**Population demographics and dynamics of coconut crabs (*Birgus latro*) on Aldabra Atoll, Seychelles**

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**Abstract**

Island species are highly vulnerable to disturbances linked to human interference and habitat loss. Increased knowledge about the remaining healthy populations is important for their conservation. The coconut crab, *Birgus latro* (Linnaeus, 1767)*,* is one such species, with population declines documented across its range. Aldabra Atoll hosts a significant and unexploited *B. latro* population. This study investigated the spatial and temporal dynamics of *B. latro* on Aldabra over a period of nine years. *B. latro* individuals were assessed; the mean density was 35.4 ± 1.69 ind./ha and has remained stable over the study period. The population exhibited high spatial and temporal variability over density, size and sex. The *B. latro* population on Aldabra is heavily skewed towards males (sex ratio 3:1 male to female) and size is sexually dimorphic with males being larger (mean thoracic length 40.9mm) than females (mean thoracic length 30.6mm). For such a dynamic species, long terms studies are necessary to provide accurate information and develop conservation measures. Aldabra represents a refuge for *B. latro* and holds the potential to repopulate other protected areas in the Western Indian Ocean.

**Key words**: crab density, moulting, reproductive season, sex ratio, spatial variability, temporal dynamics.

**Introduction**

Present extinction rates of species globally are exceptionally high, estimated to be around 100 extinctions per million species per year (Pimm *et al.,* 2014). This is 1,000 times higher than the natural background extinction rate (de Vos *et al.,* 2014). Around 10,673 species are classified as data deficient on the IUCN Red list, meaning that their threat status cannot be assessed due to uncertainties in species taxonomy, distribution, population status or unknown threats (Veron *et al.,* 2016). These uncertainties impact the likelihood of active conservation measures being adopted. Unless directly targeted for monitoring, species classified as data deficient are likely to go extinct without notice (Bland *et al.,* 2014). Taking into account information on data deficient species may therefore help fill data gaps in biodiversity indicators, as well as conserve poorly known biodiversity (Bland *et al.,* 2014). Likewise, the conservation attention paid to invertebrates lags far behind that of vertebrates (mammals, birds, reptiles, amphibians and fish) (Collen *et al.,* 2012). It is crucial to understand the conservation status and trends of invertebrates, since it is these often cryptic and overlooked species that are essential for the functioning of ecosystems (Baillie *et al.,* 2010).

The largest land arthropod, the coconut crab (*Birgus latro),* is classed as data deficient (Eldredge, 1996) due to limited information on the status of the different populations (Drew *et al.,* 2010). Although *B. latro* has a broad geographical range in the tropical Indo-Pacific region, the size and distribution of the populations have been significantly reduced in areas where the species were sympatric with humans (Schiller, 1992). This decline is mostly attributed to loss of habitat and unmanaged harvesting for human consumption (Drew *et al.,* 2010). In the Indian Ocean, the distribution is now largely confined to three populations centred on Aldabra Atoll, Chagos Archipelago and Christmas Island (Lavery *et al.,* 1996). *B. latro* is locally extinct in Mauritius (Eldredge, 1996) and is believed to be no longer present on Mayotte and the Comoros Islands (Poupin *et al.,* 2013). In the Seychelles, *B. latro* has been historically overexploited for food on the granitic inner islands and inhabited outer islands. With the exception of Aldabra Atoll, *B. latro* occurs throughout Seychelles in low incidence with recent opportunistic records on two granitic islands (Aride and Cousine Islands) and occasional sightings on the outer islands (Poupin *et al.,* 2013). Despite *B. latro*’s relative rareness and documented threats, information on the species life-history and ecological requirements is insufficient (Drew *et al.,* 2010), making it difficult to assess status and design potential conservation measures.

On Aldabra *B. latro* has benefited from complete protection since it's designation as a special reserve in 1981 and UNESCO World Heritage Site in 1982. *B. latro* is widely distributed throughout the atoll, inhabiting rock crevices, deep potholes, vegetation and sandy areas (Grubb, 1971). Individuals on Aldabra exist in two distinct colour phases, an orange-red and a purplish-blue morph, with the red morph being more common and believed to be the dominant mode of colour inheritance (Grubb, 1971). In spite of being one of the last remaining viable populations in the Indian Ocean, the status of Aldabra’s *B. latro* population has never been defined. Previous studies have established the importance of the species on the atoll’s ecosystem; Haig (1984) described *B. latro* as a scavenger of major importance on the remains of dead tortoises, tortoise and marine turtle eggs and hatchlings. Alexander (1976) identified several important ecological roles of the *B. latro* on Aldabra: as scavengers they remove rotting material and so reduce the number of carrion breeding flies, they help to decompose leaf litter, they contribute greatly to seed dispersal, particularly figs, providing a food source for birds in the juvenile stage and in turn influence the populations of crab species upon which the birds prey. They also contribute to soil aeration and erosion through their burrowing activity (Alexander, 1976).

