

Key aspects of the biology, fisheries and management of Coral grouper

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Abstract Coral grouper (genus *Plectropomus*), or coral trout, are members of the grouper family (Epinephelidae) and are one of the largest and most conspicuous predatory fishes on Indo-Pacific coral reefs. They are highly-prized food fishes that are targeted by subsistence, artisanal, commercial and recreational fisheries throughout their geographic range. *Plectropomus* have broadly similar diets and habitat requirements to other tropical groupers, but typically have faster growth and higher natural mortality rates. Although these characteristics are expected to increase population turnover and reduce

innate vulnerability to environmental and anthropogenic impacts relative to other groupers, many *Plectropomus* populations are in decline due to the combined effects of overfishing and habitat degradation. In many locations, stock depletion from uncontrolled fishing, particularly at spawning aggregation sites, has resulted in local fishery collapse. Therefore, improved management of wild populations is urgently required to ensure conservation and sustainable fisheries of *Plectropomus*. Where possible, a combination of no-take marine reserves, market-based

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management approaches, and allocation or resurrection of property rights systems are recommended to complement conventional fishery management actions that limit catch and effort. Additional investment in aquaculture propagation is also needed to reduce fishing pressure on wild stocks and support management initiatives. This global synthesis of information pertaining to the biology, fisheries and management of *Plectropomus* will assist in guiding future management actions that are attempting to address a range of stressors including fishing, reef habitat degradation, and the escalating effects of climate change.

Keywords Coral trout · *Plectropomus* · Serranidae · Coral reef fisheries · Grouper conservation · Live reef food fish trade

Introduction

Coral grouper (genus *Plectropomus*), also known as coral trout, are iconic and highly-prized fishes that support valuable fisheries throughout the Indo-West Pacific and Red Sea regions. There are seven recognised *Plectropomus* species, which are members of the grouper family (Epinephelidae), consisting of 159 species in 15 genera, including the well-known *Epinephelus* and *Mycteroperca* (Heemstra and Randall 1993). *Plectropomus* inhabit a range of shallow tropical and subtropical marine habitats, although they are best known on coral reefs, where they are often one of the largest and most conspicuous predators [70–125 cm maximum total length (TL), depending on species]. When fully grown, they are predominantly piscivorous (fish-eating) and have few natural predators, which are hallmarks of high trophic levels (Huntsman et al. 1999). In minimally exploited and undisturbed habitats at Australia's Great Barrier Reef (GBR), *Plectropomus leopardus* (leopard Coral grouper) can reach densities up to 240 fish ha⁻¹ (Kingsford 2009; Miller et al. 2012). In some areas where the abundance of *Plectropomus* has declined due to fishing, the species composition and abundance of (non-fishery) prey fishes has changed substantially (Graham et al. 2003; Watson et al. 2007; Shedrawi et al. 2014; Boaden and Kingsford 2015), suggesting *Plectropomus* may fulfil an important role in structuring reef fish assemblages.

All *Plectropomus* species are exploited throughout their ranges, both for local consumption and for export in the lucrative live reef food fish trade (LRFFT), which trades over 14,000 t year⁻¹ of live groupers and has an estimated value of US\$1 billion year⁻¹ (excludes illegal and unreported catches; Sadovy de Mitcheson et al. 2013). *Plectropomus* are major constituents of the LRFFT, comprising ~34 % of trade volume in Hong Kong (the central marketplace) (Anon. 2013). Demand for *Plectropomus* and other reef fishes has increased substantially in recent decades, resulting in an expansion of the LRFFT throughout the Indo-Pacific (Sadovy 2005; Sadovy de Mitcheson et al. 2013). As a result of high fishing pressure and poor fisheries management, two species of *Plectropomus* (*P. laevis*, black-saddled Coral grouper, and *P. areolatus*, squaretail Coral grouper) are currently listed as vulnerable to extinction (as per IUCN criteria: Sadovy de Mitcheson et al. 2013). Most major stocks of *Plectropomus* that have been assessed are considered either fully- or over-exploited, with evidence that some stocks have been locally extirpated (Scales et al. 2007; Sadovy de Mitcheson et al. 2013).

Despite the social and economic importance of *Plectropomus*, scientific knowledge of these fishes has historically lagged behind that of many other groupers, especially those from the Caribbean and Mediterranean. Of the 90 journal articles that focus on *Plectropomus*, the majority (>53 %) concentrate on a single species (*P. leopardus*) from a single geographic region (GBR). Although the biology, fisheries and management of groupers have been the subjects of two previous books (Polovina and Ralston 1987; Arreguin-Sanchez et al. 1996), these publications had a strong focus on Atlantic groupers, with little mention of Indo-Pacific species such as *Plectropomus*. Goeden (1978) produced the first exposition of *Plectropomus* biology, but his observations were largely qualitative and limited in scope, focusing on a single species (*P. leopardus*) at a single site (Heron Island, Australia).

