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REPRODUCTIVE DYNAMICS OF *P. LEOPARDUS*

Spatial variation in the effects of size and age on reproductive dynamics of common coral trout *Plectropomus leopardus*.

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Abstract

The effects of size and age on reproductive dynamics of common coral trout *Plectropomus leopardus* populations were compared between coral reefs open or closed (no-take marine reserves) to fishing and among four geographic regions of the Great Barrier Reef (GBR), Australia. The specific reproductive metrics investigated were the sex ratio, the proportion of vitellogenic females, and the spawning fraction of local populations. Sex ratios became increasingly male biased with length and age, as expected for a protogyne, but were more male biased in southern regions of the GBR (Mackay and Storm Cay) than in northern regions (Lizard Island and Townsville) across all lengths and ages. The proportion of vitellogenic females also increased with length and age. Female *P. leopardus* were capable of daily spawning during the spawning season, but on average spawned every 4.3 days. Mature females spawned most frequently on Townsville reserve reefs (every 2.3 days) and Lizard Island fished reefs (every 3.2 days). Females on Mackay reefs open to fishing showed no evidence of spawning over four years of sampling, while females on reserve reefs spawned only once every 2-3 months. No effect of length on spawning frequency was detected. Spawning frequency increased with age on Lizard Island fished reefs, declined with age on Storm Cay fished reefs, and declined with age on reserve reefs in all regions. We hypothesize that the variation in *P. leopardus*' sex ratios and spawning frequency among GBR regions is primarily driven by water temperature, while no-take management zones influence spawning frequency depending on which region the reserve is placed. Male bias and lack of spawning activity on southern GBR reefs, where densities of adult *P. leopardus* are highest, suggests recruits may be supplied from central or northern GBR reefs. Significant regional variation in

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47 reproductive traits suggests a regional approach to management of *P. leopardus* is
48 appropriate and highlights the need for considering spatial variation in reproduction where
49 reserves are used as fishery or conservation management tools.

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52 **Key words:** Batch spawn; coral reef fish; fishing; Great Barrier Reef; marine reserve;
53 reproduction.

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INTRODUCTION

Sustainably managed fisheries require the maintenance of sufficient reproductive adults and egg production (Sadovy, 1996). The importance of incorporating assessment of reproductive biology into the management of fish stocks is now recognized widely (Jakobsen *et al.*, 2009; Murua *et al.*, 2010; Bernal *et al.*, 2012), requiring increased study of the reproductive biology of fish (Lowerre-Barbieri *et al.*, 2011). A proliferation of studies has emerged in the past decade focussed on reproductive biology topics such as maturity schedules, sex ratios, fecundity, and spawning frequency to reveal species-specific variation driven, for example, by female size and age, variation in climate and region (Adams *et al.*, 2000; Portner *et al.*, 2001; Fennessy and Sadovy, 2002; Williams *et al.*, 2006), disturbance from fishing (Muñoz *et al.*, 2010), and food availability and body condition (Ganias, 2009; Somarakis *et al.*, 2012). Understanding the factors that influence the reproductive output of a population and their interaction with fishing and management measures is important for the design of fisheries management tools, such as seasonal fishing closures, no-take marine reserves and minimum sizes of retention.

Size and age influence reproductive traits of fishes in a fairly predictable way. Sex ratios of hermaphroditic fishes vary predictably with size and age as individuals change from one sex to the other (Williams *et al.*, 2006). Maturity schedules also vary with size and age, with the proportion of females that are reproductively active often increasing with female size and age as energy balances shift from somatic growth to reproduction (Fennessy and Sadovy, 2002; Shuter *et al.*, 2005). Larger and older females also generally spawn more frequently

than smaller, younger females (Claramunt *et al.*, 2007; Lowerre-Barbieri *et al.*, 2009). Less predictable is the way reproductive traits of individual species vary across geographic scales and respond to fishing pressure. Sex ratios and maturity schedules have been demonstrated to vary spatially (Adams *et al.*, 2000; Williams *et al.*, 2006) and will determine the number of mature females and spawning frequency at the local or regional scale. Spawning frequency of tropical fishes has become increasingly well quantified in recent years (Dadzie and Abou-Seedo, 2008; Maki Jenkins and McBride, 2009; van der Velde *et al.*, 2010; Ganas, 2012) but documented cases of spatial variation in spawning frequency for tropical species remains limited (although see Brown-Peterson *et al.*, 2009). Spatial variation in spawning frequency of temperate marine fishes has received particular attention and has been attributed to variations in water temperature and fish health (Korta *et al.*, 2010; Somarakis *et al.*, 2012).

Plectropomus leopardus (Lacepède 1802) is the most commercially important finfish on the Great Barrier Reef (GBR), Australia and has been heavily exploited across its Indo-Pacific range (Cornish and Kiwi, 2004). Latitudinal variation in a number of life history and population traits is well documented for *P. leopardus*. The southern GBR is characterized by male-biased sex ratios (Adams *et al.*, 2000), smaller mean length and age at sex change (Davies *et al.*, 2006), smaller mean size (Mapstone *et al.*, 2004), significantly different otolith chemistry (Bergenius *et al.*, 2005), and higher densities (Mapstone *et al.*, 2004) than in the northern GBR. *Plectropomus leopardus* are protogynous hermaphrodites (Samoilys, 2000) but can exhibit diandric male development (Adams, 2002), which is particularly prevalent in the southern GBR where the largest proportions of primary males are found (Adams *et al.*, 2000). Comparisons between fished reefs and reefs closed to fishing (no-take reserves; reserves) on the GBR have revealed that *P. leopardus* on reserves are older and larger (both

sexes combined and for females only), change sex when older and larger, and have higher densities on reefs protected from fishing (Ferreira and Russ, 1995; Adams *et al.*, 2000; Adams, 2002; Mapstone *et al.*, 2004; Begg *et al.*, 2005).

The maintenance of larger and older female *P. leopardus* within reserves may result in enhanced reproductive output, assuming there is a positive effect of female size and age on spawning frequency. Two previous studies estimated that *P. leopardus* spawn every 2-3 days during the Austral Spring spawning season (Brown *et al.*, 1994; Samoilys, 2000) and determined that there was no relationship between maternal size and spawning frequency (Brown *et al.*, 1994). These estimates were based on fish collected from one small area (two adjacent reefs near Cairns, ~17°S), however, and did not examine the relationship between age and spawning frequency, nor whether no-take reserves affect spawning frequency. Evaluation of the effects of regional variation and reserves on the reproductive dynamics of *P. leopardus* is particularly important because *P. leopardus* is currently managed as a single homogenous stock on the GBR, with the implicit assumption that reproductive productivity does not vary spatially throughout the GBR or that the stock is well-mixed during reproduction and does not result in regional variation in productivity.

The objective of this study was to examine the reproductive dynamics of *P. leopardus* to determine whether sex ratio, maturity schedules, and spawning frequency varied by female size and age, region, and between reefs open and closed to fishing on the GBR.

MATERIALS AND METHODS

FIELD COLLECTIONS

Plectropomus leopardus were collected over a four year period during structured commercial line fishing surveys from 1998 to 2001 as part of the Effects of Line Fishing (ELF) Experiment (see Mapstone *et al.*, 2004). Fish were caught during the first quarter – full moon or full moon – third quarter moon phases (Geoscience Australia, 2011) of the Austral Spring spawning season (September – December) in each of the four years. *Plectropomus leopardus* spawn throughout the complete lunar cycle, although spawning activity peaks during new moon periods when spawning aggregations averaging 44 individuals per 1000m² form at the reef edge (Samoilys and Squire, 1994; Samoilys, 1997; 2000). Sampling during the new moon was avoided in the ELF Experiment to reduce potential bias in abundance indices if large spawning aggregations were encountered. We presume that the effects on reproductive metrics we examined were not influenced significantly by lunar phase, within the spawning season, and that any relative differences among regions or zones were consistent regardless of whether sampling occurred during or outside new moon periods.

Four regions were sampled along a latitudinal gradient: Lizard Island (~14.5° S) in the northern GBR; Townsville (~18.5° S) in the central GBR; and Mackay (~20.5° S) and Storm Cay (~21.5° S) in the southern GBR (Fig. 1). Four reefs were sampled within each region: Two reefs that were zoned Marine National Park (no-take reserve reefs) and protected from

fishing for 12-15 years prior to sampling and remained closed to fishing for the duration of the years sampled; and two reefs that were zoned General Use historically and open to commercial and recreational fishing (“fished” reefs), although one of these reefs was closed to fishing for the four years of sampling and the other was closed to fishing from March 2000 onwards (Fig. 1). These historically fished reefs were considered to be fished reefs for the purposes of the analyses because the period of closure to fishing was very short (<2 – 4 years) relative to the longevity of *P. leopardus* (up to 16 years) and it was assumed that any response of spawning frequency to changes in fishing intensity or population density would be relatively slow.

Fork length (L_F) of each fish was measured (to nearest mm) at the time of capture, which also was recorded, and whole gonads were removed on the day of capture and preserved in 10% phosphate buffered formalin until histological sections were made. Otoliths were removed and age estimated by counting annuli in sectioned otoliths using the method described by Ferreira and Russ (1994).

HISTOLOGICAL PROCESSING

Sex was determined histologically from the preserved gonads of 5901 *P. leopardus*. Gonad sections were embedded in paraffin wax and sectioned at 5 μ m then stained using Myer’s haematoxylin and Young’s eosin-erythrosin (Bean *et al.*, 2003). Histological assessment was conducted on the medial section of one gonad lobe because in *P. leopardus*

oocyte development does not differ between right and left lobes (Samoilys and Roelofs, 2000) and is uniform along the length of the lobe (Adams *et al.*, 2000). Females, males, transitionals (proliferating testicular tissue in a female ovary) and bisexuals (male and female germinal tissue present with no evidence of either tissue degenerating) were categorized according to the criteria in Samoilys and Roelofs (2000), Adams (2002), and Brown-Peterson *et al.*, (2011). Transitionals made up a very small portion of the catch (<0.5%), probably because sex change commonly occurs after the Spring spawning season. Transitionals ranged from 1-7 years old, with the largest proportion of transitionals aged 3 – 4. This was consistent among all regions. Sex ratios (P_M , proportion male) were calculated from the number of mature males divided by the sum of females and males ($n = 5288$). Females were further classified histologically into reproductive phases (immature, developing, spawning capable, regressing, regenerating) according to Brown-Peterson *et al.*, (2011). The proportion of vitellogenic, reproductively active females (developing + spawning capable + regressing) (P_V) relative to the total mature female population (developing + spawning capable + regressing + regenerating) ($n = 2162$) was then calculated in each region and management zone (fished or no-take reserve) combination.

