Demography of a large exploited grouper, *Plectropomus laevis*: Implications for fisheries management

Michelle R. Heupel[A,F], *Ashley J. Williams*[B], *David J. Welch*[B,C],
Campbell R. Davies[D], *Samantha Adams*[B], *Gary Carlos*[E]
and Bruce D. Mapstone[D]

[A]School of Earth and Environmental Sciences, James Cook University, Townsville,
  Qld 4811, Australia.
[B]Fishing and Fisheries Research Centre, School of Earth and Environmental Sciences,
  James Cook University, Townsville, Qld 4811, Australia.
[C]Queensland Department of Primary Industries and Fisheries, PO Box 1085,
  Oonoonba, Qld 4811, Australia.
[D]CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, Tas. 7001, Australia.
[E]Marine Research Laboratory, Tasmanian Aquaculture and Fisheries Institute,
  University of Tasmania, Private Bag 49, Tas. 7001, Australia.
[F]Corresponding author. Email: michelle.heupel@jcu.edu.au

Abstract. Species in the coral trout complex *Plectropomus* spp. are some of the most desired and exploited in the Indo-Pacific, although data are limited for most species. Demographic parameters of blue-spot coral trout, *Plectropomus laevis*, were estimated on the basis of specimens collected from five regions of the Great Barrier Reef and Torres Strait, Australia, between 1995 and 2005 to define demography and population status over a broad range. In total, 1249 individuals were collected to estimate growth, mortality and reproductive parameters. Growth parameters based on the von Bertalanffy model were $K = 0.096$ year^{-1}, $L_\infty = 1159$ mm fork length (FL) and the best-fit model suggested non-asymptotic growth over the size and age ranges represented in the sample. Maximum age was 16 years, total mortality was estimated at 0.39 (± 0.031), and estimated size and age at first maturity were 299 mm FL (range: 299–872) and at 1 year (range: 1–6.5), respectively, with the size range over which sex change occurred at 460–872 mm FL. Population parameters and available relative abundance estimates indicated that long-term sustainable harvest rates of *P. laevis* will be lower than those for *P. leopardus* and species-specific size-based management measures are necessary to ensure the species is not overfished.

Additional keywords: coral reef, coral trout, demography, fish, growth, tropical fisheries.

Introduction

Unbiased estimates of population parameters of harvested species are an important component of assessing populations and effective management of sustainable exploitation. Many coral reef fish species have high market value and are heavily exploited in many regions of the world (Jackson *et al.* 2001; Sadovy 2005). Thus, there is an immediate need for better information on the growth and reproductive patterns of these populations to assist in development of effective management strategies. These data are scarce or absent for many large reef species. Despite a broad distribution in subtropical and tropical seas, *Plectropomus laevis* has received little scientific attention because of its rarity. Limited catch data suggested this species is in decline and has led to an IUCN Red List classification of 'Vulnerable'. The data required to define an effective management strategy for this species throughout its distribution, however, are lacking. This species currently appears to be found most reliably in waters of the Great Barrier Reef (GBR) and Coral Sea, suggesting

that studies of these populations might be used as a basis for understanding populations in the rest of the Indo-Pacific.

Serranids, particularly those of the *Plectropomus* genus, are some of the most heavily targeted species on the GBR (Mapstone *et al.* 1996; Zeller and Russ 2000; Williams *et al.* 2008*a*). Plectropomids are collectively referred to as coral trout in fisheries on the GBR and are represented by as many as four species (*Plectropomus areolatus*, *P. laevis*, *P. leopardus* and *P. maculatus*). The two closely related species of *Variola* (*V. albimarginatus*, *V. louti*) also are referred to, and commonly marketed as, coral trout. This coral trout complex has been reported to comprise 35–55% of commercial catch, 20–25% of charter catch and 15–20% of recreational catch by reef line fishers on the GBR (Mapstone *et al.* 2004). It is rare for reported catches to include species-level identification, although it is known that *P. leopardus* is the most common species in the commercial reef line fishery catch and estimated to comprise over 95% of the catch (B. Mapstone, unpubl. data).
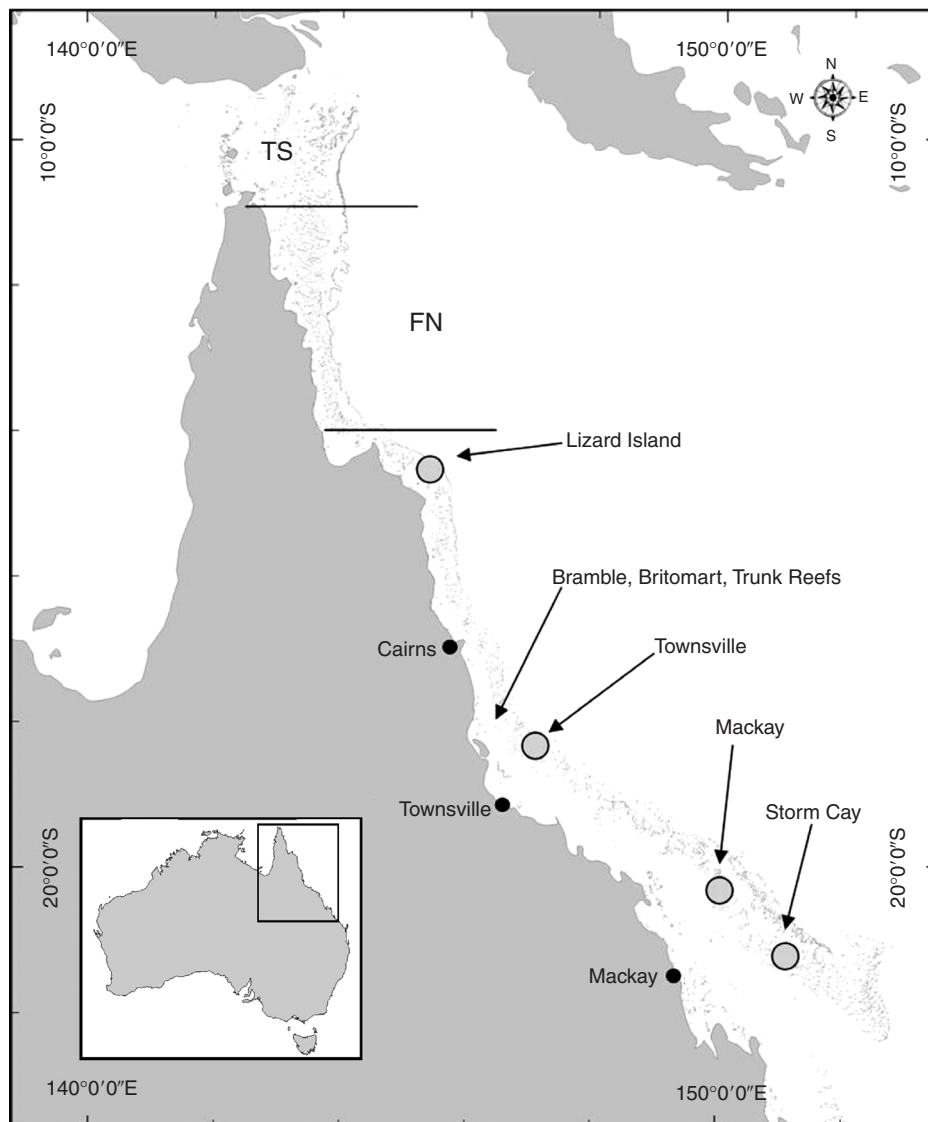
Fig. 1. Map of the Great Barrier Reef region off the eastern coast of Australia showing sampling regions used in the study, including designation of the Far North and the Torres Strait where previous work was conducted by Williams *et al*. (2008*a*, 2008*b*). Additionally, sampled reefs in the Townsville region are also indicated.