In the decades since this early work, much has been learnt about the biology, fisheries and management of *Plectropomus*. However, the literature pertaining to this group is yet to be compiled and synthesized. Intensifying threats to *Plectropomus* (such as over-fishing, coastal development and habitat destruction) provide strong and timely justification for consolidating this information, alongside consideration of

vulnerability and adaptive capacity of *Plectropomus* (and associated fisheries) to the threats of climate change. Due to the high volume, complexity and diversity of scientific information pertaining to *Plectropomus*, this review focuses on biology, fisheries and management, and the specific topics discussed in the following sections were selected to inform assessments of vulnerability and adaptive capacity, which are currently underway and will be addressed elsewhere.

Biology of Coral grouper

Morphology and phylogeny

Plectropomus have the same basic body plan as other groupers (robust body and large head) and the skin tends to be elaborately decorated with bright spots, bars and/or stripes that vary subtly within and between species (Fig. 1). In general, skin brightness (redness) increases with water depth, is apparently inflexible over short temporal scales (days to weeks), and may have a genetic basis (Cai et al. 2013). However, skin colour pattern can be changed in seconds to aid camouflage and courtship (Samoilys and Squire 1994). Furthermore, some individuals of *P. laevis* undergo a permanent radical colour transformation (from a pale body with black saddles and yellow fins to a dark body with numerous blue spots), however the onset of this event is flexible with respect to size, age and maturity (Heupel et al. 2010).

The most recent review of morphological characters (Randall and Hoese 1986) concluded that seven species warrant recognition: *P. leopardus*, *P. laevis*, *P. areolatus*, *P. maculatus* (bar-cheek Coral grouper), *P. oligacanthus* (highfin Coral grouper), *P. punctatus* (marbled Coral grouper) and, lastly, *P. pessuliferus* (roving Coral grouper) which is comprised of two subspecies (*P. pessuliferus marisrubri* and *P. pessuliferus pessuliferus*). Recent genetic analyses, however, indicate that the two subspecies of *P. pessuliferus* should be re-classified as distinct species (Ma 2014). Inter-specific comparisons of a range of nuclear and mitochondrial DNA sequences yield contrasting phylogenetic relationships (Fig. 2), suggesting incomplete lineage sorting, independent evolution of genes, and/or introgressive hybridization. Phylogeny of *Plectropomus* is therefore unresolved and warrants further investigation.

Genetic and biogeographic evidence indicate that speciation of *Plectropomus* was driven by vicariant events associated with fluctuating sea-levels that repeatedly fragmented and re-joined reef habitats during the Pleistocene (van Herwerden et al. 2006, 2009). Substantial secondary contact across much of the Indo-Australian archipelago now occurs among five of the seven species (*P. leopardus*, *P. maculatus*, *P. laevis*, *P. areolatus*, *P. oligacanthus*). A consequence of this overlap is opportunity for hybridization (interbreeding), which has been recorded between closely related species. On the GBR for example, some *Plectropomus* individuals (<1 %) have external colouration that is intermediate to that of *P. leopardus* and *P. maculatus*, and these putative hybrids have DNA sequences that are common to both parent species (van Herwerden et al. 2002; Frisch and van Herwerden 2006).

Distribution and abundance

Plectropomus species are found exclusively within the Indo-Pacific and Red Sea regions: two species (*P. laevis*, *P. areolatus*) are widespread across the Indo-West Pacific (with *P. areolatus* extending into the Red Sea), three species (*P. leopardus*, *P. maculatus*, *P. oligacanthus*) are restricted to the Indo-Australian archipelago, two species (*P. pessuliferus pessuliferus*, *P. punctatus*) are found only in the Indian Ocean, and one species (*P. pessuliferus marisrubri*) is endemic to the Red Sea (Heemstra and Randall 1993). Distinct distribution patterns are also evident across smaller spatial scales. On the GBR, for example, *P. leopardus* occurs across the full width of the continental shelf (30–200 km), whereas *P. maculatus* occurs predominately on inshore and coastal reefs and *P. laevis* occurs predominately on outer shelf reefs (Newman et al. 1997). The mechanisms that drive these patterns are not known, although comparative physiology suggests that *P. maculatus* is better suited to variable (e.g. coastal) environments than *P. leopardus* (Frisch and Anderson 2005).