Spawning frequency was determined histologically using the postovulatory follicle (POF) method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985). Postovulatory follicles encase developing eggs and remain in the ovary as ruptured follicles after hydrated eggs are ovulated (Fig. 2). Postovulatory follicles degenerate quickly, lasting 24 hours in *P. leopardus* (Samoilys, 2000), a common timeframe for POFs in the tropics (West, 1990). The predictability of POF absorption means that they can be used reliably to back-calculate time of spawning (Ganias, 2012). Postovulatory follicles were classified following the descriptions

of Samoilys and Roelofs (2000). Presence or absence of POFs, and the stage of POF (early “0-Day”, or late “1-Day”), was determined from 1676 randomly subsampled mature (vitellogenic) ovaries (Table I). The spawning fraction (P_S , proportion of mature females that were spawning per day, hereafter proportion of spawners) was calculated as the total number of mature females with 1-Day POFs present divided by the total number of mature females (Picquelle and Stauffer, 1985). These calculations only use the incidence of females with 1-Day POFs. Using the incidence of females with hydrated oocytes or 0-Day POFs is inappropriate because the presence of these structures within the ovary is dependent on time of sampling (Hunter and Macewicz, 1980) and because females who are actively spawning may be more susceptible to fishing (Picquelle and Stauffer, 1985). In this study, 1-Day POFs were found throughout the day (0730 – 1800). *Plectropomus leopardus* spawn at dusk (Samoilys 2000) and sampling occurred during daylight hours, so the presence of 1-Day POFs in the ovary indicated spawning occurred approximately 12 to 24 hours prior to sampling. Spawning frequency for the season was calculated as the days elapsed between spawns, or $1/P_S$ (Claramunt *et al.*, 2007). The number of batches spawned per season by each mature female was calculated by dividing the length of the Austral Spring spawning season for *P. leopardus*, commonly reported as lasting four months (122 day) on the GBR (Goeden, 1978; Brown *et al.*, 1994; Ferreira, 1995; Samoilys, 2000; Davies *et al.*, 2006) by spawning frequency (days).

STATISTICAL ANALYSES

Generalized linear mixed-effects models (GLMM) were used to examine the fixed effects of fork length (L_F), age (A), region (R) and management zone (Z), and the random effect of reef, on sex ratio (P_M), proportion of vitellogenic females (P_V), and spawning fraction (P_S). Each factor was modeled as an additive term and as an interaction with other factors. Three-way interactions between R , Z , and L_F or A were considered in the analyses. The factor reef was modeled as a random effect term in all models to eliminate potential bias or pseudoreplication resulting from the non-independence of samples collected at the same time from a single location. The response variables sex ratio, proportion of vitellogenic females and spawning fraction were all modeled with a binomial error distribution and logit link function. Akaike's Information Criterion (AICc) for small sample sizes (Burnham and Anderson, 2002) was used to determine the best set of explanatory factors for adequately predicting each response variable, and to compare functional forms for the relationship between factors and response variables. The best-fit model was considered to be the simplest model within two of the lowest AICc (Burnham and Anderson 2002). The best-fit model was used as a basis to predict the expected values of response variables across the observed ranges in L_F and age. All GLMMs were done in R using the *lme4* package (Bates *et al.*, 2012).

RESULTS

SEX RATIO

Sex ratios became increasingly male-biased with length and age, as expected for a protogynous hermaphrodite. Variation in sex ratio of *P. leopardus* was best described by a model that included an interaction between region, zone and L_F , and a model that included an interaction between region, zone and age (Table II). Populations at Mackay and Storm Cay had higher proportions of males across all lengths and ages compared with Townsville and Lizard Island in fished and reserve reefs (Fig. 3). Fifty percent of fish were male by the time fish reached 455 mm L_F and 464 mm L_F at Townsville and Lizard Island reserve reefs, respectively, while over 80% of 453 mm L_F and 394 mm L_F fish were male at Mackay and Storm Cay reserve reefs. The size at which 50% of fish were male was much smaller at Mackay (359 mm L_F) and Storm Cay (303 mm L_F) reserve reefs than in other regions (Fig. 3). The size at which 50% of fish were male was consistently smaller on fished reefs than reserve reefs, but the difference varied among regions. Fifty percent of the population were male at 455 mm L_F on Townsville reserve reefs and 406 mm L_F on Townsville fished reefs whilst 50% of the population at Storm Cay were male at 303 mm L_F on reserve reefs and 300 mm L_F on fished reefs (Fig. 3).

Male bias was evident in the youngest of age classes (1 and 2 years) on Mackay and Storm Cay fished and reserve reefs compared with Lizard Island and Townsville. Fifty percent of the population was male at age 6 on Lizard Island and Townsville reserve reefs, and age 1 on Mackay and Storm Cay reserve reefs (Fig. 4). *Plectropomus leopardus* populations did not reach 80% male until 10 and 12 years on Townsville and Lizard Island reserve reefs respectively, while 80% of fish were male by age 7 and 4 years on Mackay and Storm Cay reefs respectively. Sex change occurred approximately 3 years younger on Townsville fished reefs compared with reserves, while 50% sex change did not differ between management

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zones at Lizard Island (6 years, reserve and fished reefs) or Mackay and Storm Cay (1 year, reserve and fished reefs) (Fig. 4).

PROPORTION OF VITELLOGENIC FEMALES

There was an expected increase in the proportion of vitellogenic females with length and age (Fig. 5, Table II). Fifty percent of females were vitellogenic at 263 mm L_F , and 80% of females were vitellogenic by 333 mm L_F (Fig. 5). Fifty per cent of 1 year old females were vitellogenic, and 80% of females were vitellogenic by age 3 (Fig. 5).

SPAWNING FREQUENCY

Ovaries from 23.5% of mature female *P. leopardus* contained 1-Day POFs, indicating spawning on the GBR occurred approximately every 4.3 days during the Austral Spring spawning season (Table I). Sixty five per cent of mature females with hydrated ovaries contained histological evidence of two potential spawning events. That is, the ovary contained both hydrated oocytes and 1-Day POFs, indicating that 18% of mature female spawners spawned on consecutive days. Only three ovaries contained “0-Day” POFs. These females were caught in the late afternoon (1530-1630), indicative of the narrow time period between ovulation and dusk spawning reported for *P. leopardus*. Ovaries with POFs were

present during all lunar periods surveyed during the Austral Spring spawning season (first quarter, full moon, and last quarter, Table I).

A broad length range of mature *P. leopardus* was sampled (263 - 585 mm L_F) but there was little support for any of the spawning fraction models that included L_F . Variation in *P. leopardus* spawning fraction was best described by a model that included an interaction between the terms region and zone (Table II). Townsville's reserve reefs had the highest spawning fraction of any reefs at 0.43, equivalent to a spawning frequency of 2.3 days, and greater than that for fished reefs in the same region of 0.19, reflecting a spawning frequency of 5.3 days. The pattern was opposite in the Lizard Island region, where 31% of mature females on Lizard Island fished reefs contained 1-Day POFs, indicating spawning occurred on average every 3.2 days, compared with 8% on neighbouring reserve reefs, indicating spawning every 12.0 days (Table I, Fig. 6). Spawning was less frequent at Mackay and Storm Cay reefs. Storm Cay's mature females spawned every 17.2 days on fished reefs and 28.8 days on reserve reefs, though these estimates were effectively indistinguishable (Table I). There was no evidence of recent spawning on Mackay's fished reefs and on reserve reefs spawning occurred once every 83.2 days. The number of batches per season ranged from approximately 52 spawned by Townsville's females on reserve reefs, to no batches spawned on Mackay fished reefs.

The best model explaining spawning fraction involving age was an interaction between region, zone, and age (Table II). One and 2 year old *P. leopardus* spawned most frequently on reserve reefs, after which spawning fraction on reserve reefs decreased with age

in all regions (Figure 7). Spawning fraction decreased approximately linearly on Townsville and Lizard reserve reefs from 50% and 11% at age 1 respectively to 30% and 3% at age 10 respectively. Spawning fraction on Mackay and Storm Cay reserve reefs, however, declined sharply from 10-20% age 1 to zero at age 4 and did not change thereafter (Fig. 7).

Spawning fraction on fished reefs increased with age at Lizard Island from approximately 20% at age 1 to 60% at age 10 years (Fig. 7) but spawning fraction at Townsville fished reefs remained approximately 20% irrespective of age. Females with POFs were recorded only in individuals aged 3 and 4 on Storm Cay fished reefs and no females with POFs were recorded on Mackay fished reefs (Fig. 7).

DISCUSSION

This study of *P. leopardus*' reproductive dynamics provides one of the few comparisons of sex ratios, the proportion of vitellogenic females, and spawning frequency of fish collected within and outside of reserves across a broad geographic range. Spatial variation in reproductive dynamics of *P. leopardus* between reserves and among regions of the GBR was striking. Populations of *P. leopardus* at Mackay and Storm Cay in the southern GBR were characterized by male-bias and very infrequent spawning for a given size and age, relative to *P. leopardus* from Townsville and Lizard Island in the central and northern GBR. Spawning frequency was greater on reserves than on fished reefs off Townsville but the reverse in the Lizard Island region and effectively the same on both zones in Mackay and Storm Cay. There

was no significant relationship between length and spawning frequency and the effect of age varied with GBR region. These results add to the knowledge of *P. leopardus*' reproduction required for management of this commercially important species, raise some striking questions, and highlight the need for understanding spatial variation in reproduction where spawning closures and reserves are used as fisheries or conservation management tools.