This paper presents the results of a nine year study on the demographics and dynamics of *B. latro* on Aldabra Atoll. Individual counts and biometrics data were collected on *B. latro* individuals in two different sampling areas at regular intervals over the study period. Due to its isolation and protection, we hypothesise that Aldabra hosts a significant *B. latro* population with high seasonal variations in densities observed. The overall goal was to define a baseline of the population structure and its spatial and temporal variability. This is useful in order to design future monitoring and to follow the population’s trajectory. In addition, this research aims to provide information on the status and ecology of the Aldabra population and contribute to giving *B. latro* the conservation leverage it deserves. Lastly, the information can also be used to advise the potential of translocating the species to other protected areas within its known historic range.

**Materials and methods**

Study site

Aldabra Atoll (9°25′0.05″ S, 46°24′59.94″ E) lies in the Western Indian Ocean and forms part of the Seychelles archipelago. It is located approximately 1100 km south west of Mahé, the principal island of the Seychelles and 420km from Madagascar (Fig. 1). Aldabra is the second largest raised coral atoll, ca. 34 km long and 14 km wide, and it is composed of a characteristic and irregular coral limestone formation termed as ‘champignon’. The terrestrial environment is dominated by a dense scrub of varying height, either continuous or in a mosaic with open rocky ground (Hnatiuk & Merton, 1979). Aldabra’s climate is determined by two distinct seasons: the wet season of the northwest monsoon from November to April (Stoddart & Mole, 1977), while between May to October there is lower rainfall resulting from the southeast monsoon winds.

[Figure 1]

Sampling

The distribution of *B. latro* is said to be structured by distance from the coastline (Schiller, 1992). Therefore *B. latro* population surveys were conducted on two roughly parallel transects established at different distances from the shore (Fig. 1). The coastal transect was 1.4km long, composed of 27 lineal sections of 50m and separated from the shore by distances ranging between 1 and 26m. The inland transect was 1.8km long, composed of 39 lineal sections of 50m with distances from the shore ranging between 38 and 177m. The two transects were surveyed simultaneously after sunset, roughly every two weeks from January 2007 to May 2016.

All *B. latro* individuals encountered within five meters on either side of the mid transect line were recorded. For each individual encounter, the following parameters were recorded:

1. Distance to the mid transect line, estimated to the nearest meter;
2. Morph: The colour of the carapace was noted between blue and orange. Colour was judged on the underside of the front claws. Orange individuals have an orange shell and white claws whereas blue individuals have a purplish-blue abdomen with blue or white claws;
3. Sex: The sex of crabs was identified; female crabs possess three large, feathery pleopods on the ventral surface of the abdomen which are used to support their egg-masses (Fletcher, 1993). Male crabs do not have the pleopods. When a female was identified, it was noted whether it was carrying eggs or not;
4. Thoracic length; Pistorius (2006) established a highly significant relationship between weight and thoracic length for the *B. latro* population on Aldabra, corresponding to findings in other studies (Amesbury, 1980; Anagnostou & Shubart, 2014; Helagi *et al.,* 2015). Therefore the thoracic length, the linear distance between anterior and posterior borders of the thoracic groove (Helfman, 1973), of each individual encounter was measured using vernier callipers;
5. Moult; several studies (Amesbury, 1980; Fletcher *et al.,* 1990 and Held, 1963 cited by Drew *et al.,* 2010) noted a distinct expansion of the abdomen on *B. latro* prior to moulting. Pleonal expansion has also been linked to the reproductive condition of females, as it can be indicative of gonad development (Fletcher *et al.,* 1991; Sato & Yoseda, 2009). Therefore during each encounter the degree of pleonal expansion using a four-level categorical scale was recorded. In this scale, 1 was assigned to individuals in which all tergal plates are touching each other or if there is only a small gap between the most posterior tergal plate (first plate) and the next (second plate). An index of 2 was assigned to those in which the pleon was slightly swollen and the fleshy abdomen is visible between the first and second plates, and somewhat visible between the second and third plate. An index of 3 was assigned if the pleon was swollen and the fleshy abdomen is clearly present between the first, second and third plates, and somewhat visible between the third and the fourth plate. Finally, an index of 4 indicates a strongly swollen pleon and the fleshy abdomen is visible between all tergal plates;
6. Moon phase and soil humidity; *B. latro* behaviour has been hypothesised to be influenced by humidity (Schiller, 1992) and the phase of the moon (Amesbury, 1980; Sato & Yoseda, 2009; Drew *et al.,* 2010). Therefore in each survey it was noted whether the soil was moist due to ongoing or previous rain as well as the phase of the moon.