Plectropomus leopardus has been the focus of the majority of research on harvested reef species on the GBR and estimates of age-based population parameters are available only for *P. leopardus* (e.g. Ferreira and Russ 1994; Ferreira 1995; Adams *et al*. 2000) and *P. maculatus* (Ferreira and Russ 1992; Ferreira 1993) within the coral trout complex. The remaining coral trout species have received limited scientific attention largely because of their lower abundance in commercial and recreational catches and the difficulty in obtaining larger sample sizes for systematic study (but see Williams *et al*. 2008*b*). Recent research by Williams *et al*. (2008*b*) examined the population biology of four species of coral trout in the Torres Strait (at the extreme north of the GBR, and outside the GBR Marine Park, Fig. 1), including *P. areolatus*, *P. laevis*, *P. leopardus* and *P. maculatus*. The aim of their research was to assess whether coral trout populations in the Torres Strait could be managed effectively with the same management measures or required species-specific management. They concluded that combined management may be suitable for *P. leopardus* and *P. maculatus* but that *P. areolatus* should be managed separately because of the larger size at sex change for this species and low proportion of males protected by current size limits. There were insufficient samples, however, to draw a definitive conclusion for *P. laevis*.

The blue-spot or footballer trout, *P. laevis*, is the largest of the coral trout species, reaching in excess of 1000 mm total length (Randall *et al*. 1997) and displaying a distinct cross-shelf gradient in abundance, being most common on outer-shelf reefs (Newman *et al*. 1997). *P. laevis* has a monandric protogynous reproductive strategy, with mature females changing to males and populations having a biased female to male sex ratio (Adams 2002). In addition, *P. laevis* displays two distinct colour phases. Davies *et al*. (2006) suggested that the two distinct colour phases
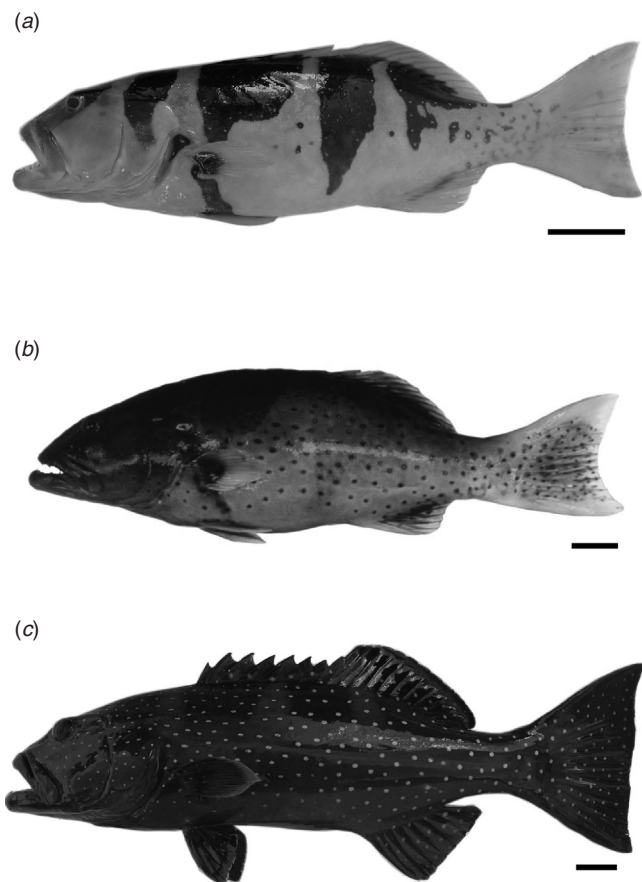
(*a*)

(*b*)

(*c*)

Fig. 2. Plate showing distinct colour phases of (*a*) footballer, (*b*) transitional and (*c*) blue-spot *Plectropomus laevis*. Scale bars = 5 cm.

are related to size at sexual maturity. Smaller individuals typically have the 'footballer' form characterised by a white body with black saddles, yellow fin markings and few blue spots, whereas larger individuals generally display the 'blue-spot' form with a dark brown or red body covered with distinctive large blue spots (Fig. 2). The two colour phases generally are distinct, but transitional individuals have been observed (Davies *et al.* 2006). This colour dimorphism is peculiar to *P. laevis* within the coral trout complex. Other members of the coral trout complex display depth-related colour variation, from dark olive in shallow water to crimson red in deeper water (Mapstone *et al.* 2001) but they do not exhibit distinct size- or age-related colour morphs and reportedly can change colour repeatedly.

Plectropomus laevis therefore warrants further research in terms of the need for species-specific estimates of population parameters to inform the development of management strategies for their conservation and sustainable use. This text provides the first age-based estimates of key population parameters for the species from samples collected over the length of the GBR to help better inform management throughout its distribution. Results of this study help define the importance of population parameters for this and other reef-associated species for which data are limited.

Materials and methods

Study area

The Great Barrier Reef (GBR) extends from the southern coast of Papua New Guinea (9°S) down the eastern margin of the Torres Strait and eastern coast of Australia to ~24.5°S, off southern Queensland. The GBR Marine Park (GBRMP) includes 344 400 km^2 of habitat and the majority of the Great Barrier Reef (10.5–24.5°S) along the eastern coast of Australia (Fernandes *et al.* 2005). This text presents analyses of samples collected from the GBRMP over a period of 10 years and compares the results with those reported for Torres Strait by Williams *et al.* (2008*b*).

Sampling methods

Most samples of *P. laevis* (*n* = 1148) were collected during the effects of line fishing (ELF) experiment (Mapstone *et al.* 2004) between 1995 and 2005 from the following four broad regions of the GBR, spanning 7° of latitude: Lizard Island, 14°S; Townsville, 18°S; Mackay, 20°S; and Storm Cay, 21°S (Fig. 1). Samples were either dissected on the day of capture and processed as described below or whole individuals or processed frames were frozen and dissected on return to the laboratory.

Additional fish were collected between January 2004 and December 2005 from reefs in Torres Strait in far-northern Australia either as frozen fish frames retained by commercial fishers or as dissected specimens collected by observers on board commercial fishing vessels (see Williams *et al.* 2008*b*). The ELF samples from the GBRMP were also supplemented with fish collected from mid-shelf reefs (Bramble, Britomart and Trunk Reefs) in the Townsville Region during monthly fishery-independent research surveys from September 1998 to December 2000 (Davies *et al.* 2006) and specimens collected by a commercial fisher between 1995 and 2005 from reefs located in the far-northern GBR (11–14°S), comprising a fifth broad region of the GBR in some analyses. Regional comparisons of population demographics were carried out where possible for ELF regions, the Far North (FN) and the Torres Strait (TS).

Sample processing

All specimens were measured to the nearest millimetre fork length (FL) and weighed to the nearest gram before dissection. Sagittal otoliths were dissected from a subsample of 597 specimens (including 23 from TS), cleaned and stored dry in paper envelopes. Otoliths were embedded in epoxy resin and cut transversely through the centrum with a diamond-tipped blade on a low speed saw to produce a thin section of 300–400 μm. Sections were mounted on glass slides with Crystalbond adhesive (Aremco Products Inc., New York). Otoliths were read under reflected light at ×40 magnification and opaque increments counted from the nucleus to the edge along the ventral margin of the sulcus acousticus. Opaque increments were assumed to be formed annually on the basis of validation in two closely related species (*P. leopardus* and *P. maculatus*; Ferreira and Russ 1992, 1994). The morphometrics of *P. laevis* otoliths are indistinguishable from the other two species (A. Williams, pers. obs.; see Ferreira and Russ 1994) and thus it was assumed that opaque increments in *P. laevis* also are formed annually.