EFFECTS OF LENGTH AND AGE ON SPAWNING FREQUENCY

The absence of a positive relationship between maternal length and spawning frequency for *P. leopardus* and the inconsistent relationship between maternal age and spawning frequency both are unusual. Larger and older females generally spawn more frequently than their smaller and younger counterparts (Claramunt *et al.*, 2007; Lowerre-Barbieri *et al.*, 2009). Assessments of the relationship between maternal length or age with spawning frequency for commercially important tropical reef fish is lacking, although a positive relationship between maternal length or age, or both, with spawning frequency has been confirmed in a number of temperate (Bani *et al.*, 2009; Ganas, 2009; Mehault *et al.*, 2010), tropical pelagic (Farley *et al.*, 2013) and tropical estuarine (Lowerre-Barbieri *et al.*, 2009) species. The lack of influence that female length has on spawning frequency is not unprecedented, however, and has been documented for northern anchovy *Engraulis mordax* (Girard 1854) (Hunter and Macewicz, 1980). A previous assessment of *P. leopardus* from reefs adjacent to Cairns (central GBR) also reported no effect of female length on spawning frequency (Brown *et al.*, 1994). Larger and older females commonly spawn more batches, however, if there is a positive relationship between female size and age with spawning season

duration (Claramunt *et al.*, 2007). For example, *E. mordax* displays no relationship between spawning frequency and female size (Hunter and Macewicz, 1980), but older females spawn more batches annually compared with young females because spawning season duration increases with age (Parrish *et al.*, 1986). Maternal effects on spawning season duration could not be determined for *P. leopardus* from this study due to the limited sampling intervals (one lunar period) in each year but warrant further research.

SPATIAL VARIATION IN REPRODUCTIVE DYNAMICS

Significant spatial variation in *P. leopardus*' reproductive traits is not surprising given the large geographic scale of this study and the variation in oceanographic influences (Wolanski, 1994; Hopley *et al.*, 2007), population density of *P. leopardus*, fishing effort, and other species, including prey species of *P. leopardus* (Mapstone *et al.* 2004), along the GBR. Variation in reef fish population biology often occurs at much finer spatial scales, such as within individual reefs or among reefs within a single region (Gust, 2004). Spatial variation in reproductive traits is influenced by genetics, the environment, or both (Wakefield *et al.*, 2013). No significant genetic variation in *P. leopardus* exists along the GBR (van Herwerden *et al.*, 2009), so spatial variation in *P. leopardus*' reproduction is more likely driven by environmental factors, which in turn affects demography and social dynamics.

Variation in water temperature is a common driver of spatial variation in fish reproduction (Danilowicz, 1995; Pörtner *et al.*, 2001), with reproductive activity commonly

reduced at higher latitudes for marine fishes with broad geographic distributions (Chauvet, 1991; Fennessy and Sadovy, 2002; Williams *et al.*, 2006; Wakefield *et al.*, 2013). Relatively low water temperatures in the southern half of *P. leopardus*' range may cause reduced spawning frequency and influence sex ratios. Mean sea surface temperature (SST) in the Mackay and Storm Cay region of the GBR is generally 1 to 2°C below mean SST in the central and northern GBR (Lough, 1999). Spawning omission at high latitudes, with reduced water temperature hypothesized to be the most likely cause, has been documented in fishes where a large proportion of female ovaries remain “resting” in a pre-vitellogenic stage during the spawning season (Fennessy and Sadovy, 2002; Williams *et al.*, 2006), the entire female population fails to mature (Wakefield *et al.*, 2013), or females mature but fail to spawn (Chauvet, 1991). Temperature also can influence sex change for hermaphrodite fishes. For example, eggs of the simultaneous hermaphrodite *Rivulus marmoratus* (Poey 1880) incubated at low temperatures resulted in the proportion of primary males increasing from 4% to 75% (Harrington Jr, 1975). Male-bias was evident on fished and reserve reefs in the southern GBR, consistent with the hypothesis that male-bias is a natural phenomenon on the GBR rather than an effect of fishing (Adams *et al.*, 2000).

Water temperature frequently operates as a “physiological switch” for the beginning and end of the spawning season (Conover, 1992; Ganas, 2009) and it may be argued that our sampling was confounded by spatial variation in spawning season along the GBR. Delayed spawning has been correlated with low water temperatures in the temperate species *G. morhua* (Hutchings and Myers, 1994; Kjesbu, 1994), and capelin *Mallotus villosus* (Müller 1776) (Carscadden *et al.*, 1997) and may confound spawning frequency estimates depending on when fish are sampled. *Plectropomus leopardus* also experience a delayed spawning

season with increasing latitude (Table III) but spawning frequency estimates in this study are unlikely to be confounded by latitudinal variation in the onset of spawning as spawning peaks in October – November regardless of latitude (Table III). Mackay and Storm Cay reefs were sampled late October – early December, and therefore were sampled during the spawning peak for *P. leopardus* on the southern GBR.

Social dynamics are known to play an important role in sex change and spawning behaviour of fishes (Munday *et al.*, 2006; Godwin, 2009), including *P. leopardus* (Goeden, 1978; Samoilys and Squire, 1994; Samoilys, 2000). Environmental conditions and social dynamics may interact to affect sex ratios, the prevalence of diandry, and spawning frequency for *P. leopardus*. The relatively low water temperature in the southern GBR may inhibit spawning and therefore diminish the reproductive benefits of maintaining a female-biased sex ratio. Perhaps the male biased sex ratio results because females that do not successfully spawn are genetically predisposed to change sex.

The estimates of spawning frequency reported here are less than Samoilys' (2000) and Brown's (1994) estimates of *P. leopardus* spawning every 2 to 3 days during the spawning season on reefs off Cairns (Fig. 1). Our estimate of spawning frequency may be conservative because samples were not collected during the new moon period when *P. leopardus* spawn most frequently (every 1.6 days) (Samoilys, 2000). Lunar phase also may have a stronger influence on spawning frequency for *P. leopardus* at higher latitudes, but no sampling occurred during the new moon period, precluding further examination of lunar effects. Lunar periodicity in batch spawning is common for tropical marine fishes, with lunar phases often

synchronizing reproduction (Taylor, 1984; Takemura and Rahman, 2004; Bushnell *et al.*, 2010). *Plectropomus leopardus* on Cairns reefs favour group spawning during the new moon and pair spawning during remaining lunar phases (Samoilys, 1997; 2000). This study and previous work (Ferreira, 1995; Samoilys, 2000) demonstrates that *P. leopardus* are capable of frequent spawning outside of new moon periods (Table I). Lizard Island and Mackay reefs were surveyed from first quarter to full moon phase, and Townsville and Storm Cay reefs were surveyed full moon to last quarter phase. The male-biased sex ratio in our samples from the southern GBR may indicate that the new moon may play a more significant role in gathering females and eliciting a spawning response in the south than in other regions.

It is unlikely that significant male bias and relatively infrequent spawning in the southern GBR reported here was due to a region-specific sampling bias where large females in spawning condition were unintentionally not accessed by the fishers. Post-settlement movement of *P. leopardus* is limited. Among-reef movement is rare (Davies, 2000), and within-reef movement to and from aggregations typically ranges from hundreds of metres to several kilometers (Davies, 2000; Zeller, 1998; Zeller and Russ, 1998). Sampling also avoided the new moon period when spawning aggregations were most likely to bias sampling (Mapstone *et al.*, 2004). Even when new moon *P. leopardus* spawning aggregations do occur, they occur at multiple sites on a reef, possibly with only one or two major aggregation sites (Samoilys and Squire, 1994). Sampling at each reef was highly structured around each reef and across the range of depths at which *P. leopardus* habitat occurred, making it unlikely that sex ratios and spawning frequency estimates were influenced by differences in reef-scale movements between sexes.

EFFECT OF FISHING ON REPRODUCTIVE DYNAMICS

There is no indication reproductive compensation occurs for *P. leopardus* at an individual level in the central and southern GBR where fishing pressure is greatest. Fishing-induced reproductive compensation is common in temperate fishes (Koslow *et al.*, 1995), where per capita reproductive output of target species in fished areas increases due to reduced competition for food and space (Rose *et al.*, 2001). For example, losses in total egg production due to increased exploitation were partially compensated for by approximately 25% due to changes in growth, maturation, and fecundity for North Sea plaice *Pleuronectes platessa* L. 1758, sole *Solea solea* L. 1758, and cod *Gadus morhua* L. 1758 (Rijnsdorp *et al.*, 1991). This pattern was only evident at Lizard Island where females spawned three times more frequently on fished reefs than reserves. This region of the GBR receives less fishing pressure than more southern regions (Mapstone *et al.*, 2004; Tobin *et al.*, 2013) and no-take marine reserve zoning has no measurable effect on mean size, age, and density of *P. leopardus* there (Mapstone *et al.*, 2004). Reproductive compensation due to fishing does not seem a plausible explanation for increased spawning frequency on fished reefs at Lizard Island, therefore, and it remains unclear why spawning frequency differed between zones in that region.

Female to male sex change occurred at smaller sizes and younger ages on fished than reserve reefs at Townsville, and on Townsville fished reefs spawning frequency was also reduced. The effect of reduced size and age at sex change with fishing pressure is well-

documented for protogynous species (Hawkins and Roberts, 2003; Hamilton *et al.*, 2007; Götz *et al.*, 2008). The effect on spawning frequency is consistent with the small amount of published research on tropical species regarding the effects of fishing on reproductive output. A complete lack of spawners of the protogynous hogfish *Lachnolaimus maximus* (Walbaum 1792) in fished areas was attributed to a total breakdown of social structure because of intense fishing pressure adjacent to the Florida Keys National Marine Sanctuary (Muñoz *et al.*, 2010). Reduced spawning frequency for *P. leopardus* on Townsville fished reefs may indicate similar fishing-induced pressures on social structure. The lack of a positive relationship between maternal length and age with spawning frequency on Townsville, Mackay, and Storm Cay reefs indicates that the key benefit of reserves for *P. leopardus* spawning frequency comes from maintaining greater densities of *P. leopardus* inside reserves and perhaps reducing disturbance from fishing, rather than from protecting larger and older individuals from harvest. Protection also led to a stronger spawning response in Townsville's females. These results indicate that reserves are beneficial for maintaining "less disturbed" spawning populations of *P. leopardus* on the GBR.