Habitat classification

Habitat composition was determined using high resolution satellite imagery (Walton, 2015) and classified into eight different habitat types. In each transect section the percentage of area occupied by the different habitat types that could affect *B. latro* detectability and/or abundance was calculated. In decreasing order of area occupied these habitats were: open mixed scrub, exposed surface, standard mixed scrub, grasses, mangrove, sand, dense *Pemphis acidula* bush, and champignon.

**Data analysis**

Density and abundance

The density of *B. latro* during each survey was estimated using the hierarchical distance sampling model of Royle *et al.,* (2004) implemented in the R package unmarked (Fiske & Chandler, 2011). The numbers of individuals within the five distance categories 0−1, 1−2, 2−3, 3−4, 4−5m from the mid-transect line were used to estimate the overall density and evaluated the impact that habitat composition had in both the detectability and abundance of *B. latro*.

To maximise differentiation between transect sites and reduce the dimensionality of the data, habitat composition percentages were transformed using a principal component analysis. Finally, the two components were included, explaining the largest proportion of the variance as covariates in the distance sampling model. Due to the large number of surveys, a fixed effects meta-analysis approach was used to ascertain the significance of the covariates. A covariate was determined to significantly affect detectability if its effect was consistent over different surveys, and to significantly affect abundance if its effect was either consistent over surveys or variable but according to the seasons. In each survey, the Akaike Information Criterion (AIC) was used to determine whether the detection process was better approximated by a half-normal, a negative exponential, a hazard-rate, or a uniform distribution function.

Next, a generalised additive model (GAM) was used to determine whether *B. latro* densities varied significantly (i) over the years, (ii) over the yearly cycle, and (iii) over the lunar cycle. Models were fitted using the R package mgcv (Wood, 2006a), and the model parsimony was assessed by comparing their AIC values. The phase of the moon during the survey was back calculated using the R package oce (Kelley & Richards, 2015) and was defined as a continuous variable from zero to one with both extremes corresponding to new moon, 1/4 for first quarter, 1/2 for full moon, and 3/4 for last quarter (Meeus, 1982).

To analyse abundance patterns at a finer spatial and temporal scale, a set of GAM was used to quantify the relative effect of the aforementioned variables on the counts of both male and female individuals. This was possible because initial analysis indicated that crab detectability did not change over time and was not influenced by habitat composition (see Results) and consequently direct counts provide an accurate index of crab abundance. As it is plausible that environmental factors interact with habitat requirements, the tensor product interaction between day of the year and distance from shore was included in the model.

Sex ratio and sizes

Sex ratios were directly calculated from the individual counts. In addition, for sake of the potential reference for reproduction, the sex ratio that would be observed if only sexually mature individuals were included was calculated. Full sexual maturity was assumed based on individuals with a thoracic length of and longer than 28mm (Fletcher *et al.,* 1990; Sato & Yoseda, 2008; Drew *et al.,* 2010). All studied island populations of *B. latro* reveals males being consistently larger than females (Drew *et al.,* 2010). Therefore thoracic length was also used to determine whether the Aldabra population also exhibits size sexual dimorphism. The difference was evaluated by visually inspecting the size distribution for both sexes and a t-test on the length measurements. A set of GAMs were used to infer the effects that time of the year, distance from shore, and phase of the moon may have on the sex ratio and sizes of individuals encountered, with competing models compared using their AIC.

Moulting and reproduction

To understand whether there is evidence of synchronous seasonal moulting, and to provide insight into the onset of reproductive season, two GAMs were constructed, one for each sex, in which the response was the index of pleonal expansion (treated as a numeric variable) and the predictor was the time of the year. To determine the reproductive season of *B. latro* on Aldabra a GAM with a binomial error distribution was constructed with the response variable whether a female was seen carrying eggs during a survey transect or not, with time of the year and phase of the moon as response variables.

**Results**

Density and abundance

Overall, 281 surveys were performed over the study period which led to a total of 8145 individual encounters. The two principal components of the habitat composition explained 81% of the variance found among transect sections (Supplementary information Fig. 1). The first component was strongly correlated with an increase on the area covered by open mixed scrub, but mainly with a decrease on percentage of exposed surface. The second component was largely correlated with an increase of grass and with a decrease of standard mixed scrub. These habitat differences, however, did not significantly affect the detectability or the abundances of *B. latro* (Supplementary Information Fig. 2 and 3). Overall, based on AIC values, the most parsimonious models were those fitting a negative exponential function to the detection process.