Sectioned otoliths were read using two different methods because ageing protocols evolved through time with the development of a set of reference otoliths. Approximately half of the otoliths ($n = 335$) were read at least once by each of two independent readers and the age was accepted if these first two counts agreed. A third count was made by one of the two readers if the first two counts did not agree and a match between this third count and either of the previous two was accepted as the age of the fish or, if the third count did not match either of the first two counts ($n = 3$), the median count was assigned as a final age estimate. The remaining processed otoliths ($n = 262$) were read by a single, experienced reader tested against a reference set of otoliths for accuracy. This reader counted each otolith once or twice with a minimum of 24 h between consecutive counts. Single counts from this reader were considered valid on the basis of a high degree of agreement between second readings of a subset of otoliths (precision) and consistent agreement with counts of the reference set of otoliths.

Gonads were dissected from 485 *P. laevis* specimens (41 from FN, 6 from TS, 438 from ELF regions) and frozen immediately after removal. Thawed tissues were preserved in a solution of formaldehyde (4%), acetic acid (5%) and calcium chloride (1.3%) (FAACC) before May 1999 and 10% buffered formalin thereafter. Paired gonads were dried of excess fixative and weighed to the nearest 0.01 g after fixation. The weights of single lobes were measured and doubled to represent a total gonad weight for both lobes if one of the lobes was lost or damaged during processing ($n = 30$). This procedure has been used previously and is accepted as providing reliable estimates of whole-gonad weight for coral trout species (Adams 2003; Williams *et al.* 2008*b*).

Histological sections were taken from all gonads following procedures for plectropomids described in Adams (2003). Medial sections were used to determine reproductive stage on the basis of consistent cell development within the central section of the gonad (Adams *et al.* 2000; Adams 2003). Stage of ovary development was based on the most advanced non-atretic cell type present (West 1990). Additional features used to classify reproductive stage included presence of brown bodies, atretic oocytes, vascularisation and the relative thickness of the gonad wall (Adams 2003). Ovaries and testes were classified on the basis of developmental stages as defined by Ferreira (1995).

Estimation of demographic parameters

The relationship between fork length (FL, in mm) and weight (W, in g) was estimated using a power function. The length–weight relationship was estimated after log-transformation of the raw data (to normalise the relationship) and differences in the estimated relationship were tested between colour phase and among regions with analysis of covariance. The distribution of residuals was examined to ensure transformed data met the assumptions of the test. Length and age frequency distributions were calculated for the sample population grouped by colour phase and (separately) by region. Tests for differences in mean length and age by region were examined with analysis of variance. Post hoc tests (Tukey unequal N HSD test) were used to identify homogeneous groups.

Growth was modelled using the von Bertalanffy growth function (VBGF) fitted using a non-linear least-squares regression

of FL (mm) on age (years). Total mortality (Z) was estimated using age-based catch curves (Ricker 1975) where the number of fish in each age class was transformed ($\log x + 1$) and regressed against the corresponding age, with the instantaneous rate of total mortality estimated by the unsigned value of the regression slope fitted to all fully recruited age classes, defined as those ages greater than the modal age class in the sample.

Patterns in the depth distribution of captured individuals were examined by fish length, colour phase and region. The relationship between depth of capture and length was tested with regression analysis. The relationships between depth and colour phase and region were examined by three-way chi-square contingency tables.

The spawning season for *P. laevis* was estimated on the basis of histological staging of reproductive tissue samples ($n = 352$) and plots by month of gonadosomatic index (GSI = gonad weight/fish weight $\times$ 100) ($n = 454$), although samples could not be obtained in June–July for either sex and no male samples were obtained in March–April of any year. The proportion of individuals in each histologically determined reproductive stage was plotted by month as an indication of ovarian and testicular development throughout the year.

A logistic function was fitted to estimate the size and age at which 50% and 95% of individuals were mature within the sampled population. The same approach was used to estimate size and age at sex change by examining the proportion of mature males (relative to mature females) by length and age class. Transitional individuals were excluded from the sex-change analyses.

Results

Samples from 781 blue-spot and 468 footballer *P. laevis* were collected during the ELF experiment and supplementary sampling. Numbers of individuals collected per region were variable, with the largest sample size from Townsville (672), followed by Mackay (237) and smaller sample sizes from Lizard Island (172) and Storm Cay (67). A further 101 specimens were obtained from outside the regions involved in the ELF experiment: 25 from the Torres Straight, 12 near Townsville and 64 from reefs in the far northern GBR (FN).

Size

The relationship between FL and W was isometric, with individuals becoming more heavy-bodied as they grew in all regions and colour phases. There was no significant difference in log-transformed length–weight relationships among the five regions with suitable sample sizes for comparison (Far North, Lizard Island, Townsville, Mackay and Storm Cay; ANCOVA, $F_{4,888} = 1.45$, $P = 0.216$). The estimated overall $W_{gm} - FL_{mm}$ relationship for the pooled sample was $W = 0.0000038\ FL^{3.21}$ ($r^2 = 0.94$, $P < 0.001$, Fig. 3).

The lengths of *P. laevis* in the sample ranged from 250 to 1150 mm FL, with the largest sample size in the 450–550-mm length class (Fig. 4*a*). Length by region was examined using data from all regions (Torres Strait, Far North, Lizard Island, Townsville, Mackay, Storm Cay). Log-transformed mean length varied significantly by region (ANOVA, $F_{5,1221} = 10.9$, $P <$
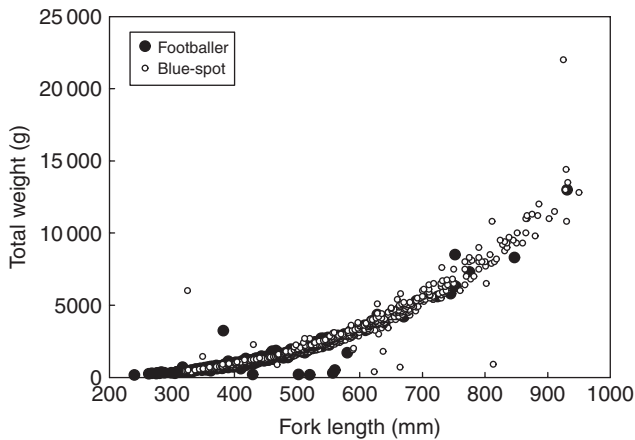
Fig. 3.   Length-at-age of all *Plectropomus laevis* sampled in all regions. Differences in points indicate footballer *v.* blue-spot individuals.
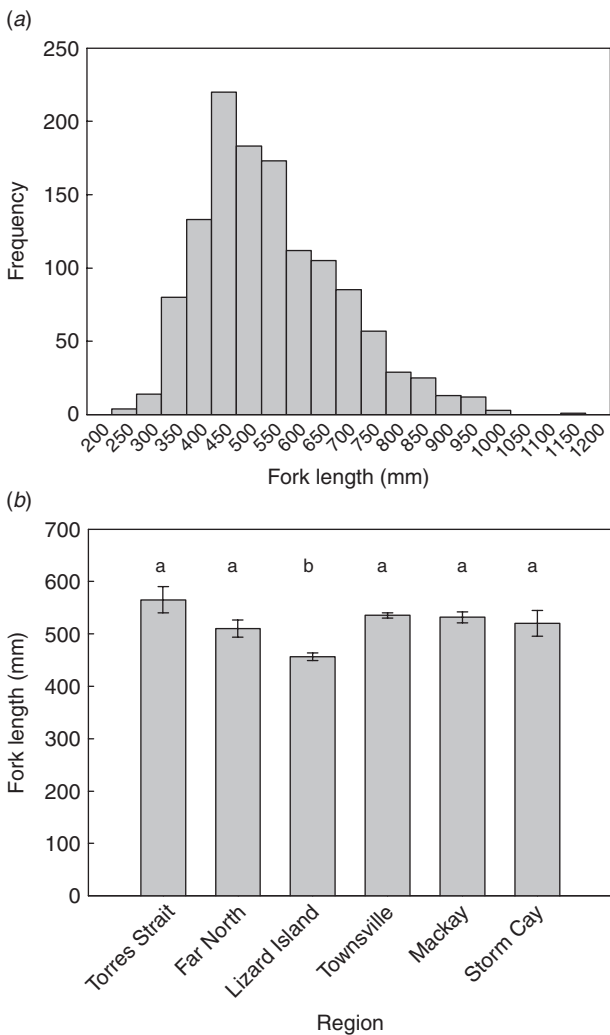

