RAFFLES BULLETIN OF ZOOLOGY Supplement No. **30**: 150–161
Date of publication: 25 December 2014
http://zoobank.org/urn:lsid:zoobank.org:pub:24DAFC98-F485-4C4E-88B9-3C3A66BA1DFD

The population structure of *Birgus latro* (Crustacea: Decapoda: Anomura: Coenobitidae) on Christmas Island with incidental notes on behaviour

Drew M. M.[1,2*] & Hansson B. S.[2]

Abstract. We report on the population size and structure of *Birgus latro* on Christmas Island, Australia. Density estimates varied seasonally from 4.3 crabs ha^{-1} to 41 crabs ha^{-1} on the mid plateau, whilst numbers on the coastal plateau peaked at 47.3 crabs ha^{-1} and recorded a low of 16.3 crabs ha^{-1}. These densities are much lower than previously recorded on the island in similar habitats, suggesting that there may have been substantial declines in the population since the late 1970s. However, methods for collecting count data varied considerably between previous studies and ours and as the population is highly mobile it is difficult to make accurate comparisons. Size sexual dimorphism was apparent, with males reaching much larger sizes compared to females. There were few crabs ≤25 mm in size despite targeted searches for this size group and this may indicate a lack of recruitment in recent years. At a minimum, our results highlight the necessity to implement an accurate monitoring programme on Christmas Island, which can effectively assess the population's trajectory and investigate the potential causes of any declines.

Key words. *Birgus latro*, Christmas Island, density, population structure, sex ratios

INTRODUCTION

The robber crab or coconut crab (*Birgus latro*) is the world's largest terrestrial arthropod, reaching weights of up to 4 kg and with a leg span close to 1 m. The crab is widely distributed on remote tropical islands in the Pacific and Indian Oceans, the Ryukyu Islands of Japan being the only population known to exist outside of the tropics (Drew et al., 2010). Populations of *B. latro* are declining throughout their range, with loss of habitat and harvesting for human consumption thought to be the key drivers of the declines. However, populations in general are poorly studied, and consequently the species is considered data deficient under the IUCN red list (Eldredge, 1996).

Christmas Island (Indian Ocean) is currently thought to support one of the largest populations *of B. latro* in the world. Since 1978 the crab has been protected from hunting and habitat destruction on over 60 % of the island, and it is therefore arguably one of the most secure populations in the species current range (Drew et al., 2010). The crab was first observed on Christmas Island in 1688, by Dampier (Gibson-Hill, 1947) and the population was later described by Andrews (1900), who noted that the species was abundant across the island both in coastal locations and high up on the central plateau. Andrews (1900) did not attempt to quantify the density of the crabs, nor were any attempts made to determine population structure such as sex ratios. He did however note the presence of many small individuals, described as "…not more than an inch or two long… were fairly common." (Andrews, 1900). Gibson-Hill (1947) provided similar information to Andrews (1900) on the population of *B. latro* on Christmas Island noting that '...the smallest free forms [living free from a shell]... were common in the forest in the first three months of the year,' and describes the species as equally common across the island, but he made no attempt to quantify the population size or structure.

No definitive attempt to describe the population of *B. latro* on Christmas Island was made until 1979. Using linear unbaited road based transects, Rumpff (1986) estimated that the population density on the island varied from between 67 and 166 crabs ha^{-1}. He noted that the crab appeared to be more common on the western portion of the island compared to the eastern side and that *B. latro* was uncommon in areas highly modified by humans such as the township and parts of the forest impacted by phosphate mining. Rumpff (1986) reported a male bias in sex ratios based on sampling that occurred in the period April–June 1979 on both the coastal terraces and on the upper/central plateau. James (2007) later reported a similar male bias based on road surveys. However, Drew et al. (2012) reported that sampling method could greatly influenced sex ratios, comparing linear transects with a grid method on Christmas Island; males dominated linear transects, whilst females dominated in grid sampling conducted during the same period and location.

---

[1] Department of Parks and Wildlife, Kensington, Western Australia; Email: myobatrachid@hotmail.com; michelle.drew@dpaw.wa.gov.au (*corresponding author)

[2] Max Planck Institute for Chemical Ecology, Hans Knoell Strasse 8, D-07745 Jena, Germany

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

To provide preliminary baseline data for future monitoring we describe the population of *B. latro* from two locations within Christmas Island National Park. Information on population structure and size will provide a starting point from which future monitoring can assess the population's trajectory. Knowledge of the population trend will then enable easier identification of potential threats to the species persistence, particularly in a population where direct human threats should be minimal. For a detailed summary on the biology and seasonal behaviour of this species on this and other islands see Drew et al. (2010).

MATERIAL AND METHODS

Mid plateau. Three grids, approximating 100 ×100 m (1 ha) were established at Aldrich Hill on the mid plateau, Christmas Island National Park, Christmas Island (Indian Ocean; Fig. 1i, ii). With the exception of January 2010, each unbaited grid was visited once a month (primary period), between August 2009 and March 2010 during daylight hours. At each primary period each grid was thoroughly searched for any *B. latro* individuals four times on a single day providing four secondary samples within each primary period for each grid. Where possible, all individuals sighted were captured, marked with a unique PIT tag and corresponding external paint mark, weighed, sexed, measured, photographed and released at the point of capture (see Drew et al., 2012 for further details). Crabs smaller than 30 mm in thoracic length (TL) or 250 g in weight were not tagged but were captured, weighed, measured and externally marked with paint before release (see Drew et al., 2012 for justification of minimum size for tagging and tagging protocol). From April 2010 to December 2010, only two secondary samples were conducted on a single day in each grid.

Coastal plateau (sub-adult searches). Very few studies have been able to collect substantial numbers of small *B. latro* (i.e., TL <10 mm) (Kadiri-Jan & Chauvet, 1998) and preliminary sampling in the mid plateau area revealed few crabs with a TL ≤25mm. Reese (1987) suggested that the relatively few numbers of small individuals in many studies was due to sampling bias and indeed Kadiri-Jan & Chauvet (1998) discovered that juveniles and sub-adults (those that have abandoned their hermit shell but are still ≤25 mm in