Plectropomus typically live at depths of 3–30 m, although they have been recorded at depths up to 150 m (Heemstra and Randall 1993). On the GBR, mean densities of *Plectropomus* (all species combined) are typically in the order of 10–100 fish ha⁻¹, which is much higher than densities of *Plectropomus*



Fig. 1 The seven species of *Plectropomus*: **a** *P. leopardus*, **b** *P. laevis*, **c** *P. areolatus*, **d** *P. maculatus*, **e** *P. oligacanthus*, **f** *P. punctatus* and **g** *P. pessuliferus marisrubri*. Photo credits: David Williamson (**a**, **b**, **d**), Gerry Allen (**c**, **e**, **f**) and Richard Field (**g**)

recorded elsewhere in the Indo-west Pacific region (Heemstra and Randall 1993). The greatest densities of *Plectropomus* usually occur on shallow reef slopes and lagoons, although moderate to high densities of

Plectropomus can also occur on deep (>40 m) low-relief shoals (Connell and Kingsford 1998; Cappo et al. 2007). Due to widespread, historical exploitation of *Plectropomus*, pristine density (carrying capacity) is difficult to discern, but is thought to be around 200–240 fish ha⁻¹ on the GBR (Kingsford 2009).

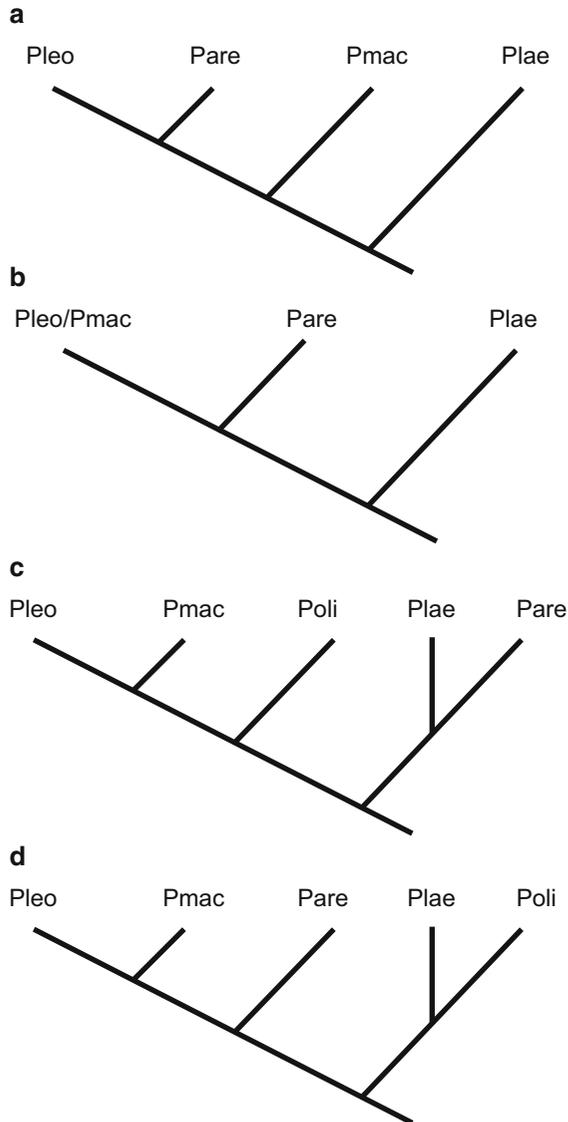


Fig. 2 Cladograms depicting phylogenies of *Plectropomus* species, inferred using different DNA sequences: **a** nuclear ETS2, **b** mitochondrial HVR I (van Herwerden et al. 2002), nuclear TMO4C4/H3 and mitochondrial 16S/12S (Craig and Hastings 2007), and **d** mitochondrial NADH2 (Zhu and Yue 2008) and ND2 (Cai et al. 2013). Pleo, *Plectropomus leopardus*; Pare, *Plectropomus areolatus*; Pmac, *Plectropomus maculatus*; Plae, *Plectropomus laevis*; Poli, *Plectropomus oligacanthus*

Habitat associations

Newly settled and juvenile stages of *P. leopardus* and *P. areolatus* are typically found on small patches of coral rubble near contiguous reef habitat with high coral cover (Light and Jones 1997; Tupper 2007). In contrast, newly settled *P. maculatus* have a strong preference for colonies of corymbose *Acropora* located over sand and/or rubble (Wen et al. 2013a). As juvenile *Plectropomus* grow, they relocate to more complex habitats, such that fish >10 cm TL are most often found in areas with high coral cover (Connell and Kingsford 1998; Hutchinson and Rhodes 2010). *Plectropomus*' strong association with live coral suggest that corals provide shelter, harbour prey, and/or aid foraging tactics. However, the extent to which *Plectropomus* are reliant upon coral or are sensitive to changes in habitat structure is poorly understood, and may vary among species. Diet of *P. leopardus* (see below) includes many prey species that depend on live coral for food and/or shelter, although *P. leopardus* also consume a substantial proportion of pelagic fishes that do not depend on coral. Similarly, adult *Plectropomus* often shelter under tabular or branching corals (Kerry and Bellwood 2012), but many individuals (particularly *P. maculatus*) also occupy rocky reefs and deep shoals where coral cover is relatively low (Cappo et al. 2007). Despite these ambiguities, several studies have demonstrated that *Plectropomus*, like many other reef fishes, decline in abundance after localised coral depletion (Pratchett et al. 2011; Frisch et al. 2012; Williamson et al. 2014). Even if coral cover is restored, occasional disturbance may prevent recovery of *Plectropomus* populations, potentially because they require structurally stable habitats to prevent bottlenecks in recruitment (Karkarey et al. 2014). Overall, this information suggests *Plectropomus* are indirectly dependent on healthy, stable coral reef habitats, but a range of intrinsic and extrinsic factors interact to generate