Fig. 4.   (*a*) Size frequency distribution of *Plectropomus laevis* specimens from all regions sampled within the Great Barrier Reef and Torres Strait and (*b*) mean length of *P. laevis* in each region. Error bars indicate standard error.
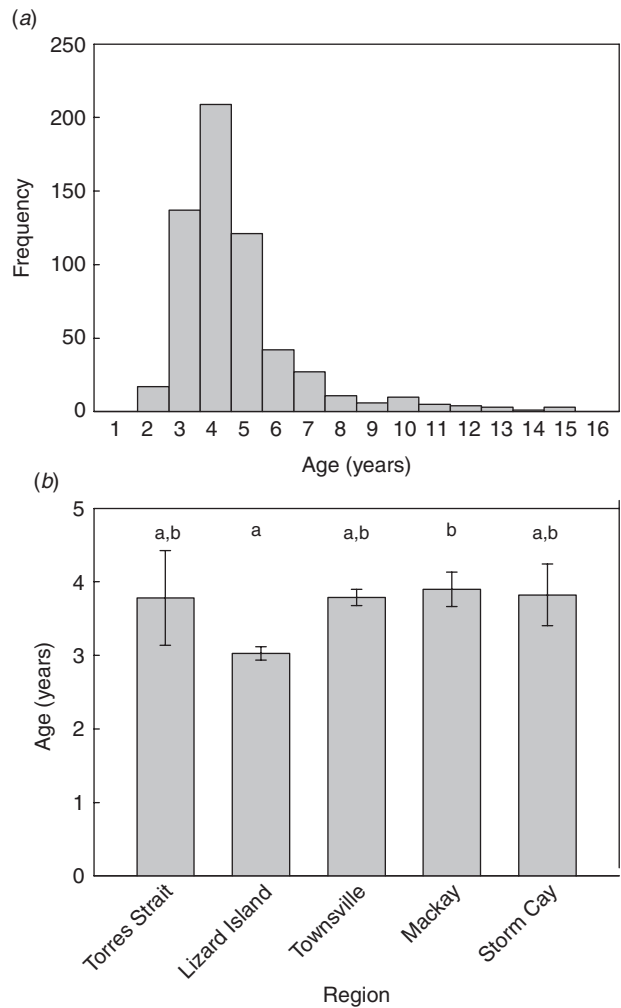

Fig. 5.   (*a*) Age frequency distribution of *Plectropomus laevis* specimens collected from four regions sampled within the Great Barrier Reef and Torres Strait and (*b*) mean age of *P. laevis* in each region. Error bars indicate standard error.

0.0001) (Fig. 4*b*), with a significantly smaller mean length at Lizard Island than in all other regions (Tukey's post hoc test, $P < 0.05$).

Age, growth and mortality

Age estimates ranged from 1 to 16 years, with a mode of 3 years ($n = 597$, Fig. 5*a*). Variation in mean age by region was examined using data from all regions for which age data were available (Torres Strait, Lizard Island, Townsville, Mackay, Storm Cay). Mean age (log-transformed) differed significantly with region (ANOVA, $F_{4, 591} = 3.16$, $P = 0.014$). Post hoc analysis indicated two overlapping homogeneous groupings of regions, as follows: (1) Torres Strait, Lizard Island, Townsville and Storm Cay, with lower mean ages; and (2) Torres Strait, Townsville, Mackay and Storm Cay, with higher mean ages (Fig. 5*b*). Thus, there was no clear latitudinal pattern in mean age.

Growth parameters calculated from the VBGF were $K = 0.096\,\text{year}^{-1}$, $L_\infty = 1159\,\text{mm}$ and $t_0 = -2.28$. The plotted growth curve was non-asymptotic over the age range observed,
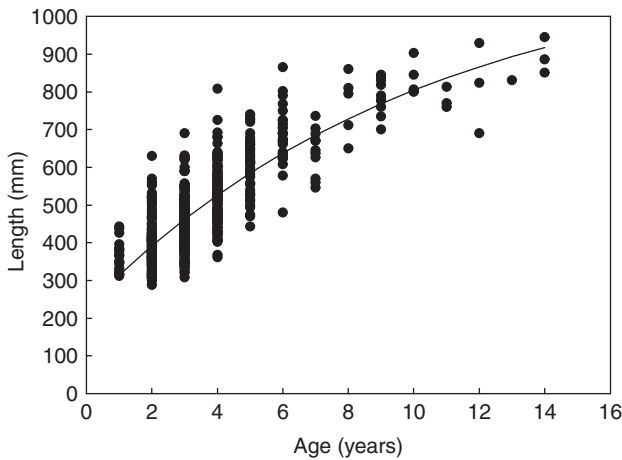
Fig. 6. Length at age data and von Bertalanffy growth curve for sampled *Plectropomus laevis*.

suggesting that individuals continue growing beyond the maximum size and age of our sample (Fig. 6). There were no size data available for the oldest individual in the sample (16 years). The distribution of size at age for the first two age classes suggests that only the larger individuals for these age classes were selected by the sampling gear. This is likely to bias the estimated K negatively and bias the estimated L_∞ positively. Limited sample sizes for some regions meant that growth curves and mortality estimates could not be compared among regions; however, comparison of the mean size at the age of 4 indicated no significant differences among regions (ANOVA, $F_{3,114} = 1.50$, $P = 0.277$). Size at the age of 4 was compared to avoid the risk that small regional variation in the proportion of individuals selected at the age of 3 (the modal age class) might have influenced the regional comparisons. Catch-curve analysis included ages 3–16 years and resulted in estimated $Z = 0.39$ (s.e. $= 0.031$, $r^2 = 0.90$, $P < 0.0001$).

Individuals were captured in depths ranging from 1 to 37 m. There was a significant but weak relationship between depth and FL, with larger individuals found in deeper water ($r^2 = 0.0041$, $P = 0.037$). There were significant differences among regions (Lizard Island, Townsville, Mackay, Storm Cay) in the proportions of individuals caught from different depth strata ($\chi^2 = 173.80$, d.f. $= 15$, $P < 0.0001$; Fig. 7). No depth data were available for samples from TS or FN.

