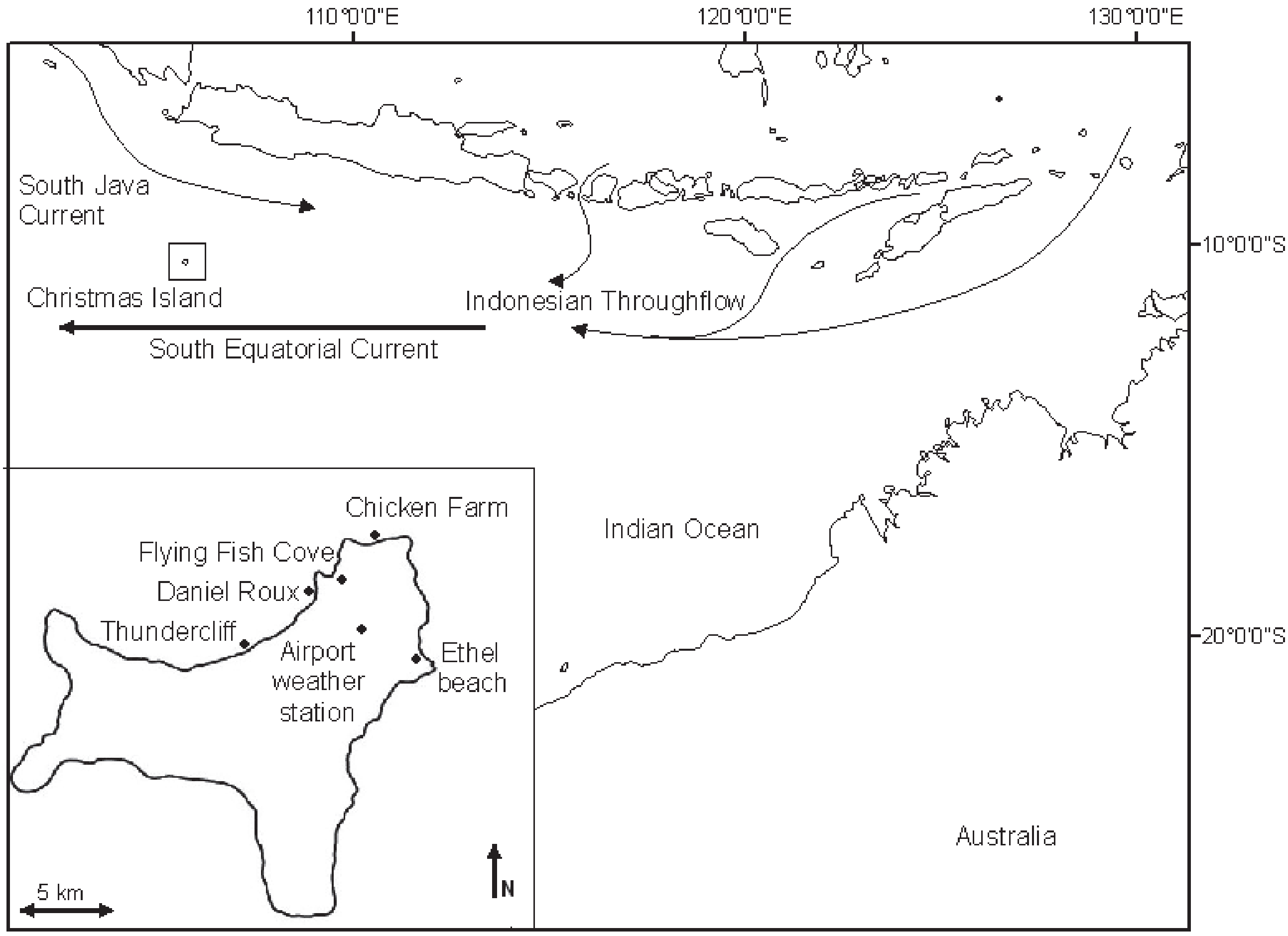

Figure 1. Location of Christmas Island in the eastern Indian Ocean. Inset shows a map of Christmas Island and indicates the sampling sites and places mentioned in the text.

Christmas Island. It was hypothesised that the abundance of plankton would be correlated with the seasonal oceanographic conditions associated with the south-east and north-west monsoons. Further, it was hypothesised that the planktonic stages of the endemic red land crab would be present in significant numbers during the spawning period over the north-west monsoon.