heterogeneous distributions, both within and among reefs.

Demography

Size-frequency distributions of unexploited *Plectropomus* tend to be strongly biased towards larger fish (>30 cm TL) because most sampling gears (e.g. hook-and-line) are size-selective (Ferreira and Russ 1995; Williams et al. 2008). Hence, there has been a strong focus on age-based metrics, which can be derived from analysis of otoliths or other calcified tissues (Hobbs et al. 2014). To this end, early studies validated otolith annuli in *P. maculatus* and *P. leopardus* (Ferreira and Russ 1992, 1994) and confirmed that growth is asymptotic and well described by von Bertalanffy growth models (Fig. 3a).

The current view is that all members of the Epinephelidae have relatively slow growth, low instantaneous rates of natural mortality and long life-spans, and that such fishes should therefore be regarded as *K*-strategists (Huntsman et al. 1999). However, congeneric comparisons of population parameters reveal that *Plectropomus* tend to have shorter life-spans, faster growth and higher natural mortality relative to other groupers of equivalent body size (Table 1). Auximetric plots of von Bertalanffy parameters, which identify the ‘growth plane’ occupied by fishes, demonstrate distinct differences in growth characteristics between *Plectropomus* and *Epinephelus*, regardless of body size (Fig. 3b). Furthermore, Munro and Pauly’s (1983) growth performance index ($\phi' = \text{Log}_{10}K + 2\text{Log}_{10}L_{\infty}$) demonstrates that *Plectropomus* tend to ‘perform’ better than *Epinephelus* of equivalent body size. All else being equal, these characteristics are expected to increase population turnover and reduce the inherent vulnerability of *Plectropomus* to environmental and anthropogenic impacts, relative to other groupers.

As is the case for most fish species, estimation of natural mortality rates in *Plectropomus* has proven to be very difficult. Only a single published study has estimated natural mortality rate using empirical data (Russ et al. 1998); all other estimates of natural mortality rate have been derived indirectly from putative relationships with other, easier-to-measure population parameters (Table 1). Given the critical importance of natural mortality rate for understanding