Reproduction

The GSI of mature females sampled in October through to December was higher, on average, than the GSI of females sampled in other months (Fig. 8a). In addition, most females with ripe ovaries were present in samples taken in August and from October to January, which included the above period of increased GSI. Females with ovaries containing hydrated oocytes, indicative of active spawning, were sampled only in October, November and January. All mature females sampled in the months February–May were reproductively inactive (Resting).

Similar to mature females, the average GSI of mature males was higher in November and December than for males sampled
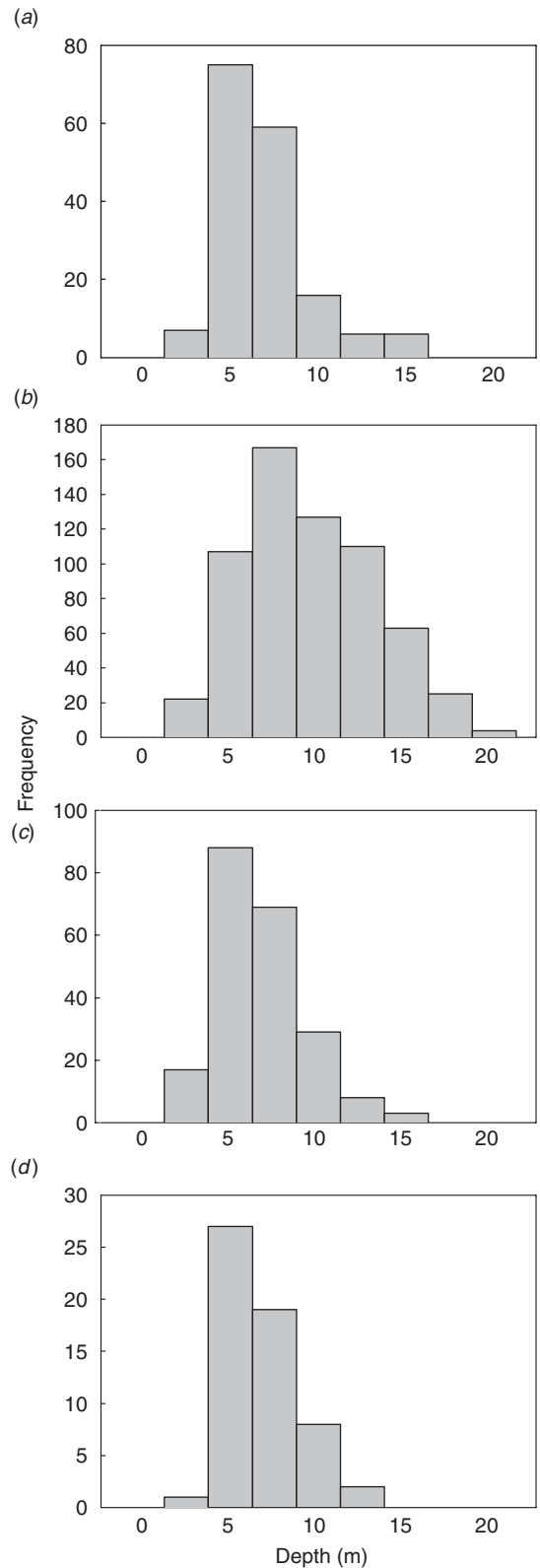

Fig. 7. Number of *Plectropomus laevis* captured by water depth in each of the following four ELF regions on the Great Barrier Reef: (*a*) Lizard Island, (*b*) Townsville, (*c*) Mackay and (*d*) Storm Cay. No depth or capture data were recorded for samples from the Far North of Torres Strait Regions.
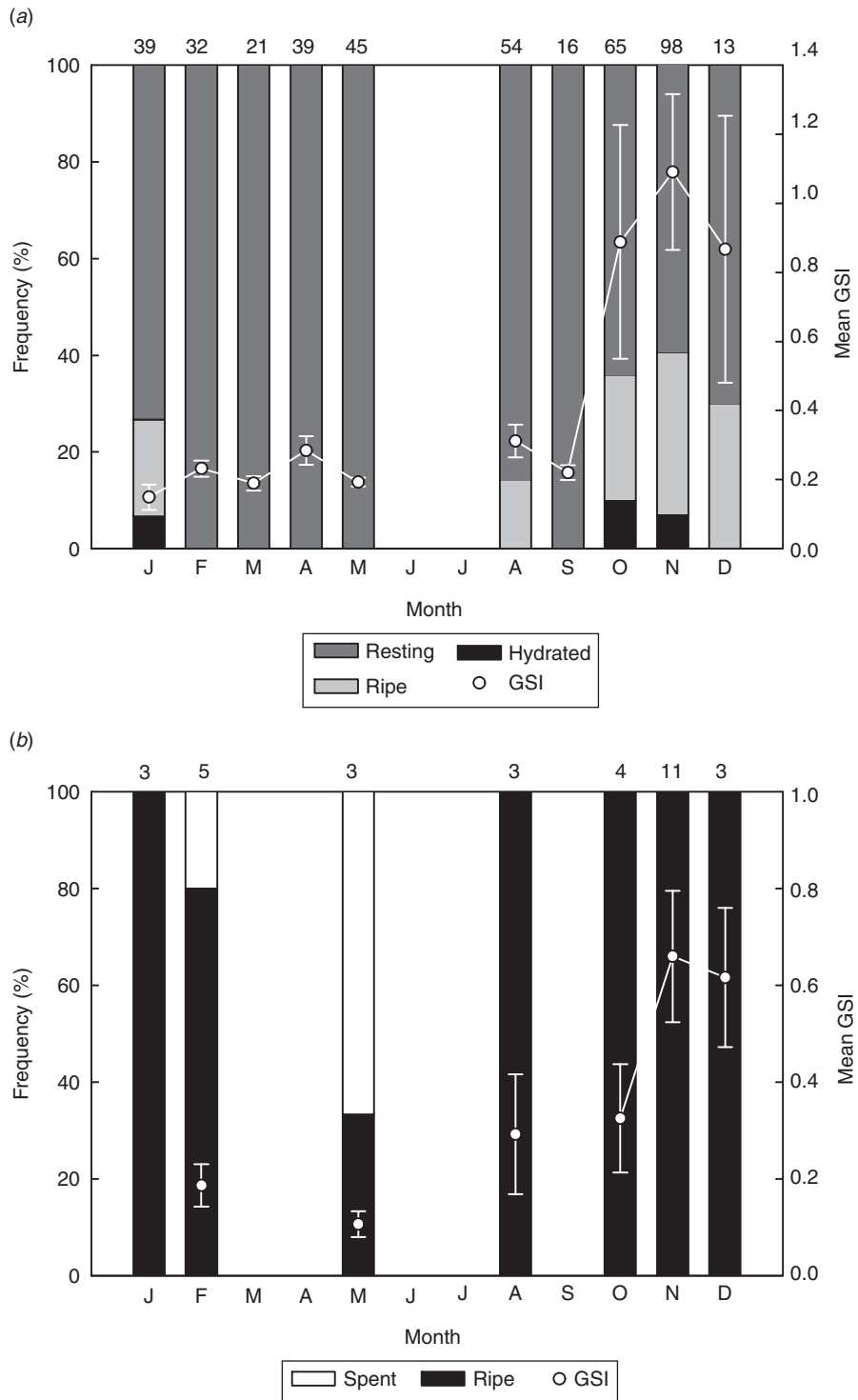
(*a*)

(*b*)