Methods

Environmental data

Meteorological data (1972–2006) were obtained from the weather station at Christmas Island airport through the Australian Bureau of Meteorology (BOM). The oceanographic conditions around Christmas Island were described from sea surface thermal imagery (6-day composite), altimetry (sea height) and surface drifter buoy trajectories (geostrophic current velocity and direction). These were accessed from CSIRO (www.marine.csiro.au/remotesensing/oceancurrents) and collated for the time periods around the plankton sampling trips.

Plankton sampling

Plankton sampling was undertaken close to the new moon period each month from November 2005 to December 2006 at three sites off the north coast of Christmas Island: Chicken Farm, Thundercliff and Daniel Roux Cave (Figure 1). These sites were chosen as they are adjacent to known red crab spawning areas and accessible with a small boat launched from Flying Fish Cove. Plankton was collected in daylight hours (09:00 to 12:00) using a 500 µm mesh net (0.6 m diameter, 3 m length), towed just below the surface at 1.5 knots, 30 m behind a small boat. At each site, two replicate tows were made parallel to the reef edge in water about 30–50 m deep. The volume of water filtered was determined using a General Oceanics flowmeter suspended in the mouth of the net. Sea surface temperature was measured using a YSI Model 85 multimeter at all three sampling sites. These temperatures were verified against Argo float data and satellite data from the aforementioned CSIRO website. Sampling was not conducted at Thundercliff in March 2006 and at Chicken Farm in June 2006 due to mechanical break down and bad weather, respectively.

Plankton samples were immediately fixed in 5 % formalin and transferred to 70 % ethanol after 24 hours.

Total settled volume of plankton (ml) was measured by allowing the samples to settle in graduated measuring cylinders for 24 hours. Plankton samples were examined under a dissecting microscope and counted following the subsampling method of Gibbons (2000). The plankton were identified to the lowest taxon possible and the counts were standardised by dividing by the volume of water filtered per tow to give a number per taxon per m^3.

Timing of spawning and rearing of red crab larvae

Eggs were collected from spawning red crabs at Ethel Beach (Figure 1) in January 2006 and transferred into a 50 L glass aquarium. The seawater in the aquarium was filtered through a 300 μm mesh sieve and replaced daily. As there were no facilities for culture of appropriate food organisms on Christmas Island, zoea were not fed anything additional to that occurring naturally in the seawater. To determine the developmental stages of the zoea, specimens were sampled at 12 hour intervals and fixed in 5 % formalin. This experiment was repeated during the spawning in December 2006 with extra plankton filtered from seawater added to the aquarium to supplement the food supply.

The zoea collected from the plankton samples were visually compared with those of the reared red crabs. The diagnostic features of the zoea were used to identify the zoea, i.e. arrangement of spines and telson shape. When this did not allow confident identification of red crab zoea the morphometrics (dorsal spine length and the body width) were measured using an eyepiece micrometer. Similar measurements were made on a selection of six brachyuran crab zoea removed from the plankton samples each month. In an attempt to identify red crab larvae in the zooplankton samples, the ratios of the maximum body width to dorsal spine length (the straight distance between the dorsal spine base and tip) were compared between the reared red crab zoea and those caught in the zooplankton samples. Zoea specimens were photographed using a Nikon dissecting microscope and digital camera.

Results

Environmental data

Total rainfall at Christmas Island over the project duration was relatively low, only 1379 mm over the fourteen months compared to 2483 mm which would be predicted from historical data (BOM rainfall data 1972–2006). The 2005–2006 north-west monsoon (December to April) was weak with long dry spells until April 2006 which was the wettest month. The 2006–2007 north-west monsoon brought rain in December 2006 with above average rainfall for that month.

The South Equatorial Current, as indicated by the geostrophic current velocities, was flowing weakly westward throughout the north-west monsoon periods and was frequently disrupted by eddies between the Indonesian Throughflow and Christmas Island. The current intensified during the south-east monsoon, reaching peak flows of >1 m/s in September 2006, before weakening as the 2006–2007 north-west monsoon developed. The maximum sea surface temperature recorded during plankton sampling was in March 2006 (29.7°C), and the lowest was in September 2006 (24.5°C).

Plankton composition and abundance

Mean filtered water volume per tow at the three sites was 170 m^3 (SE ± 52). The highest settled volume of plankton (1.9 ml/m^3 of water sampled) was recorded in September 2006 (Figure 2). From January to July 2006 plankton concentrations were consistently low, typically <0.1 ml settled volume/m^3 of water sampled. Slightly higher concentrations were observed at the start of the sampling in November and December 2005 and from October 2006 to December 2006. Two way ANOVA revealed that the settled volumes of plankton were significantly affected by the sampling site ($p<0.05$, $F_{3,2}=34.1$) and the time of year (month) ($p<0.05$, $F_{2,0}=62.3$). There was also a significant interaction between the site and the time of year ($P<0.05$, $F_{1,8}=11.8$).