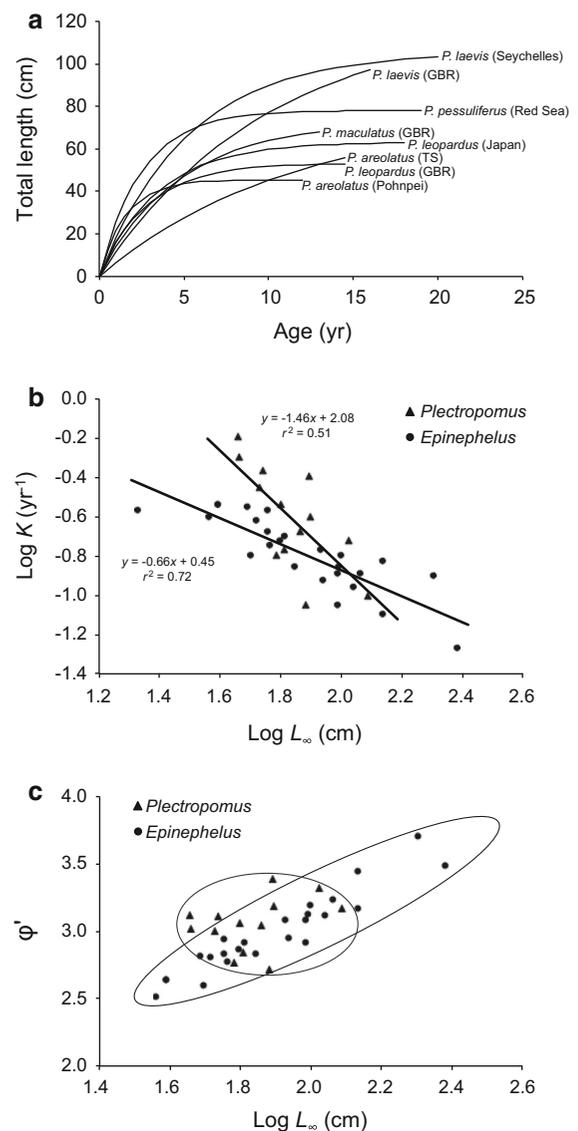


Fig. 3 **a** Von Bertalanffy growth curves of *Plectropomus*. **b** Auximetric comparison of growth between *Plectropomus* (13 populations of 5 species) and *Epinephelus* (25 species). **c** Growth performance index ($\phi' = \text{Log}_{10}K + 2\text{Log}_{10}L_{\infty}$) of *Plectropomus* and *Epinephelus* as a function of asymptotic length. Growth parameters are from published (Table 1) and unpublished sources (Froese and Pauly 2015). Regression lines for *Plectropomus* ($t_{11} = -3.30$, $p = 0.007$) and *Epinephelus* ($t_{23} = -7.64$, $p < 0.001$) are significantly different (ANCOVA, $F_{1,34} = 5.80$, $p = 0.021$). GBR, Great Barrier Reef, Australia. TS, Torres Strait, Australia

population dynamics and for estimating fishery yields, this represents a fundamental gap in our knowledge of *Plectropomus* and a priority for future research.

Table 1 Representative estimates of population parameters of Coral groupers (*Plectropomus*) and other groupers of equivalent body size (*Epinephelus* and *Mycteroperca*)

Species	T_{\max} (year)	L_{∞} (cm)	K (year ⁻¹)	M (year ⁻¹)	Location	Reference
<i>P. leopardus</i>	14	52.2 FL (53.5 TL)	0.35	0.15	GBR, Australia	Ferreira and Russ (1994), Russ et al. (1998)
	18	61.2 FL (63.2 TL)	0.29	–	Okinawa, Japan	Ebisawa (2013)
<i>P. maculatus</i>	13	60.0 SL (72.7 TL)	0.21	0.32 ^d	GBR, Australia	Ferreira and Russ (1992); Currey et al. (2010)
<i>P. areolatus</i>	14	76.4 FL ^b (76.4 TL)	0.09 ^c	0.30 ^d	Torres Strait, Australia	Williams et al. (2008); Currey et al. (2010)
	12	45.5 TL	0.64	–	Pohnpei	Rhodes et al. (2013)
<i>P. pessuliferus marisrubri</i>	19	78.1 TL	0.40	–	Red Sea	DesRosiers 2011
<i>P. laevis</i>	16	115.9 FL ^b (121.9 TL)	0.10 ^c	0.26 ^d	GBR and Torres Strait, Australia	Heupel et al. (2010); Currey et al. (2010)
	20	101.5 FL (105.5 TL)	0.19	0.21 ^d	Seychelles	Grandcourt (2005)
Mean ^a (all <i>Plectropomus</i>)	15.8	76.8 TL	0.29	0.25	–	–
<i>E. guttatus</i>	17	52.0 TL	0.24	0.18	Jamaica and Florida, U.S.A.	Manooch (1987); Ault et al. (1998)
<i>E. multinotatus</i>	27	57.0 TL	0.27	0.15 ^d	Seychelles	Grandcourt (2005)
<i>E. polyphkadion</i>	30	57.9 TL	0.18	0.13 ^d	Seychelles	Grand court (2005)
<i>E. striatus</i>	17	69.9 TL	0.14	0.18	Florida, U.S.A.	Ault et al. 1998
<i>E. fulvus</i>	17	69.9 TL	0.15	0.18	Florida, U.S.A.	Ault et al. (1998)
<i>E. fuscoguttatus</i>	42	80.7 TL	0.16	0.45 ^d	GBR, Australia	Pears et al. (2006)
<i>E. morio</i>	27	84.8 TL	0.17	0.15 ^d	Florida, U.S.A.	Lombardi-Carlson et al. (2008)
<i>M. venenosa</i>	15	86.0 TL	0.17	0.18	Florida, U.S.A.	Ault et al. 1998
<i>E. drummondhayi</i>	15	96.7 TL	0.13	0.20	Florida, U.S.A.	Ault et al. (1998)
<i>M. phenax</i>	21	100.0 TL	0.13	0.14	Florida, U.S.A.	Ault et al. (1998)
<i>E. niveatus</i>	15	109.1 TL	0.11	0.13	Florida, U.S.A.	Ault et al. (1998)
Mean (all other groupers)	22.1	78.5 TL	0.17	0.19	–	–

Mean asymptotic length (L_{∞}) and growth co-efficient (K) are von Bertalanffy growth parameters. Standard length (SL) and fork length (FL) were converted to total length (TL) for ease of comparison, and conversion formulae were obtained from the original data source or Froese and Pauly (2015). Population parameters are not known for *P. oligacanthus* and *P. punctatus*. Abbreviations: T_{\max} , maximum age; M , natural mortality rate; GBR, Great Barrier Reef