Fig. 8.   Monthly frequencies of reproductive stage (bars) and mean monthly gonadosomatic index (GSI) values for (*a*) female and (*b*) male *Plectropomus laevis*. Error bars indicate standard error. Sample sizes for each size and age class are shown above bars.

in the remaining months (Fig. 8*b*). Unlike the female data, however, reproductively active (Ripe) males were present in all available monthly samples. Spent males were observed in February and May, suggesting that some spawning activity may have continued until April. Females were more common than males in four of the sampled regions. No males were collected in the Lizard Island region, although 39 females were sampled. Sex ratios elsewhere were 14.7:1 in Townsville, 9.1:1

(a)
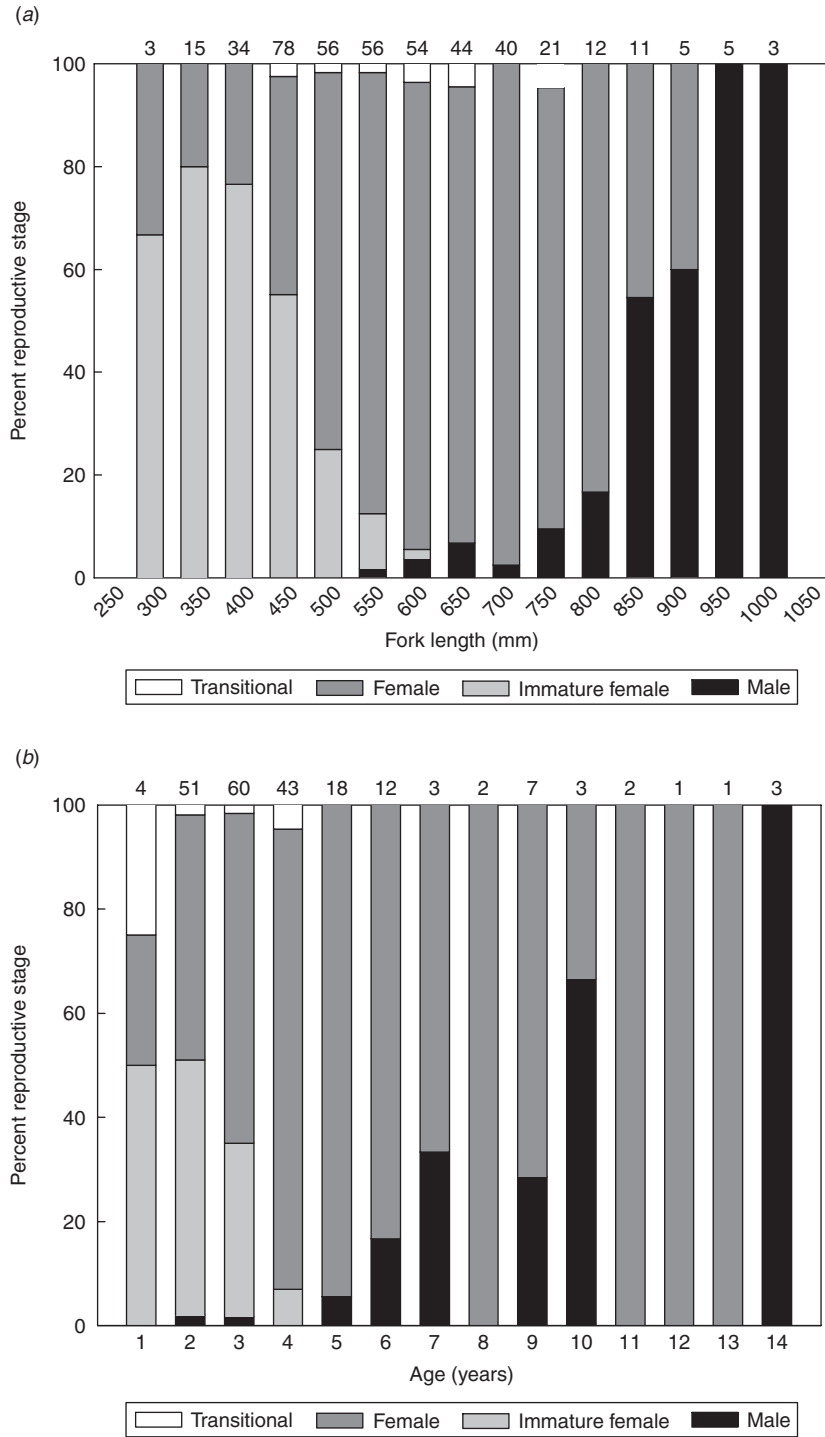

(b)

Fig. 9. Proportion of male, immature female, female and transitional *Plectropomus laevis* in each (*a*) size and (*b*) age class. Sample sizes for each size and age class are shown above bars.

in Mackay and 4.7 : 1 in Storm Cay. Insufficient sexed samples were collected from TS and FN to allow analysis of sex ratio.

Insufficient samples were available from some regions, so data were pooled for estimation of maturity and sex-change parameters. There was a large overlap in length of males and

females, although the majority of large individuals were male (Fig. 9*a*). Female size at 50% maturity was estimated to be 448 mm FL and 95% maturity was reached at 630 mm FL. The length range of mature females was 299–872 mm FL. Length at sex change showed 50% of the population was male at 874 mm

FL and 95% was male at 956 mm FL. The range in length at sex change was from 460 mm FL (smallest male) to 872 mm FL (largest female), with transitional individuals captured at lengths of 420–850 mm FL.

Males and females occurred over most of the sampled age range, although the percentage of the sample that was male was small (<5%) in age classes younger than 6 years (Fig. 9b). Both immature and transitional individuals were observed only at ages >1–4 years (Fig. 9b). Age at 50% female maturity was 1.8 years, with 95% maturity reached at 6.5 years. Fifty per cent of the population was male at the age of 9.2 years, but no estimate could be calculated for age at 95% sex change because the maximum estimated proportion of males was less than 90%.

Colour phase

There was no significant difference in log-transformed length–weight relationships between footballer and blue-spot phases (ANCOVA, $F_{1,836} = 1.37$, $P = 0.242$). Footballer individuals were most common in the smaller length classes (less than ~450 mm FL), with a mean size of 432.1 mm FL (s.e. = 4.58). Blue-spot forms were most common at larger sizes (greater than ~550 mm FL), with a mean size of 573.8 mm FL (s.e. = 5.04). Log-transformed mean length varied statistically significantly by colour phase (ANOVA, $F_{1,1140} = 294.02$, $P < 0.0001$) (Fig. 10a). Mean age also varied statistically significantly by colour phase (log-transformed; ANOVA, $F_{1,565} = 116.76$, $P < 0.0001$), with footballer individuals on average younger (mean = 2.83 years, s.e. = 0.06) than blue-spot individuals (mean = 4.41 years, s.e. = 0.14) (Fig. 10b). Depth distribution of capture also differed significantly with colour phase ($\chi^2 = 38.71$, d.f. = 8, $P < 0.0001$), with blue-spot individuals being more often captured from slightly deeper water (mean depth = 15.7 m, s.e. = 0.28) than footballers (mean depth = 13.3, s.e. = 0.34) (Fig. 10c).

Size at colour change indicated 50% transition to the blue-spot phase at 462 mm FL and 95% blue-spot at 788 mm FL. Size range of females in the blue-spot phase was identical to that for mature females (299–872 mm FL). Colour phase differed significantly with sex ($\chi^2 = 93.39$, d.f. = 3, $P < 0.0001$), with females dominating the blue-spot colour phase and immature and mature female individuals being approximately equally abundant in the footballer phase. Footballer males were rare, with most males being blue-spot colour phase, and transitionals were present in both colour phases (Fig. 11).