Marine reserve design theory suggests that in the absence of information on larval connectivity and important larval sources reserves are best placed in areas considered pristine, or where there is an abundance of targeted species (Botsford *et al.*, 2003; Bode *et al.*, 2012). Bode *et al.* (2012) recently modelled marine reserves using "connectivity surrogates" for *P. leopardus* and concluded that using the existing biomass characteristics of the species on a reef provided the best indication of transporting larvae in the GBR metapopulation. This logic would suggest that reserves would be best placed in the southern GBR where the *P. leopardus* fishery is concentrated, abundance is highest and, presumably, so too is

reproductive output. Male-biased sex ratios and the lack of spawning activity on southern GBR fished and reserve reefs, however, indicates that applying biomass as a connectivity surrogate to measure the benefits of reserves for *P. leopardus* may be flawed. The importance of considering empirically measured larval dispersal and connectivity in the design and function of marine reserves is recognized increasingly (Almany *et al.*, 2009; Jones *et al.*, 2009; Gaines *et al.*, 2010; Kininmonth *et al.*, 2011; Bode *et al.*, 2012; Harrison *et al.*, 2012; Almany *et al.*, 2013). This study highlights the importance of understanding and incorporating spatial variation in reproductive characteristics that affect the sources of larvae into the design of marine reserves, and when assessing any benefits of reserves for target species.

MANAGEMENT IMPLICATIONS

Male-bias and lack of spawning activity in the southern GBR is surprising given the southern region supports the majority of commercial catch and effort for *P. leopardus*, with catch and catch per unit effort up to four times higher than in the northern GBR (Mapstone *et al.*, 2004; Bergenius, 2007; Tobin *et al.*, 2013). Greater densities of *P. leopardus* in the southern GBR possibly indicate that southern recruits originate from more productive reefs in the central or northern GBR. The lack of genetic variation among regions indicates larval dispersal occurs along the GBR (van Herwerden *et al.*, 2009). Pelagic larval duration for *P. leopardus* is approximately 25 days and recruitment of juveniles at larger spatial scales largely appears to be driven by current patterns and geomorphology (Doherty *et al.*, 1994), with the predominant flow of water along the GBR (south of 14°S) southward due to the East

Australia Current (EAC) (Wolanski and Pickard, 1985). Larval dispersal modelling in the central GBR (Cairns region) supports the theory that there is net export of larvae from northern source to southern sink reefs, with self-recruitment accounting for less than 9% of the settling cohort in 80% of reefs (James *et al.*, 2002; Bode *et al.*, 2006). The hypothesis of long distance larval dispersal on a scale of hundreds of kilometres is contrary to recent genetic parentage analysis, however, which indicates the majority of larvae for congeners *P. areolatus* (Rüppell 1830) (Almany *et al.*, 2013) and *P. maculatus* (Bloch 1790) (Harrison *et al.*, 2012) and other reef fish (Jones *et al.*, 2005; Planes *et al.*, 2009; Saenz-Agudelo *et al.*, 2009; Harrison *et al.*, 2012) settle within tens of kilometres of their natal reef. These studies were conducted in different environments, however, where along-shore transport, such as the East Australia Current, is not as influential and transport dynamics are presumably different to those present on mid-shelf reefs of the GBR. Parentage analysis should also be applied to determine the role that central GBR reefs play as a source of recruits for southern reefs.

Alternatively, greater densities of adult *P. leopardus* may occur in the southern GBR because the relatively small numbers of eggs and larvae produced on southern reefs have a greater proportion survive to settlement compared with larvae produced at lower latitudes. Temperature has a well-known effect on larval development in marine fishes, where as water temperature decreases larvae generally experience slower growth, longer larval stage duration, smaller energy budgets, decreased larval mortality rates, and greater net survivorship (see review by Houde, 1989). Higher survival rates for *P. leopardus* larvae at high latitudes possibly could compensate for reduced spawning frequency and male bias in the GBR region. Increased survival of larvae as they enter cooler waters also might mean that larvae from central and northern reefs that reach the southern GBR experience greater

survival and so enhance recruitment to southern reef populations compared with larvae that remain in warmer, more northern waters.

Understanding spatial variation in reproductive traits is essential when assessing management policies (e.g. no-take marine reserves, minimum sizes, and spawning closures) where the management objective is maintaining sufficient reproductive adults and reproductive output of exploited species. This study highlights the pitfalls of assuming reproductive traits are homogenous when a stock is distributed over a broad geographic area, even when the stock apparently is genetically homogeneous. The current management of *P. leopardus* as a homogenous population is likely to be ineffective for maximising reproductive output, given the striking regional differences demonstrated here. A regional approach to management of the *P. leopardus* fishery may be required if a specific and confined region is disproportionately responsible for maintaining populations at a much broader geographic scale through larval source and sink relationships. If this was the case, management of exploited species would benefit by understanding where these key reproduction areas are so that management measures can mitigate effects of fishing on key reproductive components of the population. Perhaps more importantly, this study clearly demonstrates that *P. leopardus* population(s) on the GBR do not fit the conventional model of reproductive biology and sex structure following protection from fishing and highlights the need for more systematic long-term studies of the population biology of large protogynous hermaphroditic tropical reef fish.

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1 **TABLE I.** Numbers of *Plectropomus leopardus* sampled by region and management zone (fished and no-take marine reserve). Females
2 collected from four regions comprising two management zones. Spawners, 1-Day POFs present; Non-spawners, 1-Day POFs absent. Spawning
3 frequency (days) and number of batches spawned per season assuming a four month spawning season.

Region	Zone	Month	Lunar quarter sampled	Mature females			Spawning frequency (days)	Batches spawned per season
				Spawners	Non-spawners	Total mature females		
Lizard Island	Fished	October	First quarter - full moon	134	263	397	3.2	38.4
	Reserve	October	First quarter - full moon	22	209	231	12.0	10.1
Townsville	Fished	October – November	Full moon - last quarter	32	138	170	5.3	22.9
	Reserve	October – November	Full moon - last quarter	200	278	478	2.3	52.0
Mackay	Fished	November	First quarter - last quarter	0	72	72	na.	na.
	Reserve	October – November	First quarter	2	160	162	83.2	1.5
Storm Cay	Fished	November – December	Full moon - last quarter	6	88	94	17.2	7.1
	Reserve	November – December	Full moon - last quarter	3	92	95	28.8	4.2

Total	<i>N</i>	399	1300	1699	4.3	23.0
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4 na., not applicable due to absence of spawners in fished reefs.

TABLE II. Parameter estimates from generalized linear mixed effects models (GLMM) examining the effects of fork length (L_F), age (A), region (R) and zone (Z) on sex ratio (P_M , proportion male), proportion of vitellogenic females (P_V) and spawning fraction (P_S , probability of spawning) of *Plectropomus leopardus*. The four best-fitting models are shown, and the final model selected (in bold) was considered to be the simplest model within two of the lowest AICc. Models with interaction terms (*) also include main effects. Sex ratio, P_V and P_S were modeled with a binomial distribution and logit link function. β_{reef} is the random effect of reef, and ε is the error term. AIC_c is the small-sample bias-corrected form of Akaike's information criterion, Δ is the Akaike difference, and w is the Akaike weight.

Model	AIC _c	Δ AIC _c	w
Sex ratio (L_F)			
$P_M = L_F * R * Z + \beta_{\text{reef}} + \varepsilon$	5788.37	0	0.99
$P_M = L_F * R + \beta_{\text{reef}} + \varepsilon$	5800.06	11.7	<0.01
$P_M = L_F + R + Z + \beta_{\text{reef}} + \varepsilon$	5806.07	17.7	<0.01
$P_M = L_F * R + Z + \beta_{\text{reef}} + \varepsilon$	5810.00	21.6	<0.01
Sex ratio (A)			
$P_M = A * R * Z + \beta_{\text{reef}} + \varepsilon$	5912.72	0	0.82
$P_M = A + R + \beta_{\text{reef}} + \varepsilon$	5917.36	4.59	0.08
$P_M = A + R + Z + \beta_{\text{reef}} + \varepsilon$	5921.23	4.64	0.08
$P_M = A * R + \beta_{\text{reef}} + \varepsilon$	5921.52	8.51	0.01
Vitellogenic females (L_F)			
$P_V = L_F + \beta_{\text{reef}} + \varepsilon$	1569.04	0	0.36
$P_V = L_F + Z + \beta_{\text{reef}} + \varepsilon$	1569.13	0.09	0.34
$P_V = L_F * Z + \beta_{\text{reef}} + \varepsilon$	1571.11	2.08	0.13
$P_V = L_F + R + Z + \beta_{\text{reef}} + \varepsilon$	1572.99	3.96	0.05

Vitellogenic females (A)

$P_V = A + Z + \beta_{\text{reef}} + \varepsilon$	1426.71	0	0.26
$P_V = A + \beta_{\text{reef}} + \varepsilon$	1426.82	0.11	0.24
$P_V = A * Z + \beta_{\text{reef}} + \varepsilon$	1427.25	0.55	0.19
$P_V = A * R * Z + \beta_{\text{reef}} + \varepsilon$	1429.70	0.77	0.18

Spawning fraction (L_F)

$P_S = R * Z + \beta_{\text{reef}} + \varepsilon$	1547.55	0	0.90
$P_S = R + \beta_{\text{reef}} + \varepsilon$	1553.46	5.91	0.05
$P_S = R + Z + \beta_{\text{reef}} + \varepsilon$	1555.38	7.83	0.02
$P_S = L_F + R + \beta_{\text{reef}} + \varepsilon$	1555.42	7.87	0.02

Spawning fraction (A)

$P_S = A * R * Z + \beta_{\text{reef}} + \varepsilon$	1477.75	0	0.70
$P_S = A * R + \beta_{\text{reef}} + \varepsilon$	1480.24	2.49	0.20
$P_S = A * R + Z + \beta_{\text{reef}} + \varepsilon$	1482.23	4.48	0.08
$P_S = A + R + \beta_{\text{reef}} + \varepsilon$	1485.78	8.02	0.01

15 **TABLE III.** Timing and duration of spawning season for coral trout. See Fig. 1 for location of each location.