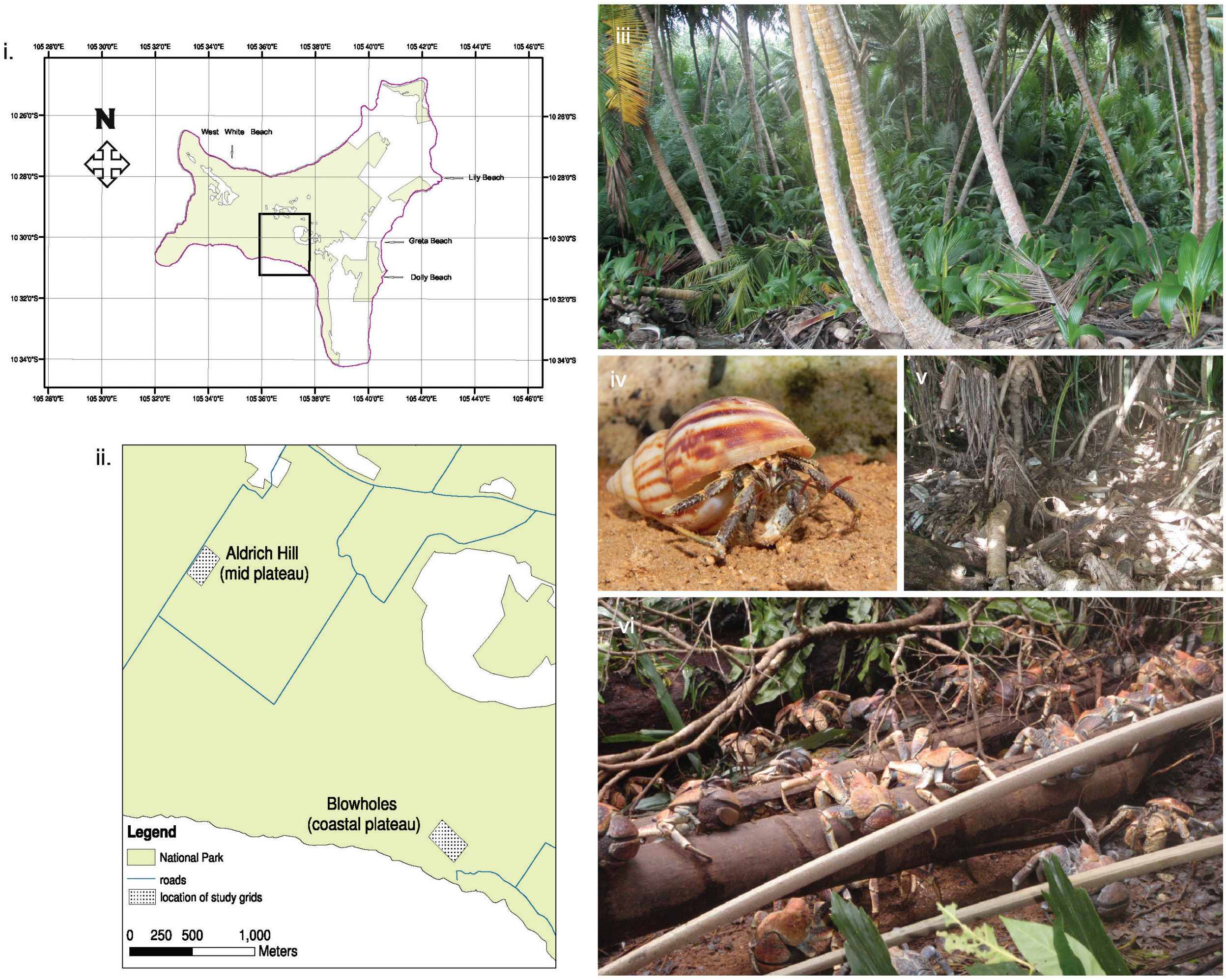

Fig. 1. (i) Map showing the location of sampling on Christmas Island. (ii) Map indicating the approximate location of the grids (show as a single block in each location) on the mid and coastal plateau. (iii) Area searched at Dolly Beach for juveniles (one of the only natural coconut palm groves present on Christmas Island). (iv) Juvenile *B. latro* discovered inhabiting the introduced giant African land snail shell at Settlement in March 2012 (image courtesy of F. Napier). (v) Typical Pandan forest leaf litter areas searched for juveniles and sub-adults on beaches and on the coastal plateau. (vi) A large congregation of *B. latro* feeding on a fallen *Arenga listeri* palm. Note the almost complete absence of females in the image but nearby searches revealed females on the periphery.

TL) are cryptic in their habits. In order to identify key sub-adult (defined for the present study as those individuals ≤25 mm in TL but no longer in their shell) habitat on Christmas Island, three grids were established on the coastal plateau (Blowholes; Fig. 1ii), incorporating relatively large areas of habitat (ca. 26% of the total area in the grid) deemed suitable for sub-adults. Unlike Lifou, where large numbers of juveniles and sub-adults were discovered at the base of coconut palms (Kadiri-Jan & Chauvet, 1998), coconut palms on the coastal plateau of Christmas Island National Park are relatively rare. Therefore, areas of thick Pandan forest (*Pandanus* spp., the primary forest type on the coastal strip, Fig. 1v) were included in the grids. It was not anticipated that juveniles in shells would be found during this search as only surface areas were searched. These three comparison grids were searched between September and December 2010. Each grid was searched thoroughly over two secondary samples each month, as per the protocol outlined for the mid plateau site.

Juvenile searches. Beach searches were also conducted in May 2010 at four of the key beach areas that have exposed sandy shorelines at high tide. These included Lily, West White, Greta and Dolly Beaches (Fig. 1i). Areas where substantial leaf litter or sea born refuse had collected (Fig. 1iii, v) were searched for a minimum of two hours at each location. All hermit crabs captured were thoroughly examined to identify the presence of any *B. latro* individuals.

In addition, five quadrats of 1 × 1 m were located on beaches in areas near potential leaf litter food sources and were searched at each beach location. Each quadrat was dug to a depth of 15 cm using a hand trowel and all hermit crabs captured examined.

Climate. Christmas Island experiences a tropical equatorial climate. The island receives a mean annual rainfall of 2133.6 mm, the majority of which falls during the wet season, December to April (BOM 2014, station 200790). Humidity ranges between 80–90% but can vary considerably across the island. The average daily maximum temperature reaches a high of 28°C in April and the average daily minimum temperature falls to 22°C in August.

Humidity and temperature data loggers were located for a number of months at both the mid plateau and the coastal plain. However an attack by ants on one of the data loggers resulted in unreliable data. Limited data from the coastal plateau is presented along with rainfall data collected from the airport meteorological station, which is approximately 10 km from both sites (Fig. 2). It is important to note that the airport is located some 261 m above sea level and there can be significant variability in conditions experienced at the airport compared to other areas on Christmas Island.

RESULTS

Morphometrics. A total of 962 crabs (525 females) were captured and measured between August 2009 and December 2010 on the mid plateau and 312 (153 female) were measured at the coastal site in the four sample periods between September and December 2010 inclusive and during the juvenile searches. There was distinct lack of small individuals (≤25 mm TL) at both the coastal and mid plateau sites and no individuals were discovered carrying a shell.

There was a clear sexual dimorphism at both sites, with male crabs dominating the larger size classes (Figs. 3, 4). On the mid plateau, captured females were on average 24% smaller than males recorded at the same site. Females ranged in size from 16.9 mm TL through to a maximum of 51.2 mm, with an average of 39.9 mm ± 0.21 (se) TL, comparatively the largest male captured was 76.1 mm TL, the smallest 19.4 mm TL. Males averaged 52.81 mm ± 0.55 (se) in TL. Only 10 crabs or <1% of those captured on the mid plateau were ≤25 mm in TL.