Discussion

Comparison to other plectropomids

Estimates of population parameters for *P. laevis* sampled from the GBR indicated that the demography of the species is in many respects generally similar to other coral trout species (Ferreira and Russ 1992, 1994). That is, *P. laevis* displays continuous, non-asymptotic growth, is protogynous, with a strongly female-biased sex ratio, and has a distinct austral spring–summer spawning season (Ferreira 1993, 1995; Samoilys 1997). Growth parameter estimates for *P. laevis* suggested rapid initial growth and early maturation, with some individuals reaching maturity in their first year and so having a long reproductive life (up to
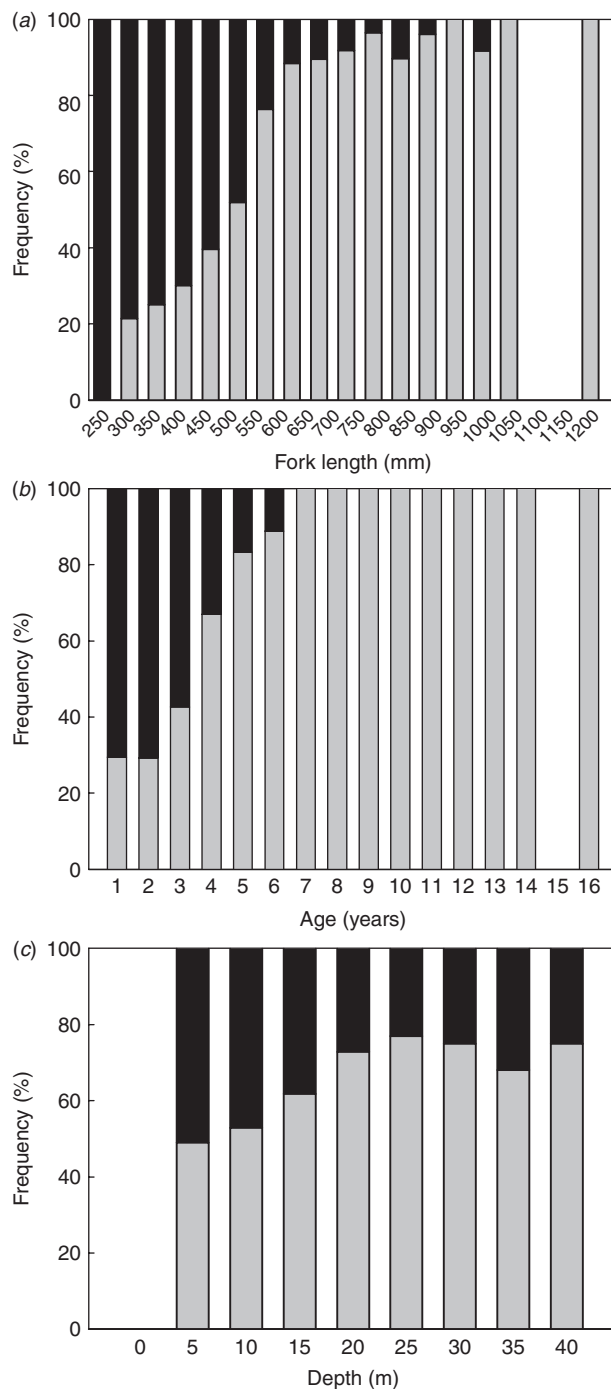

Fig. 10. Frequency of *Plectropomus laevis* individuals in footballer and blue-spot colour phases plotted by (a) size (from all regions), (b) age (from all regions) and (c) depth of capture (Lizard, Townsville, Mackay and Storm Cay Regions only) on the Great Barrier Reef and Torres Strait. Black represents the footballer phase and grey represents blue-spot phases.

15 years), with longevity similar to those of other coral trout species (12–16 years of age; Ferreira and Russ 1992, 1994; Williams *et al.* 2008b).

Although similarities are present between *P. laevis* and other *Plectropomus* species, some key differences were also identified.
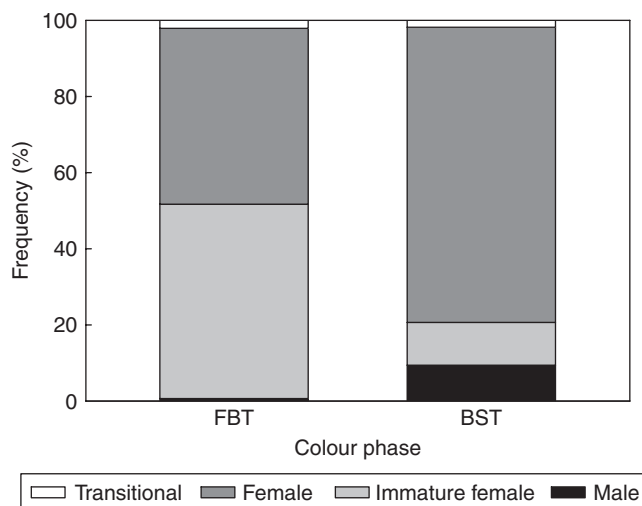
Fig. 11. Proportion of male, immature female, female and transitional *Plectropomus laevis* in each colour phase (FBT: footballer; BST: blue-spot).

P. laevis appears to attain a much larger size than the other coral trout species in the GBR and Torres Strait. Anecdotal evidence suggests that *P. laevis* grows larger than the individuals sampled in the present study. It is possible that very large individuals may have been too large to be captured by the sampling gear used. These individuals, if indeed present, may reach a greater maximum age than that estimated from our samples. Age and size results from the sampled individuals suggested that *P. laevis* grows at a faster rate than its sibling species, to obtain larger sizes at similar ages. Differences in growth rate among regions could not be tested because of low sample sizes; however, no significant regional variation was found in the mean length-at-age at 4 years.

Estimates of total mortality (Z) have been calculated for several *Plectropomus* species in the GBR and Torres Strait. Estimates of Z range from 0.57 and 0.61 for *P. maculatus* in the GBR and Torres Strait, respectively, to 0.40 and 0.44 for *P. areolatus* and *P. leopardus*, respectively, in the Torres Strait and 0.3–0.7 for *P. leopardus* in the GBR Marine Park (Ferreira and Russ 1992; Russ *et al*. 1998; Mapstone *et al*. 2004). The estimated total mortality rate of 0.39 for *P. laevis* is slightly below the range of estimates for most other coral trout species, except for those estimated for *P. leopardus* sampled on reefs in the GBR closed to fishing (0.12–0.18), which Russ *et al*. (1998) interpreted to represent natural mortality, based on the assumption that there was no (illegal) fishing mortality on the closed reefs. Individuals included in our *P. laevis* analyses were collected from reefs open and closed to fishing and so impacts of current and historic fishing may have affected estimates of Z, meaning that these estimates should not be assumed to represent natural mortality.

Demographic parameters

Smaller and younger *P. laevis* specimens were primarily in the footballer colour phase, with larger, older individuals present in the blue-spot form. Females dominated the footballer colour phase, although both sexes were present in both colour phases. This is similar to reports by Adams (2002) and Davies *et al*. (2006), who also found smaller individuals in the footballer

phase. Colour phase change observed here occurred between 300 and 900 mm FL, whereas size at sex change ranged from 450 to 900 mm FL, suggesting that colour change precedes sex change in some individuals. The size range of mature females was identical to that for colour phase change, suggesting colour change may be linked to female sexual maturity. Davies *et al*. (2006) found the same pattern in their analysis and suggested that colour change may be correlated with female maturity.