Copepods dominated the overall zooplankton composition from all sites (Figure 3) contributing 54 % (SE ± 27 %) of the individuals counted. Chaetognatha (7 %) and Cnidaria (9 %) were also consistently common. The Thaliacea were mostly salps with only a few doliolids recorded. Other Crustacea included amphipods, euphausiids, mysids, decapods, isopods, stomatopods and cumaceans. Brachyuran crab larvae were recorded throughout the year in the plankton samples at Christmas Island with a seasonal peak during the north-west monsoons (Table 1).

Timing of spawning and rearing of red crab larvae

The red crab spawning events over the 2005–2006 north-west monsoon were sporadic. The first and largest red crab spawning was around the 27th November 2005, followed by a smaller spawning event around the 26th December and

Table 1

Mean abundance of all brachyuran crab zoea each month (individuals per m^3 of water sampled) at Christmas Island during the period November 2005 to December 2006. * indicates months when red crab larvae would be expected as spawning events had been observed prior to sampling.

	Brachyuran Zoea (per m^3 water sampled)		
	Chicken Farm	Thundercliff	Daniel Roux
Nov	0.10	18.34	2.58
Dec*	6.09	0.18	0.47
Jan*	0.31	0.02	0.12
Feb*	0.30	0.02	0.08
Mar	0.10	no sample	0.24
Apr1	0.11	0.04	0.06
Apr2	0.15	0.01	0.17
May	0.35	0.11	0.00
June	no sample	0.03	0.25
July	0.09	0.12	0.11
Aug	0.20	0.01	0.11
Sept	0.50	0.05	0.31
Oct	0.75	0.02	0.14
Nov	1.48	3.38	0.34
Dec	0.46	1.39	0.52