^a Only one value per species was used to calculate the group mean. If more than one value is listed for a species, then the mean value for that species was used in the calculation

^b Likely to be an over-estimate due to biased sample

^c Likely to be an under-estimate due to biased sample

^d Derived using Hoenig's (1983) equation

Reproduction

Reproduction has been studied in five of the seven recognized species (Table 2). With the potential

exception of *P. areolatus* (Rhodes et al. 2013), sexual development in *Plectropomus* involves differentiation as immature females, followed later by sex-change to male (monandric protogyny; Ferreira 1993, 1995;

Table 2 Representative reproductive parameters of *Plectropomus* species

Species	L_m (cm)	L_m/L_∞ (%)	T_m (year)	T_m/T_{max} (%)	L_{sc} (cm)	L_{sc}/L_∞ (%)	Sex ratio (♀ ÷ ♂)	Protogyny confirmed?	References
<i>P. leopardus</i>	35.0	65	2.5	18	51.7	97	0.3–11.3	Yes	Ferreira (1995), Adams et al. (2000), Williams et al. (2008), Ebisawa (2013)
<i>P. maculatus</i>	36.0	50	2.0	15	42.0	58	1.0–2.6	Yes	Ferreira (1993), Williams et al. (2009)
<i>P. areolatus</i>	36.6	80	2.3	19	49.4	100	0.3–5.0	No	Rhodes et al. (2013), Rhodes and Tupper (2008)
<i>P. pessuliferus marisrubri</i>	62.2	80	4.6	24	63.9	82	2.1	Yes	DesRosiers (2011)
<i>P. laevis</i>	46.2	39	1.8	11	87.4	72	4.7–14.7	Yes	Heupel et al. (2010)

L_m mean total length at 50 % maturity, L_∞ asymptotic total length, T_m mean age at 50 % maturity, T_{max} maximum age, L_{sc} mean total length at sex-change

Heupel et al. 2010). Male *P. leopardus* and *P. maculatus* can also derive from either immature or mature females (diandric protogyny; Adams 2003). The process of sex-change is remarkably labile and occurs over wide size and age ranges, suggesting that it is under social control, although this is yet to be confirmed. Sex ratios of *Plectropomus* are typically female biased (up to 14F:1M) although a few (typically unexploited) populations may be male biased (up to 3M:1F; Table 2). Unlike many other fish genera (c.f. Allsop and West 2003), *Plectropomus* have a high level of inter-specific variation in mean size and age at maturity (35–62 cm TL and 1.8–4.6 year, respectively) and sex-change (42.0–87.4 cm TL), even when evaluated as a percentage of maximum size and age (Table 2). Importantly, these data suggest that the reproductive traits of *Plectropomus* are highly adaptive and thus potentially responsive to (or affected by) fishing selection and other anthropogenic pressures that are size- or age-selective.

A notable feature of *Plectropomus* (particularly *P. areolatus*) is their propensity to form large ephemeral spawning aggregations that are highly predictable in both space and time. Hundreds to thousands of individuals aggregate at the same location for several (<9) days per month, for 3–12 consecutive months (Table 3; see also Rhodes and Sadovy de Mitcheson 2012). Aggregations of *P. leopardus* tend to be much smaller (5–128 individuals) and more numerous per unit of reef area than those of *P. areolatus* (Samoilys

1997; Frisch and van Herwerden 2006). In all cases, there is a pronounced lunar influence on the timing of aggregation formation, but this varies between species and locations (Table 3). *Plectropomus areolatus*, for example, spawns around full moon in Micronesia (Hutchinson and Rhodes 2010; Rhodes et al. 2014) and around new moon in Melanesia (Hamilton et al. 2011, 2012).

Environmental regulation of spawning in *Plectropomus* appears to involve a hierarchy of variables with temperature as a primary driver and lunar phase as a secondary driver. After a long resting phase (7–8 months), rapid gonadal development is triggered when water temperature commences acclivity (*P. leopardus* on the GBR) or reaches annual minima (*P. areolatus* in Pohnpei, Micronesia) (Frisch et al. 2007; Rhodes et al. 2014). In *P. areolatus*, preliminary evidence suggests that spawning is inhibited whenever temperature exceeds a maximum threshold, regardless of moon phase or reproductive maturity (Rimmer et al. 2013; Rhodes et al. 2013, 2014; but see Hamailton et al. 2012). Further evidence of thermal regulation of spawning comes from aquaculture experiments: captive *Plectropomus* can be induced to spawn by simulating a seasonal thermal cycle that has normal amplitude but truncated wavelength, regardless of photoperiod (Liao and Leano 2008). Entrainment to a thermal cue presumably serves to synchronize reproduction with favourable conditions for larvae, such as plankton (food) blooms.