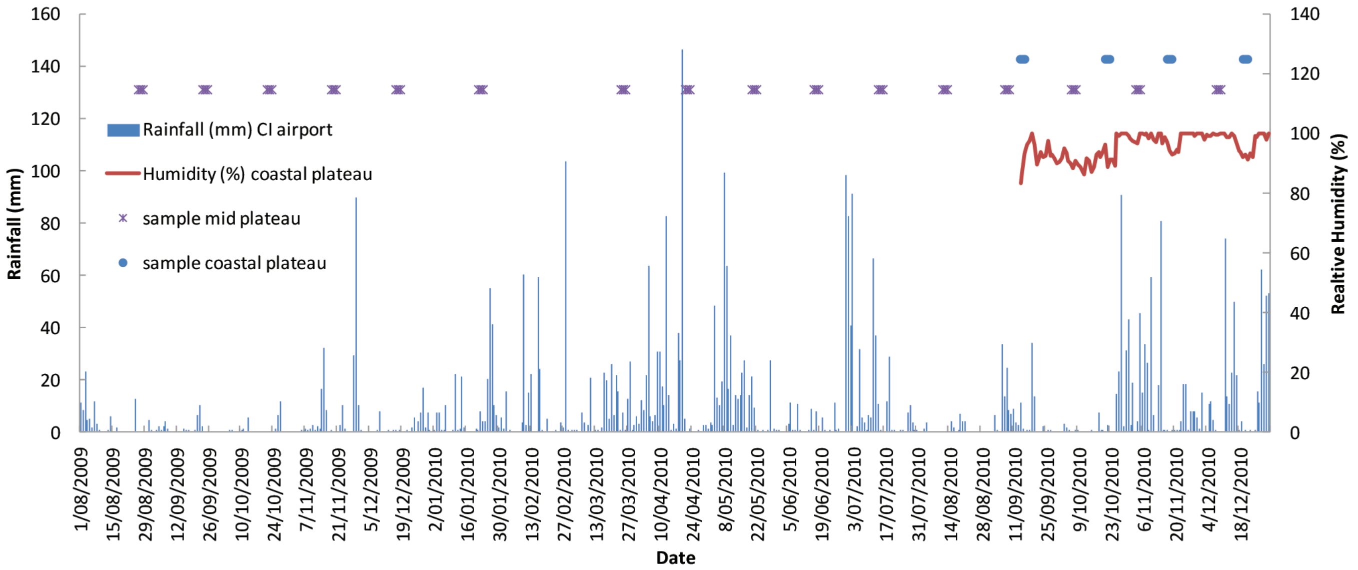

Fig. 2. Rainfall (blue bars) recorded at Christmas Island airport weather station No. 200790 (BOM 2014) and relative humidity recorded at the coastal plateau (red line) using EasyLog USB Humidity and Temperature dataloggers. Purple dots and blue dots indicate the timing of the crab sampling at the mid plateau and coastal plateau respectively.

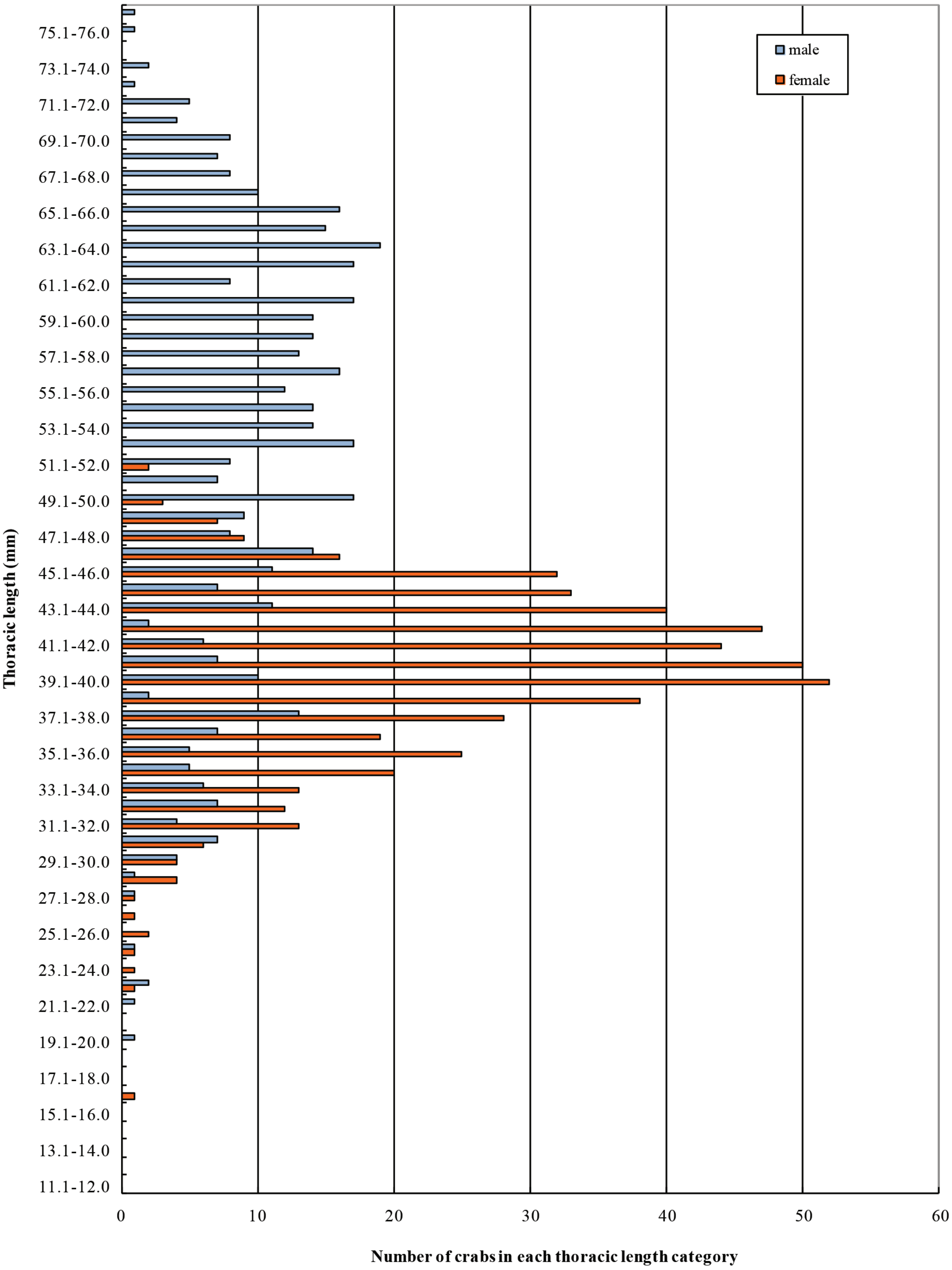

Fig. 3. Population structure of *B. latro* on the mid plateau based on 1 mm thoracic length categories, in the period between July 2009 and December 2010. A total of 962 crabs (525 females = orange bars) were recorded at this site. Males = blue bars. This data excludes recaptured individuals.