GBR Region	Location	Spawning peak	Spawning range (inclusive)	Vitellogenesis range (inclusive)	Indicator	Study duration	Author
North of GBR	Torres Strait	October-November	July – November	May - November	GSI, % frequency of gonadal stages	2004-2005	(Williams <i>et al.</i> , 2008)
Northern	Lizard Island	October	September – December*	August – December	GSI, % frequency of gonadal stages	1990 - 1992	(Brown <i>et al.</i> , 1994; Ferreira, 1995)
Central	Cairns	September-October	September – November/ December	August – December/ January	GSI, % mature females in vitellogenic state of development	1992 –1994	(Samoilys, 2000)
Central	Cairns	October	September - December	August - December	GSI, % mature	1989 - 1992	(Brown <i>et al.</i> , 1994)
Central	Townsville	October-November	September –	July – January	GSI, % mature	1998-2000	(Davies <i>et al.</i> ,

			December				2006)
Central	Townsville	October	September – November*	July – November	GSI, % frequency of gonadal stages	1990 – 1992	(Brown <i>et al.</i> , 1994; Ferreira, 1995)
Central	Townsville	October	October – December	August – December	GSI, maximum oocyte diameter, % frequency of gonadal stages	2004 – 2005	(Frisch <i>et al.</i> , 2007)
Central	Townsville	ns.	September – November	March – November	Presence of ripe females	1990-1994	(Russ <i>et al.</i> , 1995)
Southern	Swains and Capricorn- Bunker Group	October-November	October – February	ns.	GSI	ns.	(Brown <i>et al.</i> , 1994)
Southern	Heron Island	November- December	October – January	Ovaries inactive by February	GSI	1971-1972	(Goeden, 1978)

FIGURE CAPTIONS

FIG. 1. *Plectropomus leopardus* were sampled from four reef clusters on the Great Barrier Reef. Inset maps: no-take marine reserve reefs sampled (○) and reefs historically open to fishing sampled (⦿).

FIG. 2. *Plectropomus leopardus* postovulatory follicle stages used to identify recent spawners. (a) 0-Day postovulatory follicle (POF) is large with no signs of degeneration. Follicle cell layers are cord-like and convoluted and form tight folds; (b) 1-Day POF is characterized by pronounced degeneration with reduced size, fewer folds and small lumen. P, perinucleolus stage oocyte; EYG, early yolk globule stage oocyte; LYG, late yolk globule stage oocyte; H, hydrated stage oocyte.

FIG. 3. Observed and predicted trends in *Plectropomus leopardus* sex ratio (proportion male) ($\pm 95\%$ confidence intervals) with fork length (mm) at Lizard Island, Townsville, Mackay and Storm Cay from (a) no-take reserve reefs and (b) fished reefs. Predictions derived from best fit model described in Table II.

FIG. 4. Observed and predicted trends in *Plectropomus leopardus* sex ratio (proportion male) ($\pm 95\%$ confidence intervals) with age at Lizard Island, Townsville, Mackay and Storm Cay

from (a) no-take marine reserve reefs and (b) fished reefs. Predictions derived from best fit model described in Table II.

FIG. 5. Predicted trends in the proportion of vitellogenic *Plectropomus leopardus* females (\pm 95% confidence intervals) with (a) fork length (mm) and (b) age. Predictions derived from best fit model described in Table II.

FIG. 6. Predicted spawning fraction of female *Plectropomus leopardus* (proportion females with POFs) (\pm 95% confidence intervals) with region from fished reefs (\square) and no-take marine reserve reefs (\blacksquare). Predictions derived from best fit model described in Table II.

FIG. 7. Observed and predicted trends in spawning fraction (proportion female *Plectropomus leopardus* with POFs) (\pm 95% confidence intervals) with age at Lizard Island, Townsville, Mackay and Storm Cay from (a) no-take reserve reefs and (b) fished reefs. Predictions derived from best fit model described in Table II.

Figure 1

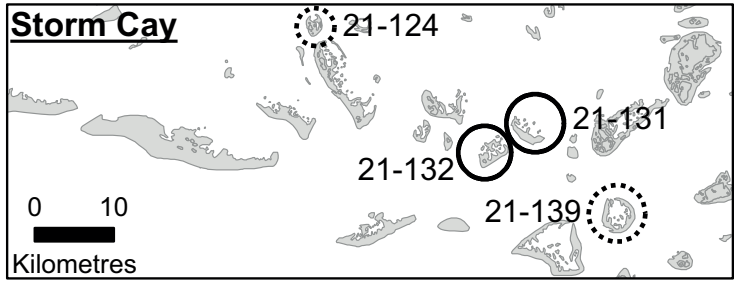
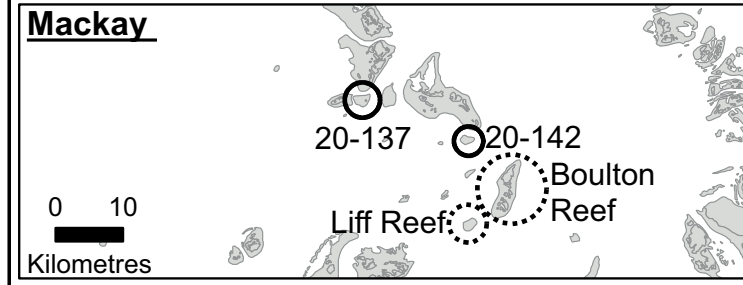
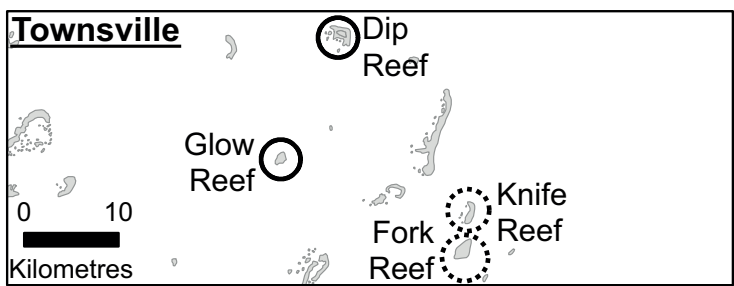
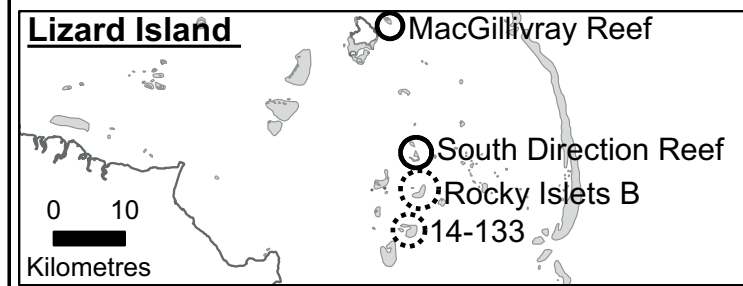
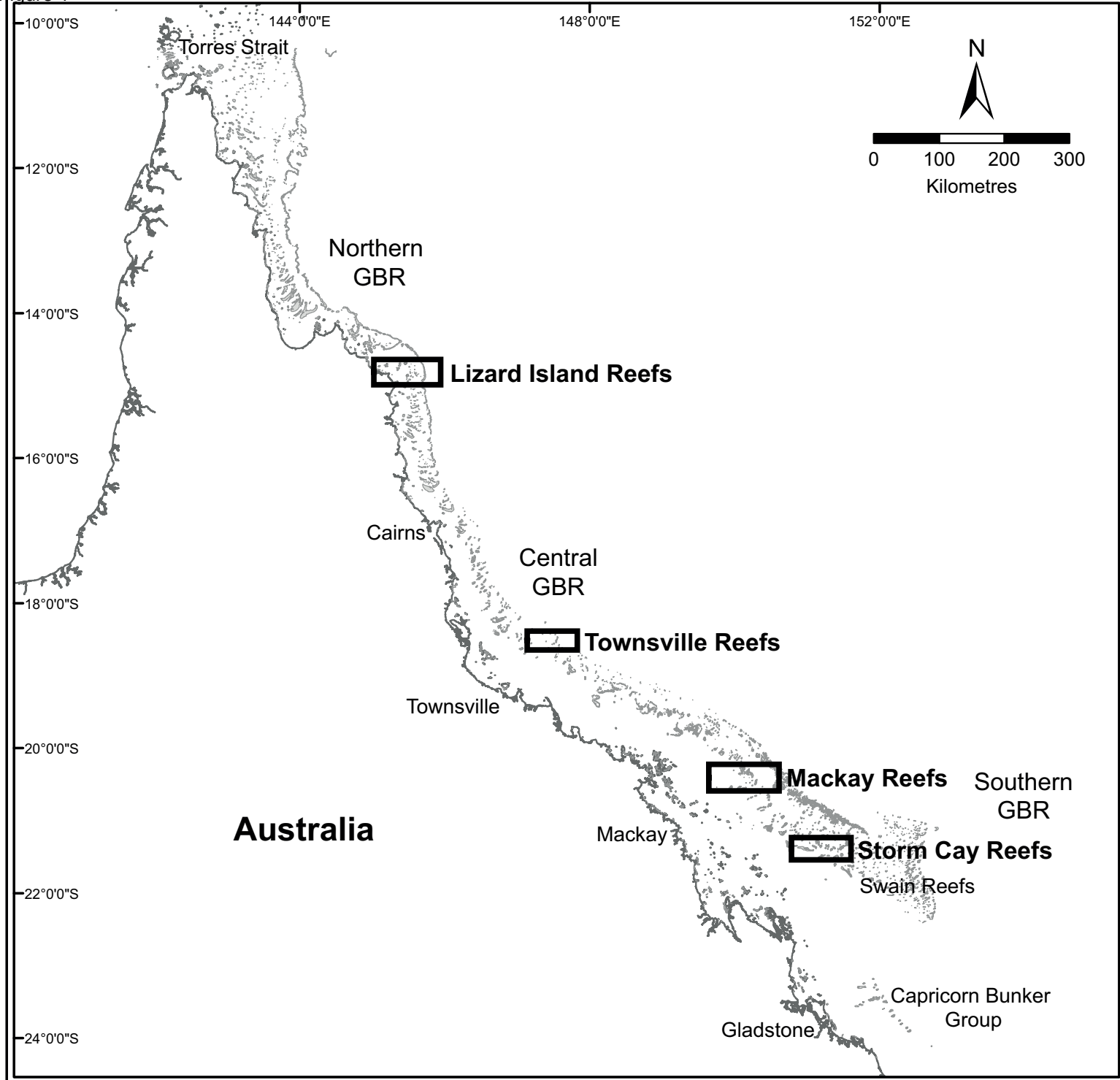