*B. latro* density in the study area varied between 3.2 and 189.4 individuals per hectare, with an overall average density of 35.4 ± 1.69 ind./ha. The overall density shows small variations over the years, but no long term trend is observable (Fig. 2A). Similarly, there was no significant variation on density with moon cycle (p=0.916). Contrastingly, there were important seasonal changes on abundance, being above average between February and June, with a clear peak in April, and below average for the rest of the year (Fig. 2B).

The number of *B. latro* males and females encountered is strongly affected by the time of the year and the distance from shore. In general, male counts in each transect section were largest during the first half of the year. Within that period, between March and April, males concentrate away from shore (Fig. 3A). During the same period, when inshore counts are high for males, female counts are higher closer to shore. In contrast, during the second half of the year when male counts are the lowest, female counts are at the highest both in coastal and inshore sections, particularly between October and November (Fig. 3A).

Although moon phase did not affect the overall *B. latro* densities, it had distinct and complementary effects on males and females (Fig. 4A). While female counts are the largest during periods of full moon, males are encountered in higher densities during new moon when the illuminated fraction of the moon is at its minimum.

[Figure 2, 3, 4]

Sex ratio and sizes

The overall *B. latro* ratio males: females was approximately 3:1 (76% male), which increases to approximately 4:1 (82% male) if only sexually mature individuals are included. As inferred by the count models, this ratio however, shows significant temporal and spatial variation, ranging between 57% of individuals encountered being male during November in areas close to shore and 86% during March in areas far from shore.

In addition to female crabs being recognized by three additional large, feathery pleopods on the ventral surface of their abdomen, a marked size sexual dimorphism was observed (Fig. 5). Overall, males were found to be significantly? (p-value if so) larger than females: male thoracic length, ranged from 9 to 78mm (mean 40.9mm), while female ranged from 6 to 76mm (mean 30.6mm). The mean size, of both male and female individuals encountered, showed two distinct peaks during the year, one between October and December, and another more pronounced between March and May (Fig. 3B). In addition, the mean sizes were found to be affected by the distance to shore. In general, females encountered close to shore were generally larger than those encountered inland. On the other hand, males found away from the coast were substantially larger than those encountered close to shore. However, this difference on male size between coastal and inshore habitats becomes inconspicuous in December and January and from June to August (Fig. 3B). Furthermore, the size of males encountered close to new moon was significantly larger than that of males encountered close to full moon. In contrast, the size of encountered females showed no variation over the moon cycle (Fig. 4B).

[Figure 5]

Moulting and reproduction

Males over 30mm were found to exhibit a yearly cycle regarding the size of their pleon, with a clear peak in April and May (Fig.6). In contrast, females encountered in November have the largest pleon. In addition, females show an additional less conspicuous peak of pleon expansion between May and July (Fig. 6).

Throughout the monitoring period, few *B. latro* females (14 out of 2071 individuals in 12 out of 438 transect surveys) were ovigerous. Nevertheless, these observations consistently pointed out to a reproductive season between December and March with an increased probability to encounter females carrying eggs just before new moon (Fig. 7).

[Figure 6, 7]

**Discussion**

The density of *B. latro* has been stable in the survey location on Aldabra over the nine years of the study period. The substantial spatial and temporal heterogeneity on observed densities suggests a highly dynamic population, similarly reported on Christmas Island by Drew & Hansson (2014). Aldabra might potentially have one of the most significant *B. latro* populations worldwide likely as a consequence of not being exploited. The other two unexploited populations on Enewetok (5.85 km2) and Taiaro (12 km2) Atolls have high densities, estimated at 147 crabs/ha (Helfman, 1973) and 190 crabs/ha (Chauvet & Kadiri-Jan, 1999) respectively, but these islands are relatively small compared to Aldabra Atoll (35 crabs/ha; 155km2). The other population with limited exploitation is found on Christmas Island; however Drew & Hansson (2014) reported a significant decline in *B. latro* densities on Christmas Island (135 km2), estimated between 4−47 crabs/ha. It is important to mention that the survey methodologies used for these above-mentioned assessments tended to be focused on areas known to be preferred by *B. latro,* and on Aldabra the survey was conducted on only one island and average densities may differ between the islands.