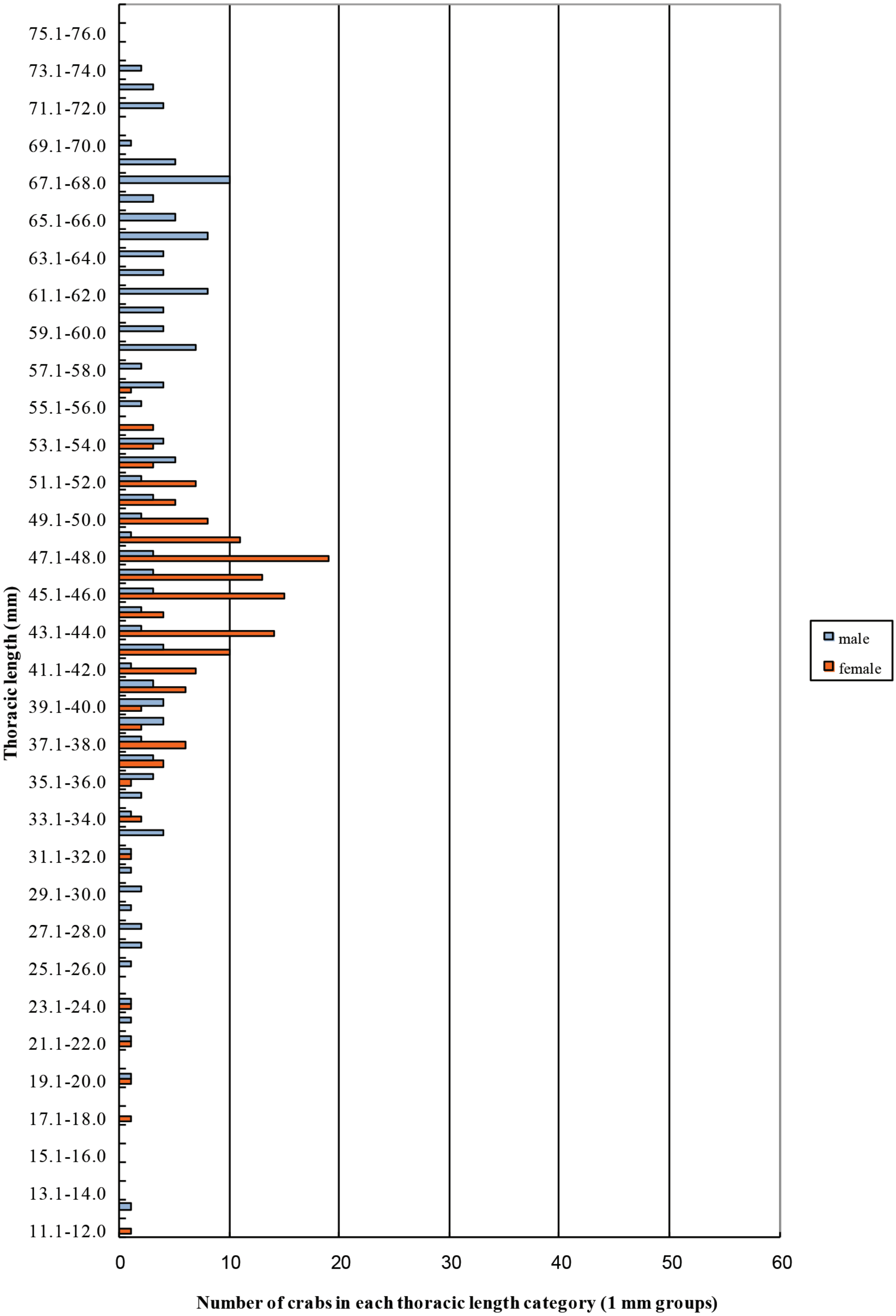

Fig. 4. Population structure of *B. latro* on the coastal plateau based on 1 mm thoracic length categories, in the period between September and December 2010. A total of 312 crabs (153 females = orange bars) were recorded at this site. Males = blue bars. This data excludes recaptured individuals.

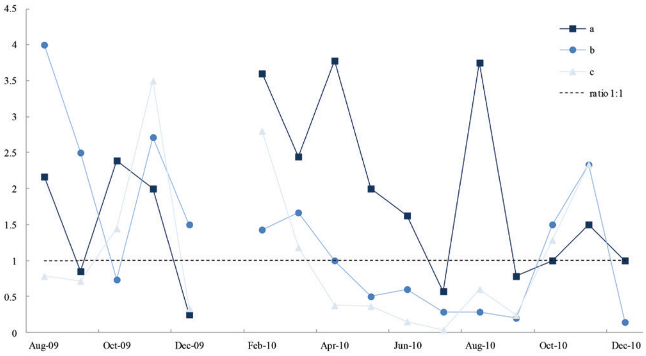

Fig. 5. Variation in the female to male sex ratio of *B. latro*, spatially (among grids a, b and c) and temporally (between sample months) for crabs captured at the mid plateau.

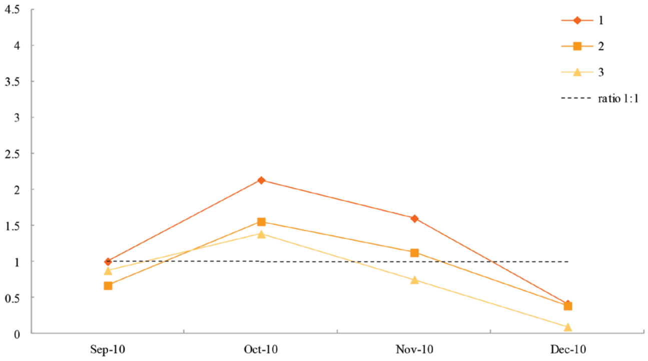

Fig. 6. Variation in the female to male sex ratio of *B. latro*, spatially (among grids 1, 2 and 3) and temporally (between sample months) for crabs captured at the coastal plateau.

On the coastal plateau (blowholes), males ranged in size from 12.5–73.9 mm TL, averaging 53.0 mm ± 1.39 (se) TL. The males were on average 13% larger than females recorded in the same location. Females reached a maximum of 56.8 mm TL, and averaged 46.11 mm TL ± 0.5 (se), with the smallest female captured being 11.0 mm in TL. Relatively greater numbers of small individuals were captured on the coastal plateau compared to the mid plateau site, with 3.2% of those captured (10 crabs) at the coastal site ≤25 mm in TL compared to <1% of those seen at the mid plateau. It is important to note that the coastal site incorporated large areas of habitat deemed important for subadults on Christmas Island.

Crabs on the coastal plateau were more evenly distributed amongst size classes compared to those recorded on the mid plateau (Figs. 3, 4). Over 95% of the female crabs recorded on the mid plateau measured in the size categories 25.1–47.0 mm TL, compared to only 57% in the same size group at the coastal site. While over 38% of females at the coastal site fell into the 47.1–55.0 mm in TL size category, compared to less than 4% of the female crabs recorded on the mid plateau.

Sex ratio. The relative abundance of each sex varied both spatially and temporally on the mid plateau. There was considerable variation in the distribution of sexes between grids within a primary period and within a grid between primary periods (Fig. 5). On the coastal plateau there was far less variability between grids within a primary period compared to the mid plateau site (Fig. 6). However, the temporal variation in sex ratios at the coastal site was relatively high, with the October 2010 primary period dominated by females, whilst December 2010 counts recorded mainly males. A comparison within months (primary periods) between the mid and coastal plateau sites shows that the sex bias at a location was not site specific, with both sites having a similar trend of higher numbers of females in October and November 2010 compared to that recorded in September or December. However, the magnitude of bias was not always equivalent between the two sites (Figs. 5, 6).

Population density/size (seasonal changes). In order to standardise the data, only the first two secondary samples for each primary period between August 2009 and March 2010 were included in the following results for Aldrich Hill. This enabled direct comparisons of seasonal changes in the relative abundance of crabs across the entire sampling period August 2009 to December 2010 despite the use of the two sampling methods (two versus four secondary samples within a primary period).

The population density varied considerably between months (Fig. 7). On the mid plateau crab numbers peaked at 41.0 crabs ha^{-1} ± 14.10 (se) in October 2009, and 31 crabs ha^{-1} ± 6.8 (se) in September 2010 (Fig. 7). By December in each year, population densities were at their lowest on the mid plateau, with only 5.3 crabs ha^{-1} ± 0.3 (se) in 2009 and 4.5 crabs ha^{-1} ± 0.4 (se) in 2010. The density of crabs increased from the December low in February with 22.33 crabs ha^{-1} ± 0.88 (se), slightly above the average for the site of 21.02 crabs ha^{-1} ± 2.56 (se). There was also a slight decrease in crab numbers observed in June 2010, with 18.33 crabs ha^{-1} ± 4.81 (se). The maximum number of crabs seen on a single one hectare grid using the two replicates was 69 crabs in October 2009 (Fig. 8).

The highest densities recorded on the coastal plateau were in September 2010 with 47.3 crabs ha^{-1} ± 3.52 (se). Post this date, the density of crabs declined to a low of 16.3 crabs ha^{-1}, but the densities in the four sampled months were consistently higher than that recorded on the mid plateau in the same period (Fig. 7). However, crab counts were only significantly different between the two sites in December 2010 ($t(4) = -3.36269$, p (2-tail) = 0.0282). The average density of crabs over the four sampling months on the coastal plateau was 29.5 crabs ha^{-1} ± 7.1 (se) and the maximum number of crabs seen on a single grid over the entire sample period was 52 crabs in September 2009.

Of note is the significant reduction in population numbers at the mid plateau site in December compared to previous months. Over 72% of the population seen in November of 2009 and 73% of the population seen in November 2010 were no longer available for capture by December of the same year. In comparison, counts at the coastal site between November and December only reduced by ca. 20% between the two sample periods (Fig. 7).