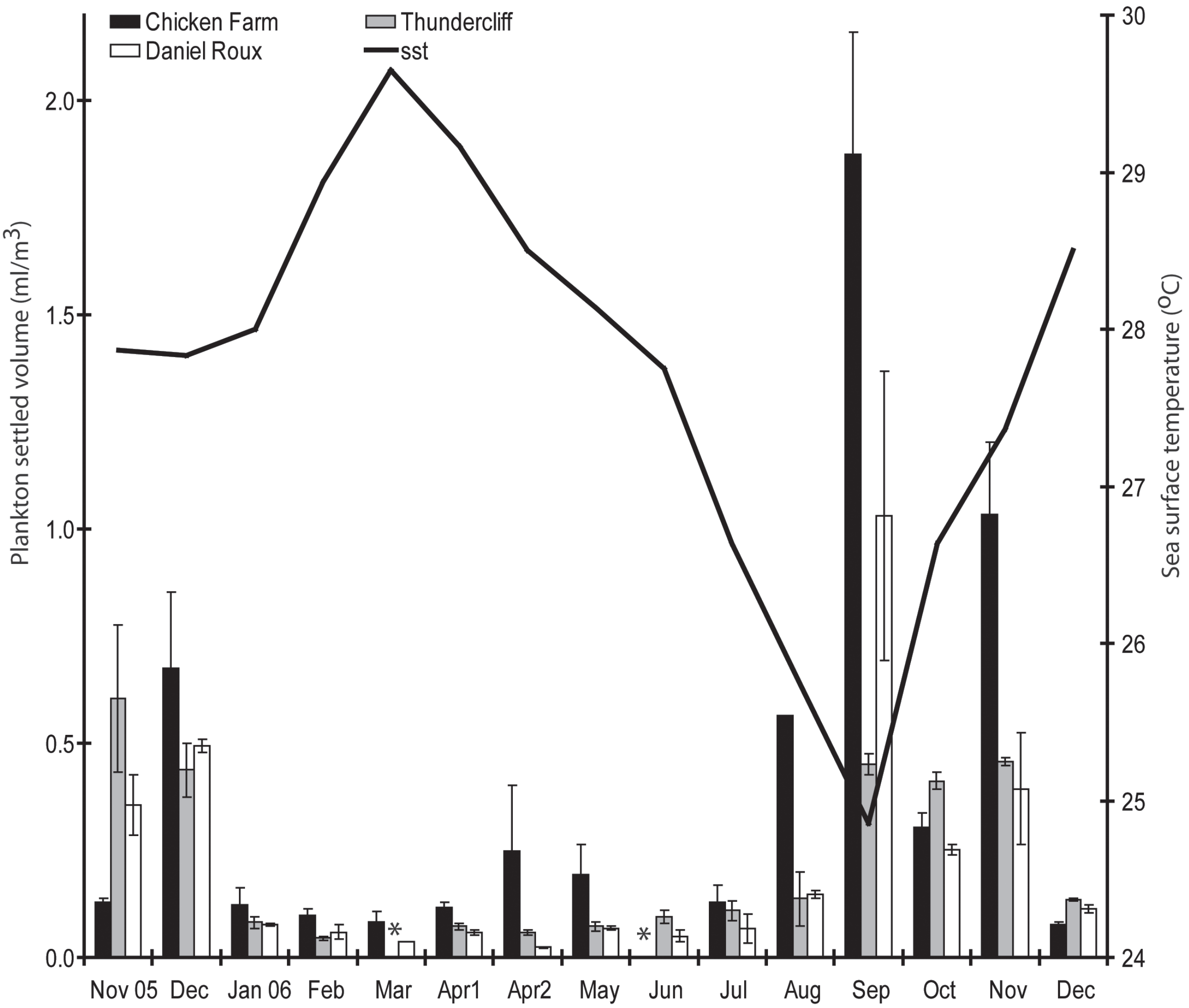

Figure 2. Mean (and SE) monthly settled volumes at each site (ml of plankton /m^3 of water sampled) and sea surface temperature measured at the time of sampling. * indicates that no samples were taken at Thudercliff in March 2006 or Chicken Farm in June 2006.

very small spawning events around 26th January and 27th February (C. Davies pers. obs.). During the January 2006 spawning event, eggs were collected as the female crabs spawned them into the water at Ethel Beach. The first migration of the 2006–2007 season occurred in December 2006 after the sampling and eggs were collected at Flying Fish Cove Beach as they were being spawned.

The red crab zoea from January 2006 survived for a week in the aquarium but did not moult into a second zoeal stage. Similarly, zoea from the December 2006 spawning that were reared with supplementary filtered plankton added to the aquarium only survived for four days and did not moult to a second zoea.

The first zoeal stage of the red crab measured approximately 2 mm in length from the carapace (excluding dorsal spine) to the end of the furcae, had lateral spines on the carapace and a furcated telson with three pairs of inner setae. Exospines developed on the larger zoea larvae.

The standard error for dorsal spine to body width ratio was low in the reared red crab zoea, n=32 (Figure 4). Measurements of the dorsal spine to body width ratio from the selection of zoea from the monthly plankton samples revealed a wide scatter indicating that there were zoea of many crab species in the samples. Zoea that had a similar dorsal spine to body width ratio to that of the reared land crabs were found in December 2005 and February, April, September and October 2006.

Discussion

The plankton concentration in the waters around Christmas Island was highest in September 2006 at the end of the south-east monsoon when the sea surface temperature was lowest. The South Equatorial Current is strongest in this region towards the end of the south-east monsoon when the wind stress over the region is strongest (Meyers *et al.* 1995; Donguy & Meyers 1995).