Table 3 Spawning season and lunar periodicity of *Plectropomus* species

Species	Location	Spawning season ^a	Moon phase ^a	Evidence	References
<i>P. leopardus</i>	GBR	Sep–Dec	New	Aggr/GSI/Hist	Samoilys (1997), Frisch et al. (2007)
	Japan	May–Jul	New	GSI/Hist	Ebisawa (2013)
<i>P. maculatus</i>	GBR	Sep–Dec	New	Aggr/Hist	Ferreira (1993), Frisch and van Herwerden (2006)
<i>P. areolatus</i>	Pohnpei	Jan–May	Full	Aggr/GSI/Hist	Rhodes et al. (2013, 2014)
	Solomons	Jan–Dec	New	Aggr	Hamilton et al. (2012)
	PNG	Jan–Dec	New	Aggr	Hamilton et al. (2011)
	Torres Strait	Jul–Sep	–	GSI/Hist	Williams et al. (2008)
	Indonesia	Sep–Feb (Apr–Jul)	Full (new)	Aggr	Pet et al. (2005)
<i>P. punctatus</i>	Seychelles	Dec–Feb	New	Aggr	Robinson et al. (2008)
<i>P. pessuliferus</i> <i>pessuliferus</i>	Maldives	Apr–May, Nov–Dec	Full	Surv	Tamelandar et al. (2008)
<i>P. laevis</i>	GBR	Oct–Dec	–	GSI/Hist	Heupel et al. (2010)

Evidence for spawning activity includes fish aggregation (Aggr), elevated gonadosomatic index (GSI), presence of hydrated oocytes in histological sections (Hist) and fisher surveys (Surv). GBR, Great Barrier Reef. PNG, Papua New Guinea

^a Secondary spawning periods are in parentheses

Larval biology and recruitment

The early life-history of *Plectropomus* was an enigma for many years due to the small, fragile nature of larvae, and current knowledge is based largely on just one species: *P. leopardus*. Larvae hatch at ~1.6 mm TL after 26 h, but they have no fins and the mouth remains closed until 2 d after hatching (Masuma et al. 1993). The yolk provides nourishment for the first 3–4 days, after which larvae switch to exogenous food sources (plankton). After 25–35 days, planktonic larvae undergo metamorphosis to pigmented juvenile fish (25–30 mm TL) with a benthic habit (Doherty et al. 1994). Late-stage larvae are excellent swimmers and have considerable control over their depth, direction of movement, and hence dispersal (Leis and Carson-Ewart 1999). They also have well developed otoliths and fully formed nares (Leis 1986; Masuma et al. 1993), and they respond to auditory and olfactory signals with a degree of sensitivity that strongly suggests they use their sensory systems to navigate, select suitable habitat, and avoid predators (Wright et al. 2008). As in other reef fish species

(Dixson et al. 2008), the sensory and locomotory systems of larval *Plectropomus* are probably sufficiently well developed to facilitate self-recruitment and be major determinants of fine-scale patterns in the supply of larvae to reefs.

Due to the highly cryptic habit and low density of early life stages, knowledge of *Plectropomus* recruitment patterns is limited and comes from just a few studies undertaken on the GBR. In particular, Russ et al. (1996) identified a strong cohort of *P. leopardus* that subsequently dominated the adult population in two no-take marine reserves (NTMR) for at least 3 year thereafter, and Wen et al. (2013b) identified the existence of recruitment hotspots that disproportionately contributed to adult populations of *P. maculatus*. Together, these results suggest that patterns of recruitment can vary considerably through space and time, and that variability in recruitment may be a strong and lasting determinant of adult population size.

Aquarium-based experiments indicate that water temperature and food availability are likely to influence larval survival and, by inference, affect the

supply of larvae to reefs. The transition from endogenous to exogenous nutrition is a critical phase for larvae because there is a very short temporal window (~ 6 h at 28°C) during which larvae must eat or starve (Yoseda et al. 2008). If ambient conditions are not within narrow thresholds, then mass mortality ensues. Changes in temperature influence metabolic rate and may shift the timing of critical developmental events (e.g. opening of the mouth) so that they occur when conditions are undesirable (e.g. at night). Furthermore, early-stage larvae are poor swimmers, so availability of suitable food at the time of first feeding profoundly affects larval survival. Thus, it is easy to conceive how extreme weather events (e.g. tropical cyclones or intense rainfall) or sustained environmental change could sufficiently alter water temperature and food availability to engender recruitment failures or pulses. Given that spawning occurs during a limited number of days each year for some species, extreme weather events need only be short lived to have a significant and enduring effect on the demographic structure of *Plectropomus* populations.