As observed in all other studied populations, *B. latro* on Aldabra is size sexually dimorphic, with males being substantially larger than females. Interestingly, the mean thoracic length of *B. latro* recorded on Aldabra is much smaller than all the other studied populations (see Drew *et al.,* 2010 for review) for both males and females. One reason for this can be the result of intense interspecific competition for resources. Hermit crabs of the genus *Coenobita* are abundant on Aldabra (Grubb, 1971). As reported by Amesbury (1980) in areas with high abundance of *Coenobita*, the amount of scavengeable material available to *B. latro* may be limited, as well as the availability of gastropod shells for the glaucothoe stage. A second reason may be due to the drought frequency on Aldabra reported to have increased from two to six months per year between 1970 and 2013 (Haverkamp *et al.,* 2017). *B. latro* is suggested to exhibit a decrease in the frequency of their foraging activity during the dry season compared to the wet season (Fletcher, 1993), thereby resulting in a slower growing population on Aldabra.

At the relatively small spatial scale of this study, sex ratio appears to be extremely biased towards males, most likely as a result of the cryptic nature of the species and the sampling design. Transect studies typically report male bias ratios compared to grid sampling, suggested to be associated to variations in habitat use between sexes (Drew *et al.,* 2012). Female crabs have been recorded to be more dominant in denser vegetation and are therefore less likely to be encountered on transects along existing paths than in grid areas covering more vegetated areas (Drew *et al.,* 2012). In addition, James (2008) postulated a more sedentary behaviour of female *B. latro* outside of the breeding season, suggesting that the males are wider ranging, increasing their chances of being encountered in surveys along pathways.

The high spatial and temporal variability of *B. latro* density, size and sex is most likely linked with a complex life cycle associated with reproductive migrations, moulting requirements, availability of resources and potentially behavioral variations associated with environmental conditions at a site (Drew & Hansson, 2014). From February to May, the overall number of crabs observed is higher than average. This is largely due to an increase in the number of males. During this time, large dominant males favour areas further from shore, presumably with more resources, while females and smaller males are mostly encountered in near-shore habitats. Drew & Hansson (2014) noted that large males often actively exclude females and potentially smaller males from desirable feeding locations. Afterwards, roughly from June to December, the overall number of crabs is lower than average. Again, this is largely due to a decrease on the number of males, particularly of large ones, which are potentially undergoing moulting during the drier months of the year as suggested by Fletcher *et al.,* (1991). *B. latro* undergo moulting in shallow burrows to minimize their vulnerability to predation and desiccation during the moulting process (Drew *et al.,* 2010). During this period, in stark contrast with the lower male density, female counts increase on the second half of the year both in the coastal and inshore areas, likely opportunistically exploiting the available resources left by dominant males (Drew & Hansson, 2014). Female densities peak between September to December close to shore which coincides with a period in which males of sexually active sizes are commonly encountered. This advocates a breeding migration of female *B. latro* which involves females migrating to the coast for the purpose of releasing larvae into the ocean (Schiller *et al.,* 1991). There are few studies detailing the mating behavior in *B. latro,* copulation is believed to be brief and not preceded by elaborate courtship behavior (Brown & Fielder, 1991).

Based on the encounters with ovigerous females the reproductive season on Aldabra occurs with most likelihood between December and March, during the rainy season, though no actual observations of females extruding their eggs have been made. This also corresponds with the period of highest peak of female pleonal expansion in November to December, which is believed to be related to gonad development (Fletcher *et al.,* 1991; Sato & Yoseda, 2009). This period coincides with the reproductive seasons observed in other *B. latro* populations in the southern hemisphere (Drew *et al.,* 2010). Moreover, signs of synchrony with the moon cycle were found as ovigerous females were mostly encountered during surveys performed close to new moon. This synchrony is likely related to the timing of spawning, nevertheless, it can also be related to timing of egg extrusion (Sato & Yoseda, 2009). The timing between mating and egg extrusion is unknown. As female individuals don't possess a seminal receptacle, it is believed that egg extrusion occurs shortly after mating (Sato & Yoseda 2009; Drew *et al.,* 2010).

Despite several failings, this study has provided a good baseline which can be used to design further *B. latro* surveys on Aldabra. Given the relatively small spatial scale of this monitoring and the large variability in spatial densities, it is advisable that other islands of the atoll are sampled to give better insight on the dynamics of *B. latro*. The subjective assessment categories of abdomen expansion should be replaced with measurement of the ‘index of pleonal expansion’ as described by Sato & Yoseda (2009). Moreover, alternative sampling methods such as grid sampling is recommended which has shown to increase sampling efficiency and reduces bias in sex ratios (Drew *et al.,* 2012). Nevertheless it is advisable that transect methods should be continued, at a reduced frequency, to provide continuity to the long term dataset so as to detect future changes in trends. A mark-recapture study would be useful to estimate the total population size on Aldabra. Drew *et al.,* (2012) found Passive Integrated Transponder (PIT) tags to be a suitable tagging system for use in *B. latro*, providing good apparent retention rates and good return rates relative to other mark-recapture methods. Lastly, a recent black rat (*Rattus rattus*) eradication trial on Aldabra recorded substantial interference by *B. latro* and other hermit crabs to poison bait (Harper *et al.,* 2015). Due to their gregarious behaviour, this poses a potential threat to the species either through direct bait consumption or scavenging on dead animals that have taken bait. Further studies on the factors affecting the gregarious nature of *B. latro* should be investigated as well as other precautionary measures, such as use of crab deterring bait masks. This, together with the information on density and seasonality will be useful in planning future eradication programs to prevent declines in the population.