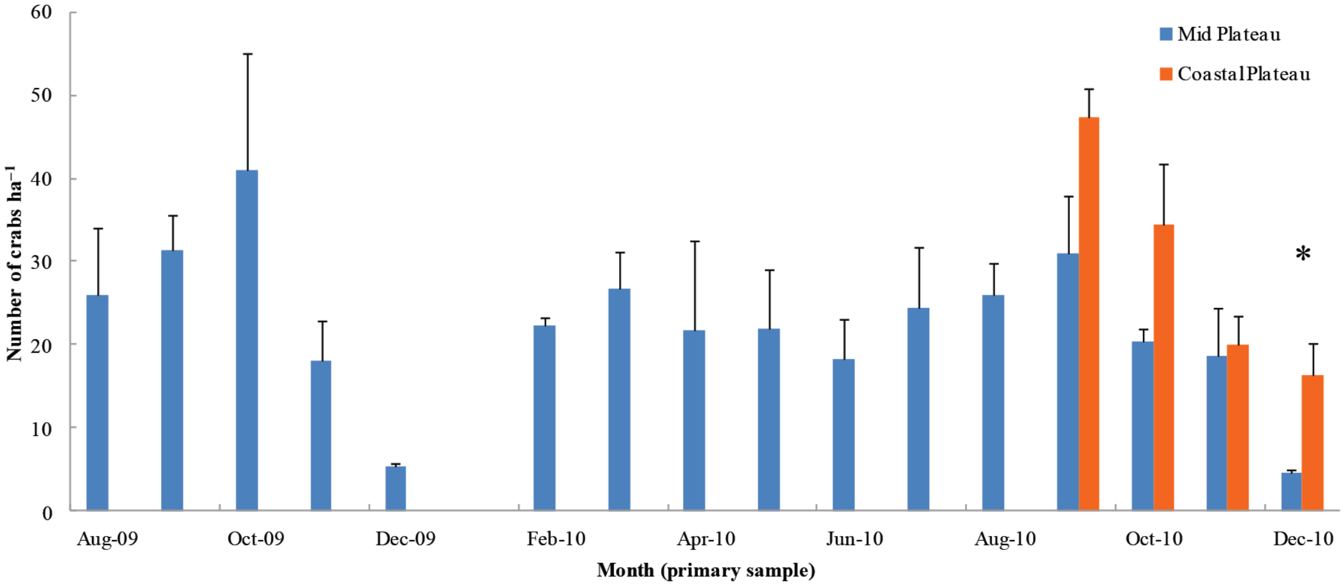

Fig. 7. Seasonal changes in the density of *B. latro* per hectare based on two standardised secondary samples at the mid plateau (blue) and the coastal plateau (orange). Error bars = standard error; * indicates months where numbers of crabs at the two sites were significantly different at the $p < 0.05$ level

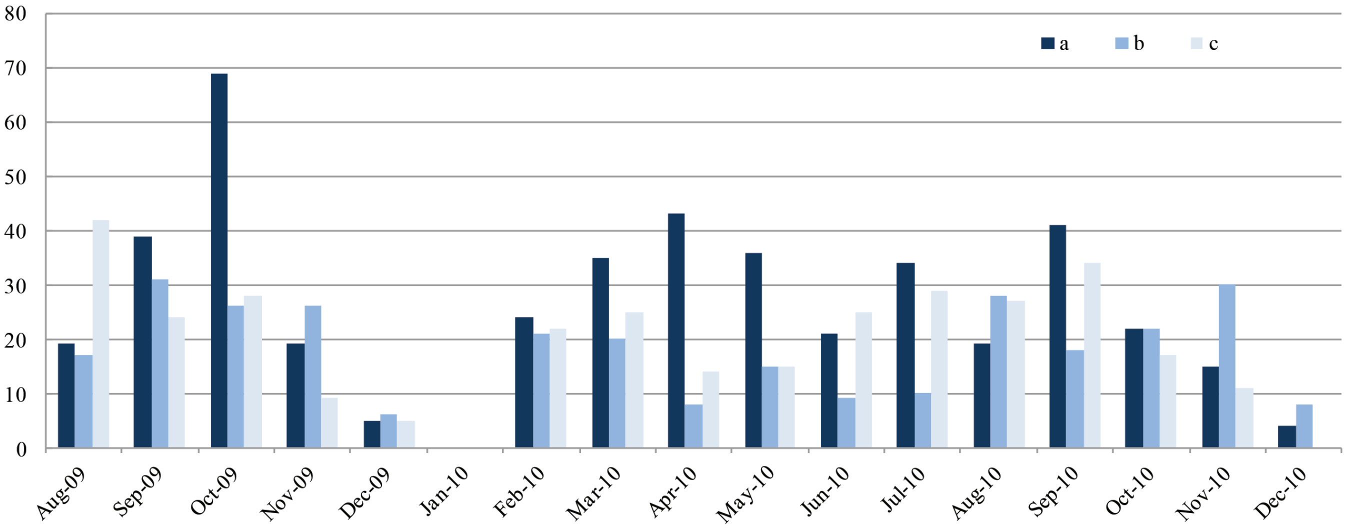

Fig. 8. Seasonal variation in number of *B. latro* observed in each grid on the mid plateau using data from the first two replicates only.

Detectability on the mid plateau. In order to determine the percentage of the population missed as a result of different sampling intensity, a comparison was done between the two sampling protocols (four versus two secondary samples within a primary period) conducted on the mid plateau. Density was estimated from the two methods by dividing the number of crabs seen in each method by the area searched to give a density ha^{-1} for each method and standard error for each (Fig. 9). Results indicate that between 12.8 and 35.5% (average: 20.7%) of the population is missed using the lower intensity two secondary sample method.

Maximum density of crabs at the mid plateau using the four secondary sample method resulted in a peak density of 47 crabs ha^{-1} ± 14.2 (se) in October 2009. A maximum of 75 crabs were seen on a single one hectare grid on one day using the four replicate sampling method (Fig. 10) in the period August 2009 to March 2010, compared to 69 on the same grid in the same month using data from just the first two replicates (Fig. 8).

Juvenile beach searches. Extensive beach searches of both beach debris and sand habitats revealed no juveniles. The only individual in a shell with a TL of <10 mm reported to us on the island in the period between 2009 and 2012 was discovered and photographed by a local Parks Australia North officer in the town centre (coastal plateau) on the evening of 17 March 2012 (Fig. 1iv). The crab occupied the shell of a giant African land snail (*Achatina fulica*). An additional anecdotal record was noted in 2010 when a small *B. latro* was discovered in its shell hiding under leaf litter in a resident's garden in the area known as Drumsite (on the mid plateau), within the township of Christmas Island. No photographs or measurements were taken, however the resident reports noting the crab inhabited the discarded shell of the introduced giant African land snail.

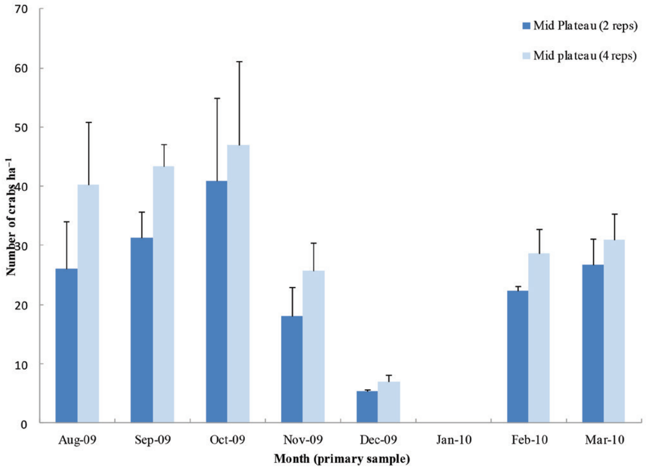

Fig. 9. Detectability of *B. latro*: the variation in the density of *B. latro* ha^{-1} recorded using the first two secondary samples (2 replicates = dark blue) and four secondary samples (4 replicates = light blue) within a grid on the mid plateau in the period August 2009 to March 2010. Note: This data includes both crabs captured and those that were only observed (but could not be captured) to give the most accurate estimate of density. Error bars = standard error (N = 667 crabs).