Figure 2a

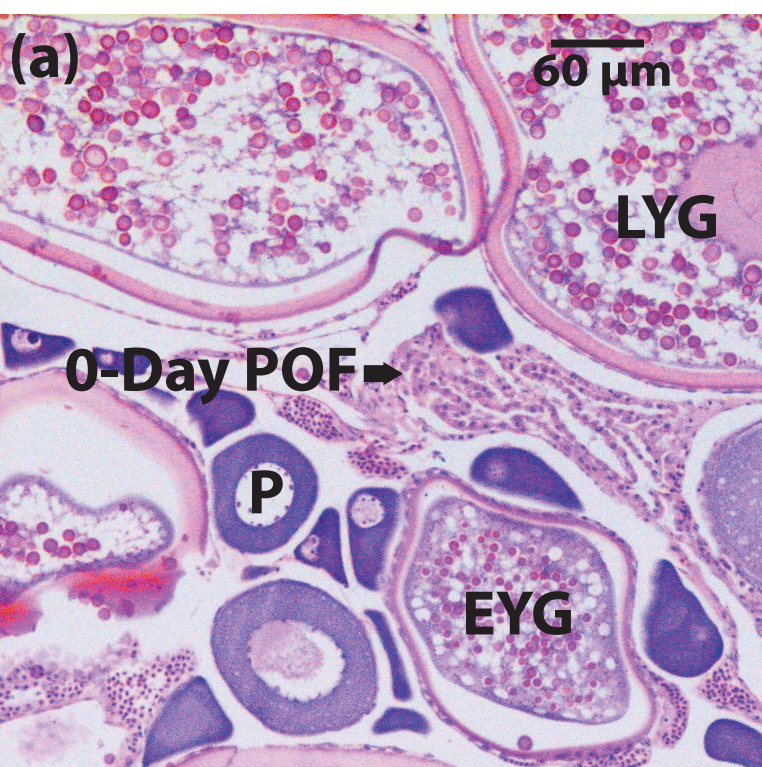
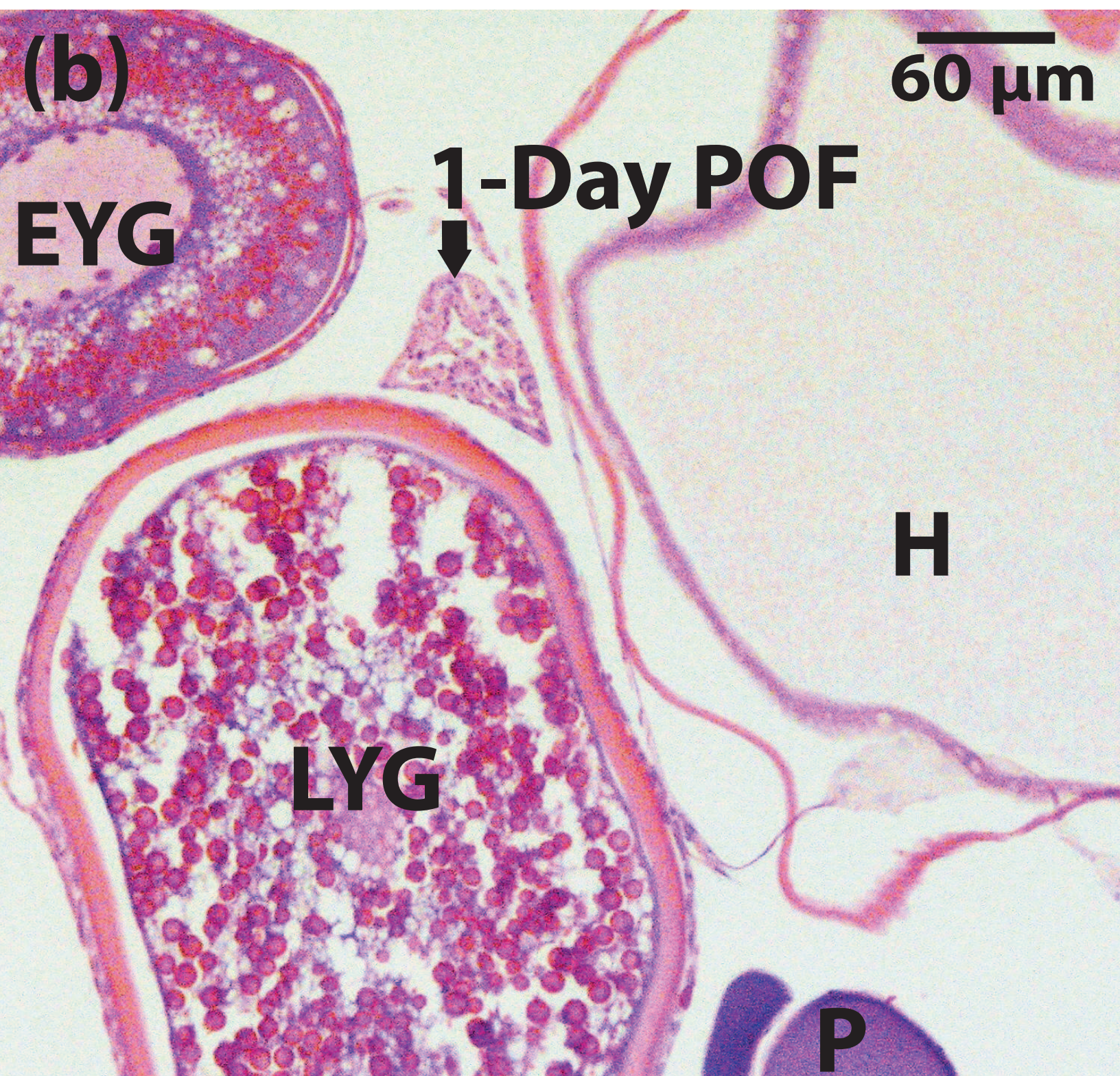