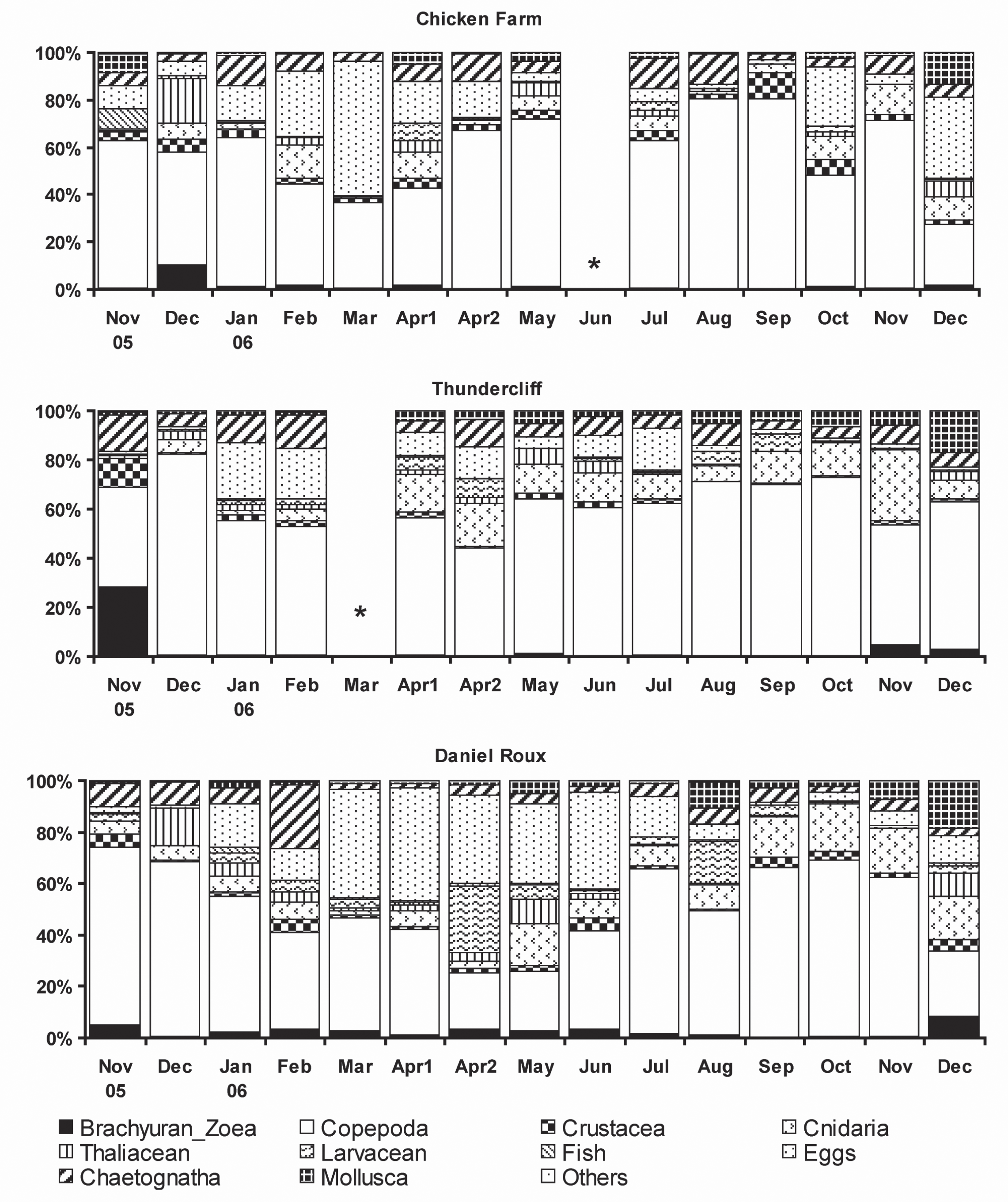

Figure 3. The monthly composition of the zooplankton sampled at three sites on Christmas Island, November 2005 – December 2006. * indicates that no samples were taken at Thundercliff in March 2006 or Chicken Farm in June 2006.

Upwelling on the northern flank of the South Equatorial Current has been linked to the increase in plankton concentration (Wyrtki 1962). During the Indian Ocean Expedition, Tranter & Kerr (1977) found that plankton concentration increased in the Eastern Indian Ocean at the end of the south-east monsoon and they ascribed this to increased productivity from the upwelling along the flank of the South Equatorial Current (Wyrtki 1962) or simply due to horizontal water movements (Tranter 1967).

The plankton concentration was consistently low from January, in the north-west monsoon, until July 2006 when the south-east monsoon strengthened. The low plankton concentration found when the South Equatorial Current is weak may reflect a return to the prevailing plankton impoverished waters of the South Indian Ocean gyre (Tranter & Kerr 1977).

This may infer that much of the recruitment at Christmas Island is from external sources dependent on the South Equatorial Current. This would be supported by the fish fauna which is typical of the Indo West Pacific region (Allen 2000) and by a low diversity of benthic invertebrates such as corals, molluscs and echinoderms (Done & Marsh 2000, Marsh 2000, Wells & Slack-Smith