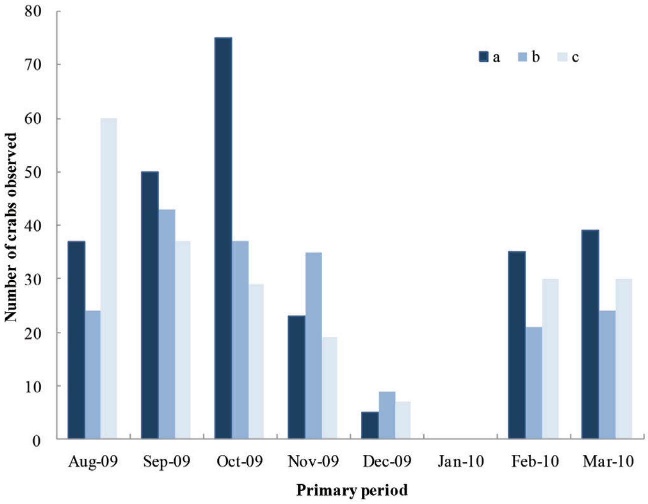

Fig. 10. Seasonal variation in the number of *B. latro* observed in each grid on the mid plateau using the four replicate per primary period method. Note: This data includes both crabs captured and those that were only observed (but could not be captured) to give the most accurate estimate of density.

Incidental notes on juveniles. Incidental sampling identified a number of sub-adults moving up to the mid plateau in February 2011. Two females <12 mm in TL were discovered moving up the primary hill between the coastal plateau and mid plateau near Middle Point, just south of the mid plateau sampling site. In general there were many more small individuals sighted during the early part of the year in both 2010 and 2011. This may indicate that coastal sampling had not been timed to intercept the period of highest activity for sub-adults.

Incidental records on movement. Records incidentally collected on the coast 2 km directly south of the mid plateau site between December 2010 and February 2011 revealed nine males and one female that had been tagged at the mid plateau. Of these, three males and the female had been recaptured multiple times on the mid plateau over several years and it is likely that the grids on the mid plateau could be considered to be within their usual home range. Similar surveys conducted during the non-breeding period in 2011 revealed a total of three males that had been tagged on the mid plateau. Discovery of tagged individuals at the coast indicates that both males and females move between the coast (despite previous reports to the contrary, see Drew et al., 2010 for details) and the forest on the mid plateau, and records from our study would indicate that this movement is more common during the wet season.

Incidental notes on mating behaviour. No females were discovered at the mid plateau with any indication that they had mated during the peak reproductive period (October and November), in either 2009 or 2010 despite examining over 230 females. In contrast, of the 107 females examined at the coastal plateau in October and November 2010, five females had clearly been sexually active with spermataphores present near their gonophores and a number of males were captured that had traces of spermataphores on their undersides indicating recent sexual activity. A similar number of females were discovered with spermataphores on the coastal plateau in late November 2009 during incidental monitoring for another experiment. No ovigerous females were found at either site.

DISCUSSION

Morphometrics. As with other populations throughout the species range (see Drew et al., 2010 for a review) the population of *B. latro* on Christmas Island is size sexually dimorphic, with males on average attaining much larger sizes than females in the same locations. Drew et al. (2010) compared the average size variation between the largest males and females recorded in eight of the studies reviewed and noted an average variation of 21.9 mm ± 7.7 (se) TL between males and females in each location. Variation in the sizes recorded in the present study are similar to that recorded in other studies with the sexual variation between the largest male and female on the mid plateau being 24.9 mm TL and 24.5mm TL on the coastal plateau.

The variation in size distribution of crabs between the two sites is worth noting. On the mid plateau there were few crabs smaller than 25 mm in TL compared with those recorded at the coastal site. As the coastal site was established primarily to incorporate primary sub-adult habitat it is not surprising that more of sub-adults were noted at this site. Kadiri-Jan & Chauvet (1998) noted that on the island of Lifou (New Caledonia) crabs >25mm in TL (around sexual maturity) were commonly noted to move from the coastal region to higher elevations. The limited number of sub-adults in our study on the mid plateau may therefore be a result of immature crabs remaining in coastal locations and therefore not available for capture at this relatively elevated site.

Sex ratios. Interestingly, and unlike most other previous studies on this and other islands (e.g., Helfman, 1973;

Amesbury, 1980; Rumpff, 1986; Kadiri-Jan, 1995, James, 2007), our study recorded a predominately female bias population. Notably this bias was not consistent, neither spatially nor temporally, and the large variability in sex ratios and population density at a single location over time and space illustrates a highly dynamic population. It is likely that spatial and temporal variability is linked with a complex life cycle associated with reproductive migrations, moulting requirements, availability of resources and potentially behavioural variations associated with environmental conditions at a site.

Birgus latro has been described as a highly mobile omnivorous predator. The species has been noted to feed on a wide variety of fruit as well as scavenge carcasses and actively hunt conspecifics and other crustacean species (see Drew et al., 2010 for a review). As all these food sources are likely to be highly variable in space and time, the variation in densities of crabs is hardly surprising. What is of interest however is the apparent clustering of sexes. Clear variations in the sex ratios within a primary sample between grids show a highly patchy sexual preference for particular areas. The dynamic nature of the site preferences recorded in this study suggests that a single sex is actively choosing an area and/or excluding the opposite sex from a site at certain times. Large males often actively exclude females and potentially smaller males from desirable feeding locations (Fig. 1vi; Rumpff, 1986, Drew et al., 2012), and this may explain some of the sexual differentiation between sites. Females may be congregating in nearby habitats in order to be able to exploit a resource once the dominant males have moved on. Alternatively, males and females may require different resources at different times of the year, which could result in this apparent temporal and spatial sexual partitioning.

Schiller (1993) noted that most females moved to very humid locations such as coastal caves during incubation, presumably to prevent desiccation of the egg mass, which is carried in a relatively exposed location on the underside of the female's abdomen. Schiller (1993) also noted that berried females were less likely to be seen foraging during the day and were more likely to be seen moving to the coast to forage during the hours of dark. The large change in sex ratio at the coastal location in December (a month after we noted a peak in sexual activity in the area) may be linked to this behaviour—post-copulation females moving to nearby caves to extrude and incubate eggs.

Variation in sex ratios between this and previous studies on this and other islands is most likely linked to survey methods. Drew et al. (2012) compared transect and grid methods in the same location during the same period. They identified that linear transects had a male bias, whilst the grid sampling revealed a female bias in the same location.

Changes in long-term density estimates. As no previous studies on *B. latro* densities on Christmas Island have used the grid method, no direct comparison can be made to determine if there has been a change in density of the crabs over time between this and other studies. Rumpff (1986) estimated density, using both diurnal and nocturnal unbaited road-based transects in sites to the west of the mid plateau, and to the east of our coastal site. He estimated the population of *B. latro* in 1979 to be approximately 112 crabs ha^{-1} using a 3.9 km portion of track (approximately 4 km south west of the mid plateau site in our study) and 80 crabs ha^{-1} using a 6.8 km section of the south point track (on the coastal plateau, which finished within 1 km of our coastal site). In more disturbed habitats, such as a drill line located between North-South Rd and the cliff edge of the plateau on the east coast, Rumpff (1986) reported densities of about 67 crabs ha^{-1}. Whilst in 1987, Schiller (1988) estimated a total population of 1,257,342 ± 335,854 (se) crabs on the island or approximately 93 crabs ha^{-1} ± 24.87 (se) based on 15, 500 m nocturnal linear forest transects set across the island both within and outside of the National Park (no dates were given).