Figure 2b



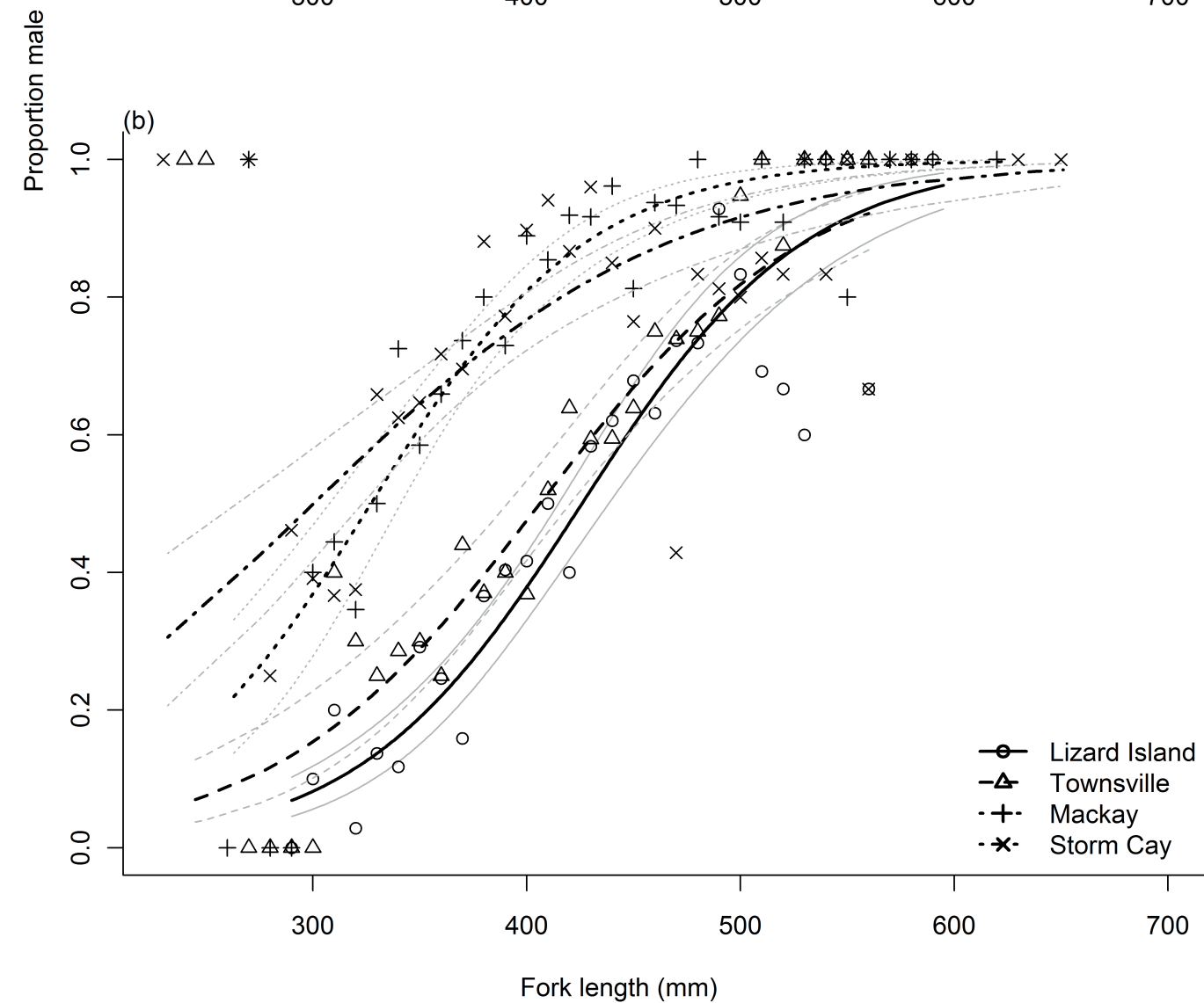
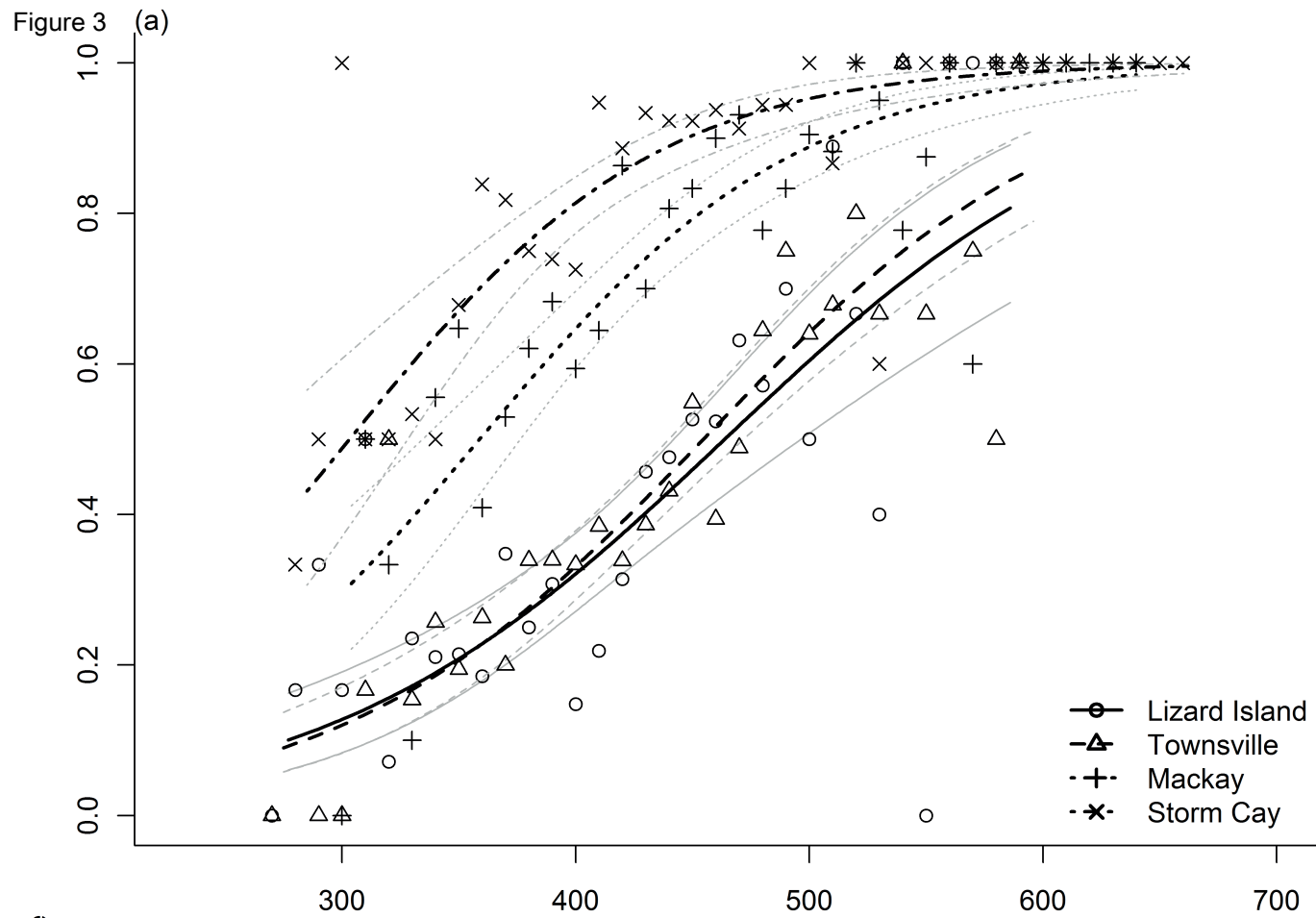