Males were also represented in the footballer colour phase, however, and immature females were present in the blue-spot colour phase, suggesting that the underlying causal process is more complex, or different from, the 'female maturity' hypothesis suggested by Davies *et al*. (2006). The large number of males in the blue-spot phase may suggest that colour change is in some way related to sex change. The picture is further complicated by the distinctive spawning colouration of large male *P. laevis* which, during courtship display, become very pale, almost white, and are adorned with dark saddles similar to the footballer form (G. Carlos, pers. obs.). Unfortunately, the very limited observations of *P. laevis* behaviour, and spawning behaviour in particular, means there is no basis to assess the potential importance of social or environmental factors in colour transition. It is also unclear whether colour phase change strictly occurs in one direction, with anecdotal evidence suggesting transitions from blue-spot to footballer colouration may occur (G. Carlos, pers. obs.). The apparent recent divergence of the plectropomid clade from other epinepheline clades (van Herwerden *et al*. 2006) raises interesting questions about the evolution of the genus, the origins of the two colour phases of *P. laevis*, and their adaptive significance.

Variability in sex ratios has been documented several times for *Plectropomus* species, with differing results. *P. laevis* in all sampled regions showed a female bias, as expected for a monandric protogynous species (Adams 2003), with greatest bias occurring on reefs in the northern regions. Gear selectivity cannot be ruled out as a factor in this bias, especially if very large individuals had a low likelihood of capture with the gear used either because of large gape compared with hook size or because lines were broken by larger individuals. However, Williams *et al*. (2008*b*) also found female bias in *Plectropomus* populations sampled in the Torres Strait, although these ratios (5 : 1, 2 : 1, 1.1 : 1 for *P. areolatus*, *P. leopardus* and *P. maculatus*, respectively) were not as high as those observed for *P. laevis* (up to 14.7 : 1). Adams *et al*. (2000) found *P. leopardus* to be female-biased in the Townsville region, but male-biased in the Swains (Storm Cay) region. The authors hypothesised that the high relative abundance of males in the Storm Cay region reflected a natural regional difference in sexual strategy because fishing pressure on smaller female individuals in the region was limited and the pattern occurred on both reefs open and closed to fishing. They inferred that the biased ratio observed was unlikely to be attributable solely to removal of females by fishing and was most likely related to a diandric sexual pathway whereby males are derived from mature and immature females.

The presence of a diandric sexual strategy in *P. leopardus* on the GBR was subsequently confirmed by Adams (2003) and has been reported for other epinepheline serranids (Liu and Sadovy 2004). No male bias was observed in *P. laevis* in the Storm Cay

region in the current analysis, although the lowest ratio (4.7 : 1) was observed there, suggesting some difference in female : male distribution in southern sections of the GBR. The lower female bias in the Storm Cay region could be due to regional differences in the size at sex change (i.e. changing sex at a larger size or older age in southern regions). Unfortunately, there were insufficient samples in the present study to examine regional patterns in sex change; however, this pattern has been observed previously in *P. leopardus* on the GBR (Davies *et al.* 2006). Thus, *P. laevis* may show regional variability in sex change, which results in population level differences in sex ratio.

Histological and GSI analyses suggested that *P. laevis* has a seasonal spawning pattern whereby mature individuals spawn during the austral spring and summer, with minimal or no spawning activity in autumn and winter. A similar seasonal spawning pattern has been found in other coral trout species (Ferreira 1993; Samoilys 1997). Female and male *P. laevis* appeared to exhibit multiple spawning during a season, on the basis of histological analyses, consistent with *P. maculatus* and *P. leopardus* (Ferreira 1993, 1995; Adams 2002). Even though reproductively active males were present in all monthly samples, it is unlikely that males exhibit spawning activity throughout the year.

Size and age at maturity data for *P. laevis* indicated larger sizes of maturation and sex change than for other coral trout species, but different from those reported previously for this species. For example, Adams (2002) estimated the age of 50% female maturity to be 5 years, considerably older than the 1.8 years estimated here. The size at 50% female maturity reported by Adams (2002) (450–499 mm FL), however, was similar to the 448 mm FL estimated here. Davies *et al.* (2006) reported 50% female maturity for *P. laevis* at 391 mm FL and 2.2 years of age. Differences among results of these three studies may be due to differences in sample sizes and sampling duration, with Davies *et al.* (2006) and, especially, Adams (2002) having few individuals from fewer years available than in the present analysis. Size at maturity in the present analysis agrees closely with that from Adams (2002), despite other differences, and age at maturity agrees closely with Davies *et al.* (2006). Estimated size and age at sex change was also similar between Davies *et al.* (2006) and the present analysis. Davies *et al.* (2006) reported size at 50% male of 828 mm FL and size at 95% male of 940 mm FL, in comparison with 874 mm FL and 956 mm FL, respectively, in the current analysis.

Regional variation in the characteristics of sampled *P. laevis* may reflect, in part at least, cross-shelf differences in distribution, as suggested by Newman *et al.* (1997) and Davies *et al.* (2006). For example, more of the reefs sampled in the Townsville region were outer-shelf reefs and also tended to have steeper drop-offs and deeper surrounding water, anecdotally reported to be preferred habitat of *P. laevis*, than mid-shelf and near-shore reefs. The Townsville region had both the largest number of blue-spot individuals and significantly different depth distribution of captured individuals than did the other three regions. Differences in ranges of available depths could also have accounted for regional differences in capture depth. It was not possible to separate the confounded influences of relative shelf position and region with samples available because too few individuals were collected from the mid-shelf reefs in the Townsville region to allow a cross-shelf comparison.

Implications for management

Estimation of demographic parameters of high-value coral reef species is crucial for developing appropriate management measures. For example, harvest of *P. laevis* on the GBR is managed by a slot-size limit, allowing take of individuals between 500 and 800 mm in total length, on the basis of Adams' (2002) earlier work. The reproductive characteristics described above confirm that those size restrictions are appropriate and would allow many females to reach maturity and spawn at least once before recruiting to the legal fishery and also protect large males. The absence of species-specific reporting observed in many reef line fisheries, combined with a generally lower abundance (A. Ayling and B. Mapstone, unpubl. data), however, may represent a potential risk for *P. laevis* because over-exploitation might go largely unnoticed, especially if compliance with size limits is low. Stricter requirements for retention of fish in identifiable form (e.g. not skinned and filleted), species-specific reporting requirements and increased education of recreational fishers in identifying various coral trout species would go some way to attenuating that risk. The results of the present study have shown that without detailed knowledge of the demography of a species, it is not possible to define whether management strategies are appropriate. This type of data is required for many other reef-dependent species that have high fishery value.

Results presented here support the suggestion in previous studies that there is a need for broader spatial scale studies of targeted species such as serranids to ensure adequate data are collected to resolve complex variations in distribution and spatial variation in population parameters and perhaps also population dynamics (e.g. Adams *et al.* 2000). The data presented here expand our understanding of the demography of *P. laevis* and provide evidence that appropriate size-based regulations on harvest can provide protection from overexploitation. Results from our analyses support the strategy of managing *P. laevis* populations differently from other coral trout species to ensure long-term sustainability of populations. Presumably, *P. laevis* is not the only species with demographic characteristics different from those of closely related species. Thus, demographic characteristics must be considered when assessing the efficacy of management strategies and determining whether strategies designed for one species are suitable for other closely related species.

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