As both these studies identified densities that are substantially higher than recorded in our study, it may suggest that the *B. latro* population has declined on the island substantially since the late 1980s. However, it is important to note that the survey methods differed significantly between previous studies and ours. As humidity levels strongly influence crab activity (Rumpff, 1986; Hamasaki et al., 2011), the nocturnal surveys conducted by Rumpff (1986) and Schiller (1988) may have improved crab capture rates. But, regardless of the potential variability associated with different survey methods, the substantial differences in densities recorded between the surveys are notable and should not be overlooked. Although *B. latro* is protected on most of the island, road kills have increased substantially in recent years due to an increasing human population and activities such as phosphate mining in nearby habitats (Smith, pers. comm.). In addition, the crab has experienced localised declines on the island due to the introduced yellow crazy ant, *Anoplolepis gracilipes* (Smith, pers. comm.), whilst information collected in the present study suggests they may have seen reduced recruitment in recent years. Efforts should be made to ensure that this apparent decline is not a true illustration of the trajectory of the population on the island.

Seasonal changes in density. Previous studies have noted that only females migrate to the coast for breeding (Schiller, 1988). However, the significant reduction in both male and females at the mid plateau site on all grids in December 2009 and 2010 in our study indicate that male crabs are either migrating to the coast with the females or males may change their behaviour significantly during this period making them less available for capture. Krieger et al. (2012) recently reported on the long-distance migration of male *B. latro* on Christmas Island. Their GPS-based tracking showed that males frequently undertake coastal migrations during the wet season (November–April), which also coincides with the period of highest reproductive activity on Christmas Island. In comparison, few long-distance migrations were recorded on male crabs monitored during the dry season at the same location. Krieger et al. (2012) suggests a number of theories for these wet season coastal migratory events ranging from resource motivated movements through to reproductive motivations, however they had no direct evidence to link the movement with a particular theory.

Incidental records from our study indicate that more males appear to migrate to the coast during the breeding period compared to non-breeding periods, a result similar to that reported by Krieger et al. (2012). However, as none of the individuals tagged on the mid plateau and subsequently recaptured at the coast showed any evidence of recent sexual activity, we cannot directly link this movement with reproductive motivations. But, two patterns are worth noting:

1) The relatively large numbers of females and males seen at coastal locations with evidence of recent sexual activity during November 2009 and 2010. The sex ratio at the coastal site during November 2010 was almost 1:1 compared with a relatively strong female bias in October 2010. A month later, in December 2010, the sex ratio at the site became heavily male biased despite relatively similar numbers of crabs being recorded at the site between the two months.

As noted previously the large change in sex ratio at the coastal location in the month following peak sexual activity is most likely related to the post copulation females moving to nearby caves to extrude and incubate eggs. We suggest that peak sexual activity occurred at or around 19 November 2010, to coincide with a dusk high tide (1.47 m at 1749 hours, sunset 1800 hours) and four days before the full moon recorded to occur on 22 November 2010 at 0027 hours (Time and Date AS, 2013).

2) On the mid plateau where no sexual activity was recorded during any sampling period in 2009 or 2010, there was a strong female bias in the captured population in both November 2009 and 2010. A month later in December 2010 almost all the crabs at the site were no longer available for capture, with over a 70% reduction in the numbers of crabs captured from November to December in both years, and almost all of the crabs captured in December in both years being male.

In this situation we theorise that the sampling in September, October and November 2010 coincided with large numbers of crabs moving through the site on their migration to the coast at the commencement of the wet season. Crabs migrated to the coast in preparation for the first large copulatory event thought to occur roughly 30 days (the average incubation period for eggs as reported by Schiller, 1988) before a dusk high tide after the first major rain of the season. By the December 2010 sample, all crabs that were reproductively active for the year had moved to the coast and were no longer available for capture at this site. This may explain the large reduction in the number of crabs at all grids at the mid plateau site.

The slight drop in numbers in June 2010 may be linked to increased numbers of crabs retreating to burrows to moult. Limited data collected on burrow densities during the study suggest that burrow densities peaked around June.

Detectability. Despite the large size of many *B. latro* individuals, the species can be highly cryptic, with crabs often found concealed in cryptic refuges such as logs, tree hollows, in the crown of dense trees and rock crevices or subterranean spaces. Efforts were made to ensure that all accessible trees and hollows were searched, however repeated surveys within a single day highlighted that a large proportion of the population remained concealed for at least part of the day. Attempts to undertake a similar survey at night indicated that this type of search method in forested areas was difficult (compared to linear searches) and preliminary results indicate that it did not increase capture rates substantially.

Drew et al. (2012) compared transects and grid sampling methods and discovered that sampling method can influence sex ratios. Our study highlights that sampling effort can increase population counts in the same locality from between 12.7 and 35.5% of the sampled population and like Rumpff (1986) we have observed anecdotally that local weather conditions (humidity and rainfall) can strongly influence crab activity during certain times of the year. As the numbers of crabs captured using the higher intensity sampling was not significantly different to the 2 replicate sampling, the increased effort required to do the higher intensity sample may negate any benefit of conducting higher intensity sampling. However, given the large variability in densities between locations it is advisable that multiple locations are sampled simultaneously and at least some of these should be subjected to higher intensity sampling to determine the detectability between sites over time and space.

Recruitment. This study, like almost all previous quantitative studies (Rumpff, 1986; Schiller, 1988; James, 2007) on this and other islands, discovered few small *B. latro*. Both Amesbury (1980) and Kadiri-Jan & Chauvet (1998) concluded that a lack of small individuals in most studies is primarily due to the largely cryptic habits of these individuals in comparison to their larger counterparts. However, numerous searches targeted in habitat described as ideal by Kadiri-Jan & Chauvet (1998) were searched by Rumpff (1986), Schiller (1993) and by us, and very few individuals <20 mm and only a few individuals in the 20–30 mm TL size range were found. Yet reports from early descriptions of the population of *B. latro* on Christmas Island (Andrews, 1900; Harms, 1937; Gibson-Hill, 1947) indicate that both the glaucothoë and small individuals described as not more than an inch or two long were common. Gibson-Hill (1947) specified that crabs of approximately 12 months of age (he provided no size information but referred to age estimates based on laboratory experiments by Harms (1937), so we assume individuals were most likely 8–10 mm TL) were most commonly encountered in the forest in the first three months of the year. Assuming the correct identification of young individuals by these early researchers and our assumptions on size are correct, there appears to have been a massive shift in recruitment success from the early half of the 20th century to now.

As postulated by both Rumpff (1986) and Schiller (1993), recruitment success in *B. latro* is likely to be highly dependent on a multitude of local biotic and abiotic factors. The larval phase of the species requires approximately one month in the open ocean before returning to shore whereby the glaucothoë must locate and inhabit a suitable shell (Reese, 1968; Reese & Kinzie, 1968; Wang et al., 2007; Hamasaki et al., 2011). The individual will remain in a shell for approximately two years before becoming free living (Reese & Kinzie, 1968).