Similar long term studies under natural conditions should be prioritised for other *B. latro* populations due to the species highly dynamic behaviour. This will provide conservation managers with more accurate information when determining population size and demographics, especially in exploited locations. More long term studies will also assist in revision of the threat status of *B. latro* on the IUCN redlist. Even with full protection of the species and its habitat, the density of *B. latro* population in the survey location on Aldabra did not increase over the study period suggesting a fragile species potentially vulnerable to climatic changes, or at a carrying capacity. More studies into the species’ ecological requirements throughout its life history are therefore necessary. This can also advise conservation measures for inhabited island populations, for example protecting natural crab habitats in addition to limitations on crab harvesting. In the Seychelles, several inner granitic islands are now fully protected and strictly managed for conservation purposes. The feasibility of translocation of *B.latro* from Aldabra to these sanctuaries should be investigated to re-establish the species on these islands, further securing the Seychelles’ population.

**Conclusion**

This study provides one of the longest continuously recorded data set on *B. latro* populations and provides additional insight into the ecology of this species. *B. latro* on Aldabra is highly dynamic due mainly to their life history traits and resource availability. With a significant, stable and unexploited *B. latro* population, Aldabra Atoll represents a refuge for this species recorded to be on decline elsewhere throughout their range and potentially a crucial reservoir for repopulating other suitable islands in the Western Indian Ocean (Poupin *et al.,* 2013). Aldabra as a research base is in a privileged position to unravel long held questions on *B. latro*. Its strict protection from human disturbance provides the opportunity to investigate the potential for this species to persist in the face of global climatic changes and provide important lessons for other managed and unmanaged populations elsewhere.

**Acknowledgements**

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**Figure legends**

**Figure 1.** Location of Aldabra Atoll in the Western Indian Ocean and location of the monitoring transects for *Birgus latro*.

**Figure 2.** *Birgus latro* density over (A) the years and over (B) the yearly cycle. The solid lines show the values predicted by the Generalised Additive Model, while grey ribbons represent the standard error. The dashed line indicates the average crab density.