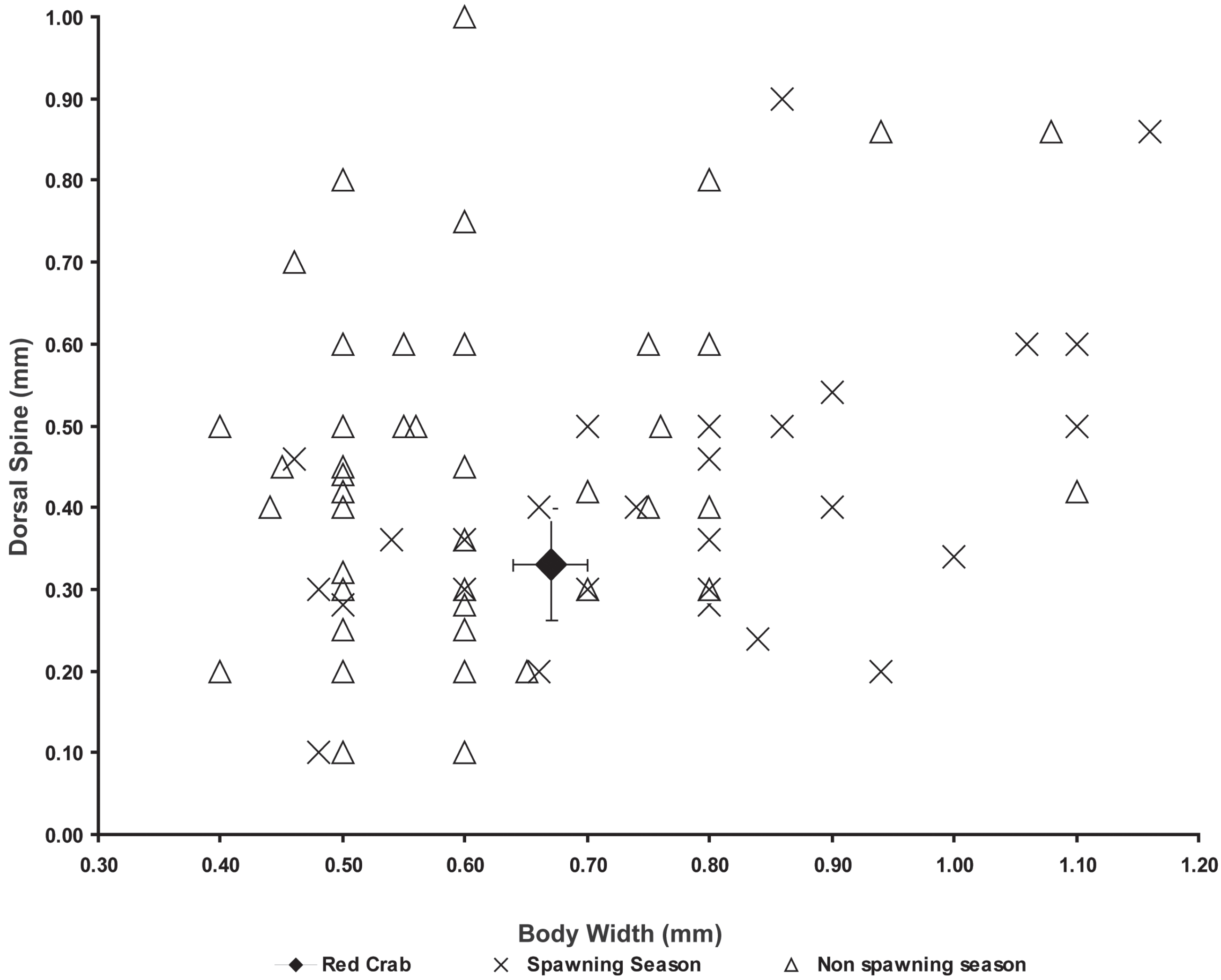

Figure 4. The relationship between the length of dorsal spine to body width for reared red crab zoea larvae (with SE bars) compared to those of a monthly selection of zoea collected in the plankton samples at Christmas Island. Note that two outlying data points of crabs with extended dorsal spines (1.6 mm) were omitted from the graph.

2000) as the pelagic larval duration of many species is not long enough for transport from neighbouring Indonesian or Australian populations.

The plankton concentrations at the three sites were significantly different throughout the sampling period. This difference may be explained by the bathymetry and conditions at the three sites. The Thundercliff and Daniel Roux sites both have little fringing reef and steep drop offs although the Daniel Roux site is more sheltered from the prevailing currents. The Chicken Farm site, in a small embayment on the north-east side of the island, has a wider fringing reef extending up to 50 m offshore and is more exposed to strong currents.

The concentrations of plankton caught at Christmas Island were low when compared to plankton studies in other coastal tropical areas (Nair *et al.* 1981; McKinnon *et al.* 2005). This can partly be explained by the use of a 500 μm mesh net which did not retain smaller plankton and also the location of Christmas Island in tropical, oceanic waters where plankton concentrations are expected to be lower (Nair *et al.* 1981). The oceanic nature of the plankton sampled at Christmas Island was highlighted by presence of taxa such as hyperiid amphipods, euphausiids and salps (Gibbons 2000).

Over the sampling period, copepods were the most abundant component of the plankton accounting for 54 % of the individuals counted per m^3 of water sampled at Christmas Island. This is lower than the value of 74 % for the tropical Indian Ocean determined by Longhurst (1985) from analysis of 4000 global plankton samples. However, his review was of studies which sampled with nets of 200– 300 μm mesh, finer than our 500 μm mesh net.