Success at these early stages is likely to be highly dependent on a multitude of biotic and abotic factors including for example local winds, tides, currents, predators, humidity, and food and shelter. Further, recent genetic investigations have revealed that populations of *B. latro* on Christmas Island appear to have been genetically isolated from Pacific Ocean populations most likely since the Pleistocene (Lavery et al., 1995, 1996). As the closest Indian Ocean population (on Cocos (Keeling) Islands) is located some 800 km away, it is reasonable to suggest that in terms of external recruitment capacity Christmas Island could be considered largely isolated compared with Pacific island counterparts, which often have a multitude of islands in relatively close proximity. This isolation along with the multitude of stochastic factors impacting on larval survival and return indicate that it is highly likely that annual recruitment on the island is on average very low. This may explain the absence of many small individuals despite targeted searching in this and previous studies (Rumpff, 1986; Schiller, 1993). However, the contrast with recent reports and those made during the early history of the island, indicate that the frequency of high recruitment events may be declining and this should be investigated further.

CONCLUSIONS

Large variations in density and sex ratio of *B. latro* both temporally and spatially suggest that the population on Christmas Island is highly dynamic. Short-term surveys, which do not account for this variability, are unlikely to adequately reflect the actual population size or structure. This highlights the necessity of ensuring that surveys monitor all habitat types adequately and are designed to accommodate for seasonal behavioural changes associated with large events such as breeding migration and moulting. For example, surveys conducted during a moult period may miss a large proportion of the population, whilst conducting coastal surveys during the breeding period may positively bias counts, resulting in a much inflated population size estimate. Monitoring programmes should be designed to ensure this short-term variability in population and the species detectability are accounted for to ensure a robust estimation of population size.

Our study has noted that there is a substantial difference in the density of *B. latro* collected here and in previous studies. Although survey method and location varied between studies, the discrepancy in densities is substantial and should not be overlooked. The apparent decline in numbers over time may indicate a very real and potentially catastrophic decline in the population and long-term monitoring should be designed to determine the actual trend. Further behavioural studies will provide more comprehensive knowledge on the mechanisms of migratory behaviour on the island and further knowledge on recruitment on the island will be vital to the ongoing management of this species.

We have also noted that there appears to be a very low recruitment in recent years, however it is likely that the survey methods used either missed key habitat or it is possible that searches were not timed for peak juvenile and sub-adult activity. It is recommended that targeted searches should be conducted year round in order to assess the current recruitment success of the population.

ACKNOWLEDGEMENTS

We would sincerely like to thank the following people for their invaluable efforts in the field, without which much of this project could not have been achieved: Kevin Moorman, Kristin Schwartz, Dr Dave Hunter, Don Hardwick, Julie Cope, Julia Bignall, Alison Derry, John Woinarski, Jakob Krieger, Meike Kilian and the tireless team from Parks Australia North (Christmas Island): Michael Smith, Dion Maple, Jess Bolton, Tanya Detto, Caitlyn Pink, Peter Smith, Rachel Barr, Robert Taylor, Finnuala Napier, Chris Boland, Claire Humphries, and Meryl Jenkins. This project was funded by the Max Planck Society.

LITERATURE CITED

Amesbury SS (1980) Biological Studies on the Coconut Crab (*Birgus latro*) in the Mariana Islands. Marine Laboratory Technical Report Number 66. University of Guam, Guam, vii + 36 pp.

Andrews CW (1900) A Monograph of Christmas Island (Indian Ocean): Physical Features and Geology. British Museum (Natural History), London, 337 pp.

Drew MM, Hartnoll RG & Hansson BS (2012) An improved mark-recapture method using passive integrated transponder (PIT) tags in *Birgus latro* (Linnaeus, 1767). Crustaceana, 85: 89–102.

Drew MM, Harzsch S, Stensmyr M, Erland S & Hansson BS (2010) A review of the biology and ecology of the Robber Crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). Zoologischer Anzeiger–A Journal of Comparative Zoology, 249: 45–67.

Eldredge LG (1996) *Birgus latro*, 2008 IUCN Red List of Threatened Species. www.iucnredlist.org (Accessed 23 February 2014).

Gibson-Hill CA (1947) Christmas Island–terrestrial crabs: field notes on the terrestrial crabs. Bulletin of the Raffles Museum, 18: 43–52.

Hamasaki K, Sugizaki M, Sugimoto A, Murakami Y & Kitada S (2011) Emigration behaviour during sea-to-land transition of the coconut crab *Birgus latro*: effects of gastropod shells, substrata, shelters and humidity. Journal of Experimental Marine Biology and Ecology, 403: 81–89.

Harms JW (1937) Lebenslauf und Stammesgeschichte des *Birgus latro* L., von den Weihnachtsinseln. Zeitschr Naturwiss Jena, 75: 1–34.

Helfman GS (1973) The Ecology and Behaviour of the Coconut Crab *Birgus latro* (Linneaus). MSc thesis, University of Haiwaii, Honolulu.

James DJ (2007) Christmas Island Biological Monitoring Programme: population structure and road mortality in red crabs (*Gecarcoidea natalis)* and robber crabs (*Birgus latro*) on Christmas Island. In: Christmas Island Biodiversity Monitoring Programme. Parks Australia North, Christmas Island.

Kadiri-Jan T (1995) Biology and Population Dynamics of the Coconut Crab (*Birgus latro*) in Loyalty Island, New Caledonia. Thesis, Universite Francaise du Pacifique, New Calendonia

Kadiri-Jan T & Chauvet C (1998) Distribution of the juvenile coconut crab, *Birgus latro* (L.), on the island of Lifou, New Caledonia. Ecoscience, 5: 275–278.

Krieger J, Grandy R, Drew MM, Erland S, Stensmyr M, Harzsch S & 1Hansson BS (2012) Giant robber crabs monitored from space: GPS-based telemetric studies on Christmas Island (Indian Ocean). Plos One, 7: 1–14.

Lavery S, Moritz C & Fielder DR (1995) Changing patterns of population structure and gene flow at different spatial scales in *Birgus latro* (the coconut crab). Heredity, 74: 531–541.

Lavery S, Moritz C & Fielder DR (1996) Indo-Pacific population structure and evolutionary history of the coconut crab *Birgus latro*. Molecular Ecology, 5: 557–570.

Reese ES (1968) Shell use: an adaptation for emigration from the sea by the coconut crab. Science, 161: 385–386.

Reese ES (1987) Terrestrial environment and ecology of Enewetok Atoll. In: Devaney DM, Reese ES, Burch BL & Helfrich P (eds.) The Natural History of Enewetok Atoll Volume I The Ecosystem: Environments, Biotas and Processes, Book 1. U.S. Department of Energy, Office of Scientific and Technical Information, Oak Ridge, pp. 187–202.

Reese ES & Kinzie RA (1968) The larval development of the coconut crab or robber crab *Birgus latro* (Linneaus) in the laboratory (Anomura, Paguridea). Crustaceana, Supplement 2: 117–144.

Rumpff H (1986) Ethology, Ecology and Population Biology Field Studies of the Coconut Crab, *Birgus latro* L. (Paguridea, Crustacea, Decapoda), on Christmas Island (Indian Ocean). PhD thesis, Westfaelische Wilhelms-Universitaet, Muenster, Germany.

Schiller C (1993) Early Development and Larval Ecology of the Coconut Crab *Birgus latro* (Linneaus). PhD thesis, University of Queensland, Brisbane.

Schiller CB (1988) Spawning and larval recruitment in the coconut crab *Birgus latro* on Christmas Island, Indian Ocean. In: Australian National Parks and Wildlife Service, Consultancy Report prepared for the Australian National Parks and Wildlife Service.

Time and Date AS (2013) Moonrise and Moonset in The Settlement, Christmas Island, Australia November 2010. http://www.timeanddate.com/worldclock/astronomy.html?n=695&month=11&year=2010&obj=moon&afl=-11&day=1 (Accessed 26 April 2014).

Wang F-L, Hsieh H-L & Chen C-P (2007) Larval growth of the coconut crab *Birgus latro* with a discussion on the development mode of terrestrial hermit crabs. Journal of Crustacean Biology, 27: 616–625.