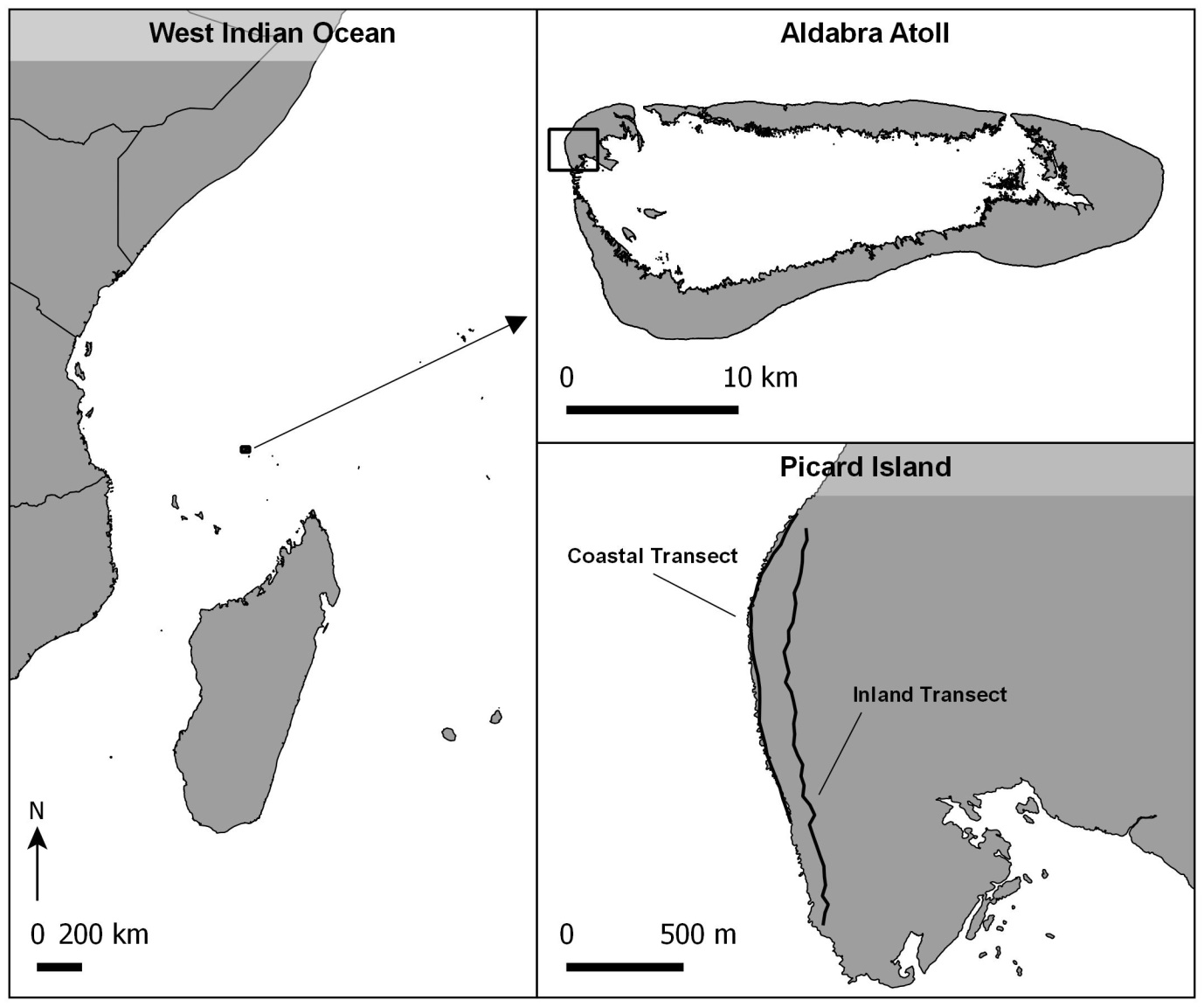
**Figure 3.** Contour plots of the effect of time of the year and distance from shore on A) the counts and B) the size of both males (top panels) and females (bottom panels). In all panels, shades of red and blue indicate values larger and smaller than the average respectively.

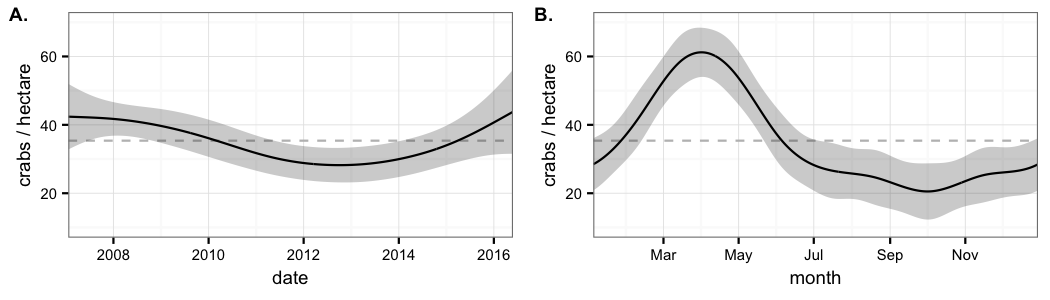
**Figure 4.** Association between the phase of the moon and A) the count and B) the size of encountered *Birgus latro* females (green) and males (orange). The y-axes show the effect on the mean counts (0.36 females and 1.13 males) or the mean sizes (30.5mm thoracic length for females and 40.6mm for males) per transect section. The solid lines show the values predicted by the Generalised Additive Model, while ribbons represents the standard error. The phase of the moon is defined as 0 and 1 for new moon, 0.25 for first quarter, 0.5 for full moon, and 0.75 for last quarter (Meeus, 1982).