Figure 4

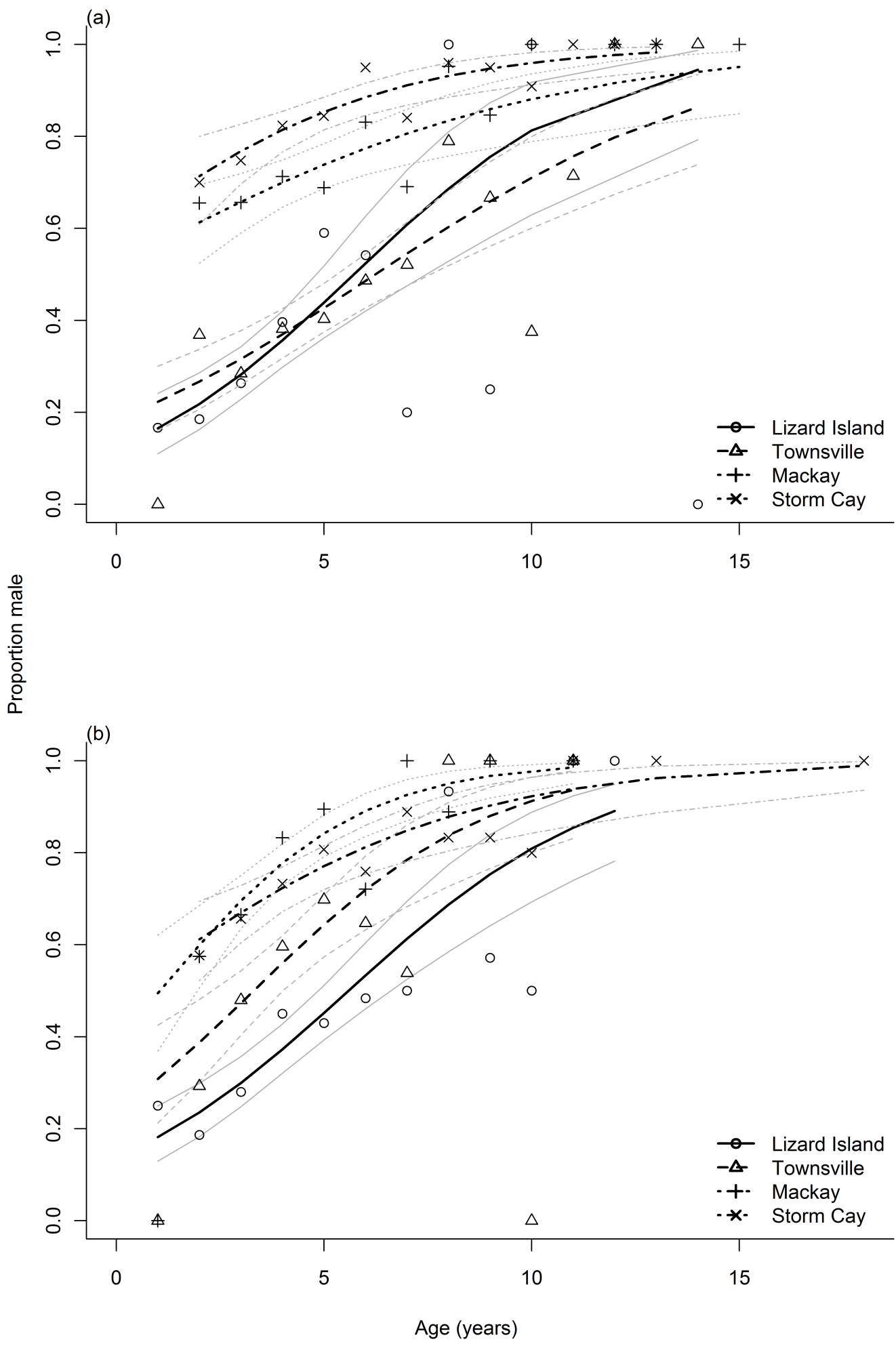


Figure 5a

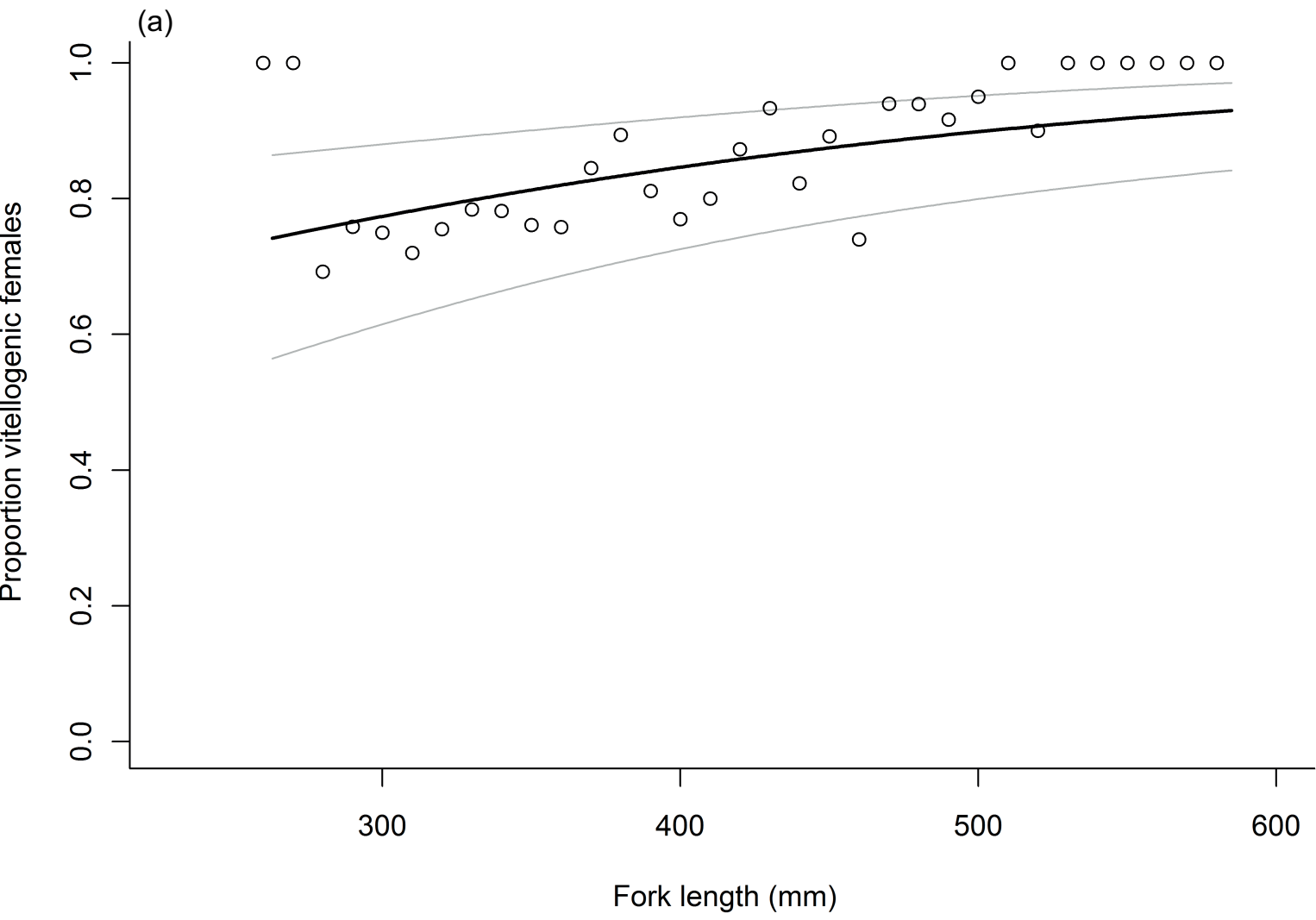


Figure 5b

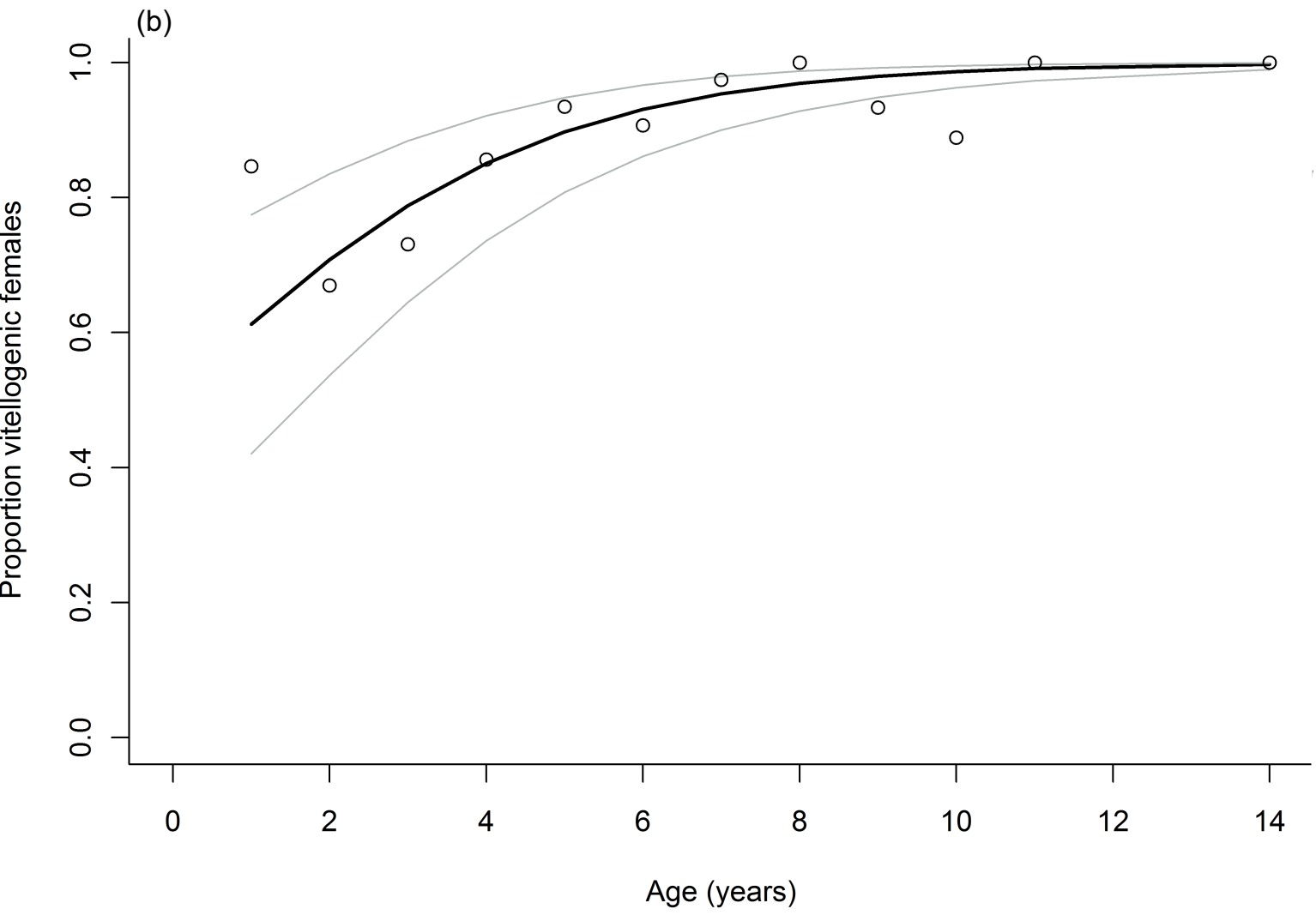


Figure 6

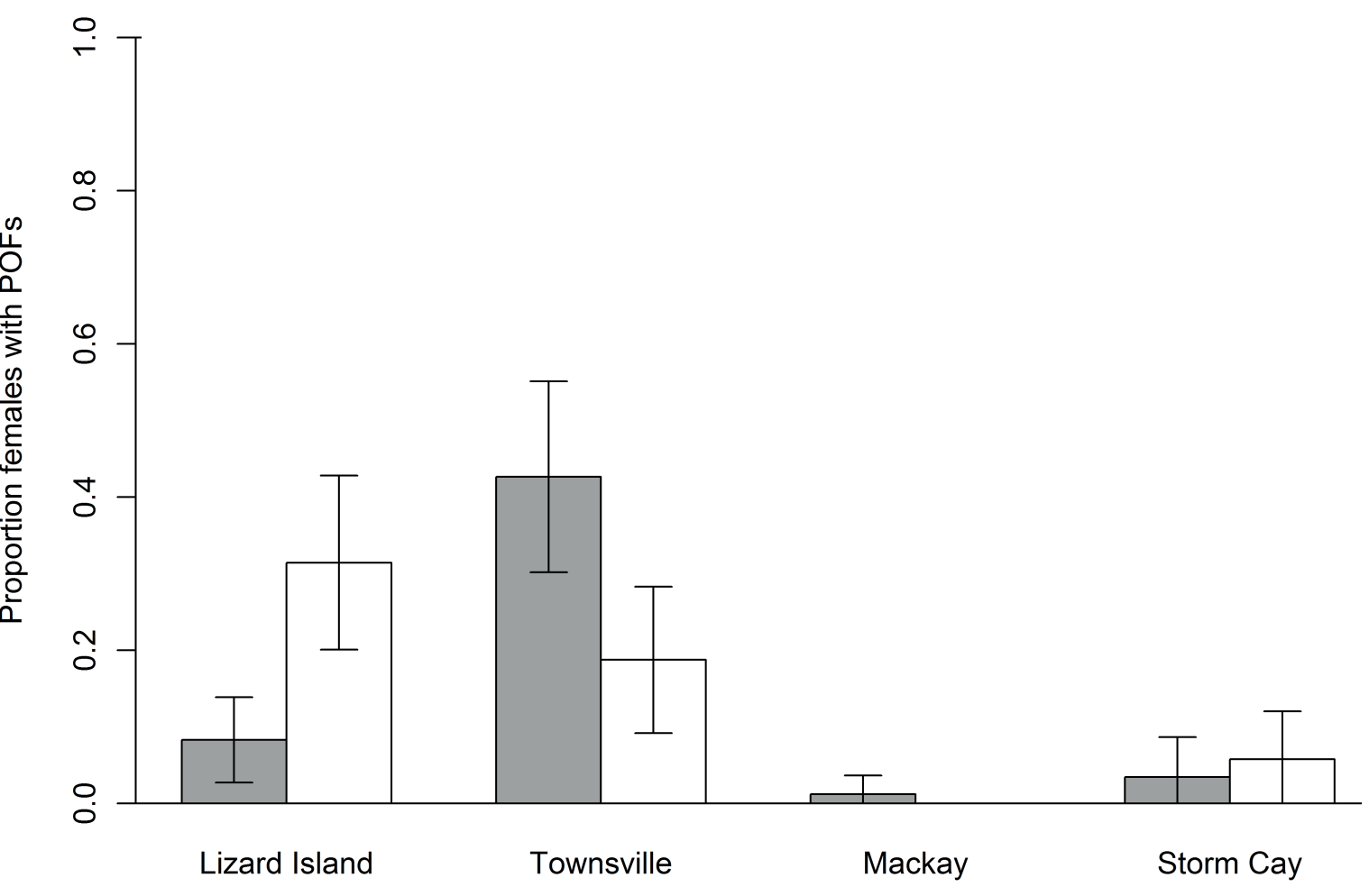


Figure 7