Brachyuran zoea were found in almost every plankton sample over the project duration. Surprisingly, the highest concentrations occurred in the samples collected in early November 2005, before the first red crab spawning later that month. This suggests that at least one other brachyuran crab species was spawning at that time. It was originally hypothesised that large numbers of red crab larvae would be present in the plankton during the spawning season. However, this was not the case. Sporadic, lower than average rainfall over the 2005–2006 north-west monsoon resulted in only three small migrations, rather than one large migration, producing less crab larvae and identification of the zoea could not be inferred through high abundance levels.

Many of the 142 marine brachyuran crab species recorded from Christmas Island (Morgan 2000) have undescribed larval stages so to confirm the presence of red crab zoea in the plankton we compared those raised in the aquarium to those caught in the samples. There was a large variety of zoea in the plankton samples and some matched the morphometrics of the reared red crab zoea. However, some of the matching zoea occurred during months outside of the red crab spawning season indicating that the measured morphometrics do not provide conclusive identification. Chromatophores are recognised as the best way to positively identify brachyuran zoea as they do not change with growth, but they do fade with preservation (Boltovskoy 1999; Shanks 2001). Unfortunately, the chromatophores of the reared red crab larvae faded rapidly on preservation and hence could not be used for identification purposes.

The highest plankton concentrations, and potentially recruitment from external sources, coincided with the strongest westward flow of the South Equatorial current. Conversely, the red crabs spawned when the South Equatorial Current had weakened and westward transport was lowest. It is unknown where the red crab larvae develop. Based on observations that the highest returns of juvenile crabs occur in areas where the fringing reef is widest it has been suggested that they stay close to shore (Gray 1981). At Chicken Farm, where the fringing reef is wide, spawning crabs were observed in November and December 2005 and January 2006. A maximum of 6 crab zoea/m^3 was recorded in December, four days after a spawning and 0.3 zoea/m^3 in January and February, seven to nine days after spawning events. However, no subsequent juvenile returns were observed at this site (pers. obs. C. Davies). Although the red crab migrations were relatively small in 2005–2006, many million eggs would have been released over each spawning period and higher concentrations would have been expected in the samples if the zoea had remained inshore.

The larvae of many other crab species are known to develop offshore. For example, the blue crab, *Callinectes sapidu,* spawns in estuaries off the mid Atlantic coast of America and the larvae are immediately carried out into the open ocean where they develop in the surface waters (Johnson *et al*. 1984; Epifanio 1995). Blue crab recruitment is also sporadic but wind stress has been shown to be very important for successful recruitment with wind-driven onshore currents responsible for retaining the larvae in the general area and then returning the megalopae to the coast (Johnson *et al*. 1984; Garvine *et al*. 1997; Perry *et al.* 2003). Brachyuran crab larvae have also demonstrated active vertical movement to accomplish horizontal transport towards the shore (Cronin 1986; Blackmon & Eggleston 2001; Lee *et al.* 2005).

Whilst inshore development was not ruled out by this study, we suggest that red crab larvae might develop further offshore than previously thought, and that recruitment is dependent on oceanographic conditions being favourable for the return of megalopae to the island. The irregular recruitment of juvenile red crabs to Christmas Island, noted as once or twice a decade by Clark (1994), and the absence of high numbers of red crab zoea in the plankton during this study would support this hypothesis. Detailed exploration of the oceanography, in particular, eddy fields and lee effects from the island would probably be necessary to unravel the larval ecology of red crabs during their obligate marine phase.

Acknowledgements: Parks Australia on Christmas Island provided the laboratory and equipment for this project and their boat was also used on some occasions to collect the samples. Many other people on Christmas Island volunteered to help with sampling and we thank them for their time and effort. The plankton samples taken during this project and the reared zoea larvae are lodged in the Western Australian Museum in Perth

References

Allen G R & Steene R C 1988 Fishes of Christmas Island Indian Ocean. 1st Edition, Christmas Island Natural History Association.

Allen G R 2000 Fishes of Christmas Island, Indian Ocean. Records of the Western Australian Museum 59: 83–95.

Berry P F 1988 Survey of the marine fauna of Christmas Island, Indian Ocean. Western Australian Museum, Perth, WA.

Blackmon D C & Eggleston D B 2001 Factors influencing planktonic post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathburn). Journal of Experimental Marine Biology and Ecology 257: 183–203.

Boltovskoy D 1999 South Atlantic zooplankton. Vol 2, Backhuys publishers, Leiden.

Clark R 1994 Christmas Island Naturally. 2nd Edition, Christmas Island Natural History Association.