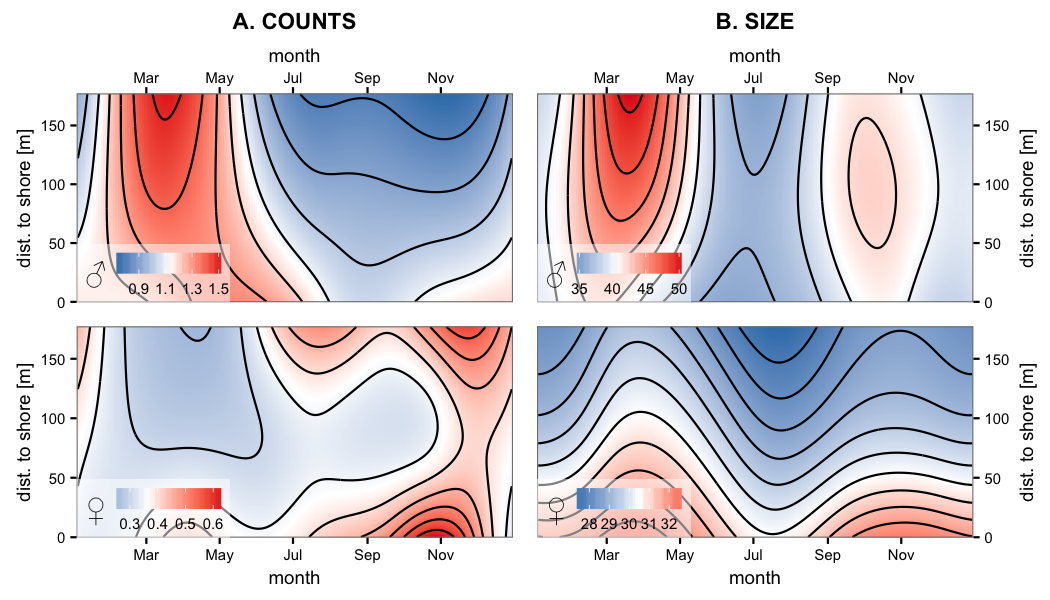
**Figure 5**: Size distribution of *Birgus latro* on Aldabra for female (green) and male (orange) individuals.

**Figure 6**: Effect of time of the year on the mean pleon size for *Birgus latro* females (green) and males (orange). Pleon size was estimated using an index between 1 and 4. An index of 1 indicates that all tergal plates are touching each other of there is only a small gap between the most posterior tergal plate and the next. An index of 4 indicates a strongly swollen abdomen and all tergal plates are divided by thick gaps.

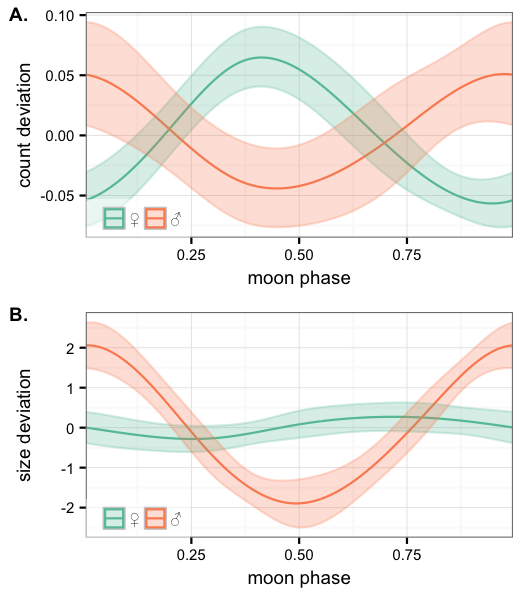
**Figure 7:** Probability of encountering an ovigerous female during a survey. The solid line and dashed line correspond to the maximum and minimum encounter probability during the moon cycle respectively. A moon phase of 0.41 corresponds to about three days before full moon and 0.94 to around two days before new moon (Meeus, 1982). Grey ribbon indicates confidence interval of the mean probability across the year.

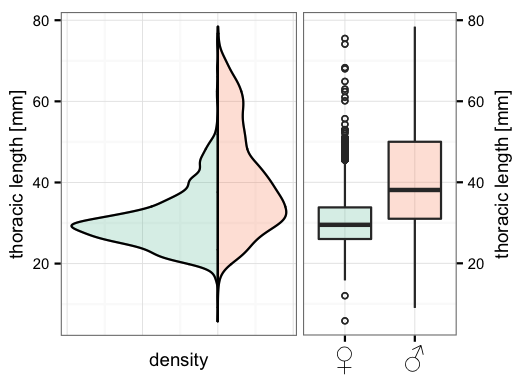
**Figure 1.**

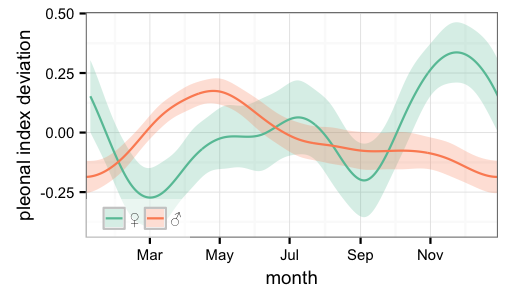
**Figure 2.**

**Figure 3.**

**Figure 4.**

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**Figure 5.**

**Figure 6.**

**Figure 7.**