Cronin T W 1986 Vertical migration cycles of crab larvae and their role in larval plankton dispersal. Bulletin of Marine Science 39(2): 192–220.

Done T J & Marsh L 2000 Reef-building corals of Christmas Island. Records of the Western Australian Museum 59: 79–81.

Donguy J R & Meyers G 1995 Observations of geostrophic transport variability in the western tropical Indian Ocean. Deep-Sea Research I 42(6): 1007–1028.

Epifanio C E 1995 Transport of the blue crab (*Callinectes sapidus)* larvae in the waters off Mid-Atlantic States. Bulletin of Marine Science 57: 713–725.

Flores A A V, Cruz J & Paula J 2002 Temporal and spatial patterns of settlement of brachyuran crab megalopae at a rocky coast in Central Portugal. Marine Ecology Progress Series 229: 207–220.

Garvine R W, Epifanio C E, Epifanio C C & Wong K-C 1997 Transport and recruitment of blue crab larvae: a model with advection and mortality. Estuarine, Coastal and Shelf Science 45:99–111.

Gibbons M J 2000 An introduction to the zooplankton of the Benguela Current region. Marine & Coastal Management, Cape Town.

Gray H 1981 Christmas Island Naturally. 1st Edition, Christmas Island Natural History Association.

Hicks J W, Rumpff H & Yorkston H 1984 Christmas Island Crabs. Christmas Island Natural History Association.

Hicks J W 1985 The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). Australian Journal of Zoology 33: 127–142.

Johnson D R, Hester B S & McConaugha J R 1984 Studies of a wind mechanism influencing the recruitment of blue crabs in the Middle Atlantic Bight. Continental Shelf Research 3(4): 425–437.

Lee T L, Coleman R A & Jones M B 2005 Vertical migration during tidal transport of megalopae of *Necora puber* in coastal shallow waters during daytime. Estuarine, Coastal & Shelf Science 65: 396–404.

Longhurst AR 1985 The structure and evolution of plankton communities. Progressive Oceanography 15: 1–35.

Marsh L 2000 Echinoderms of Christmas Island. Records of the Western Australian Museum 59: 97–101.

McKinnon AD, Diggan S & De'ath G 2005 Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. Estuarine, Coastal & Shelf Science 63: 497–511.

Meyers G, Bailey R J & Worby A P 1995 Geostrophic transport of Indonesian Throughflow. Deep-Sea Research I 42(7): 1163–1174.

Morgan G J 2000 Decapod crusatcea of Christmas Island. Records of the Western Australian Museum 59: 117–123.

Nair S S R, Nair V R, Achuthankutty C T & Madhupratap M 1981 Zooplankton composition and diversity in western Bay of Bengal. Journal of Plankton Research 3(4): 493–508.

Parks Australia North Christmas Island (PANCI) 2005 Island Wide Survey, Unpublished Report, Parks Australia North Christmas Island, Department of Environment & Heritage.

Perry H, Johnson D R, Larsen K, Trigg C & Vukovich F 2003 Blue crab larval dispersal and retention in the Mississippi Bight: testing the hypothesis. Bulletin of Marine Science 72:2: 331–346.

Quadfasel D, Frische A & Cresswell G 1996 The circulation in the source area of the South Equatorial Current in the eastern Indian Ocean. Journal of Geophysical Research 101(5): 12,483–12,488.

Shanks A 2001 An identification guide to the larval marine invertebrates of the Pacific Northwest. 1st Edition, Oregon State University Press, Corvallis.

Tranter D J & Kerr J D 1967 Seasonal variations in the Indian Ocean along 110°E. Australian Journal of Freshwater Research 20: 77–84.

Tranter D J & Kerr J D 1977 Further studies of plankton ecosystems in the Eastern Indian Ocean III. Numerical Abundance and Biomass. Australian Journal of Marine & Freshwater Research 28: 557–583.

Wijffels S, Sprintall J, Fieux M & Bray N 2002 The JADE and WOCE I10/IR6 Throughflow sections in the southeast Indian Ocean. Part 1: water mass distribution and variability. Deep-Sea Research II 49: 1341–1362.

Wells F E, Slack-Smith S M 2000 Molluscs of Christmas Island. Records of the Western Australian Museum 59: 103–105.

Wolcott T G & Wolcott D L 1982 Larval loss and spawning behaviour in the land crab *Gecarcinus lateralis* (Freminville). Journal of Crustacean Biology 2(4): 477–785.

Wyrtki K 1962 The upwelling in the region between Java and Australia during the south-east monsoon. Australian Journal of Marine & Freshwater Research 13: 217–225.