Stock structure and connectivity

The stock structure of *Plectropomus* has been investigated using a range of techniques, yielding information at multiple spatial and temporal scales (Welch et al. 2015). Studies of otolith morphology and microchemistry in *P. leopardus* on the GBR identified discrete stocks (i.e. independent populations of non-juvenile fish) at scales of tens to hundreds of kilometres (Bergenius et al. 2005, 2006). However, a study of genetic variance in *P. maculatus* on the GBR revealed a single panmictic population, suggesting high levels of contemporary and (or) historic gene flow among reefs from 18° to 23°S (Evans et al. 2010). In contrast, both *P. maculatus* and *P. leopardus* were found to have extensive genetic subdivision across the Indo-Australian archipelago, suggesting limited gene flow at scales of hundreds to thousands of kilometres (van Herwerden et al. 2006, 2009). Given the limited movements of adult fish (see next section), stock structure of *Plectropomus* seems to be driven primarily by larval dispersal. However, it is apparent that larvae tend not to traverse large expanses of open water or unsuitable coastal habitat, which act as potential barriers to dispersal. When occasional gene flow does occur, it is typically unidirectional and

aligned with major oceanic currents (van Herwerden et al. 2009).

Recent breakthroughs in larval tagging (Williamson et al. 2009) and genetics (Harrison et al. 2014) have enabled quantification of small-scale dispersal trajectories of *Plectropomus*. At the Keppel Islands, Australia, $\sim 30\%$ of *P. maculatus* offspring were found to settle within 1–2 km of their parents, although there was also significant bi-directional exchange of larvae among reefs separated by up to 28 km (Harrison et al. 2012). Similarly, at Manus Island, Papua New Guinea, 17–25 % of *P. areolatus* offspring were found to settle within 6 km of their parents, and 50 % were predicted to settle within 13 km (Almany et al. 2013). Dispersal of larvae to distant reefs (>33 km away) has never been examined, but is considered likely given the swimming abilities of larvae (Leis and Carson-Ewart 1999) and the panmictic stock structure of *P. maculatus* on the GBR (Evans et al. 2010). Together, these results indicate that *Plectropomus* populations are maintained by both high levels of self-recruitment and larval exchange between discontinuous reefs separated by intermediate distances (tens to hundreds of kilometres). Adaptive capacity of *Plectropomus* populations is expected to be relevant across spatial scales of the same magnitude.

Behaviour

Plectropomus are cryptic as juveniles but relatively conspicuous as adults, since they are less sedentary than other groupers. Ultrasonic telemetry data indicate that adult fish occupy distinct home ranges in the order of 1–12 ha for *P. areolatus* and 1–50 ha for *P. leopardus*, with no apparent relationship between body size or gender and home range area (Zeller 1997; Hutchinson and Rhodes 2010; Matley et al. 2015). Individuals are diurnally active, regularly using a small number of locations within their home-ranges, and often return to the same location each night (Zeller 1997; Bunt and Kingsford 2014). Long-distance (>3 km) and inter-reef movements of *Plectropomus* are rare (Sumpton et al. 2008; Matley et al. 2015), although individual *P. leopardus* and *P. areolatus* have been shown to travel up to 5 and 23 km (respectively) to participate in spawning aggregations (Zeller 1998; Hutchinson and Rhodes 2010). Together, these results indicate that movement

Table 4 Diet of *Plectropomus leopardus* from various Indo-Pacific locations

Size range ^a (cm)	Location	Major dietary items (in order of importance)	Unit of measure ^b	References
8–71 SL	Heron Island, GBR	Unidentified teleosts (37 %), Atherinidae (25 %), Scaridae (12 %), Pomacentridae (11 %), Labridae (5 %)	1	Choat (1968)
23–47 FL	Solomon Islands	Unidentified teleosts (58 %), Pelagic teleosts (42 %)	2	Blaber et al. (1990)
~10–60 SL	One Tree Island, GBR	Unidentified teleosts (32 %), Pelagic teleosts (13 %), Scaridae (7 %), Blenniidae (8 %), Crustacea (13 %), Pomacentridae (10 %), Labridae (6 %), Apogonidae (4 %)	1	Kingsford (1992)
6–52 SL	GBR	Clupeidae (22 %), Pomacentridae (19 %), Crustacea (9 %), Labridae (12 %), Gobiidae (5 %), Caesionidae (5 %), Scaridae (4 %), Synodontidae (4 %), Unidentified items (2 %)	3	St John (1999)
13–59 FL	GBR	Unidentified teleosts (60 %), Pomacentridae (10 %), Labridae (8 %), Pelagic teleosts (7 %), Caesionidae (3 %), Synodontidae (2 %), Scaridae (2 %)	3	St John et al. (2001)
24–79 FL	New Caledonia	Teleosts (88 %), Crustacea (8 %), Mollusca (4 %)	4	Kulbicki et al. (2005)

Minor prey groups are not listed. Pelagic teleosts are the Clupeidae and/or Engraulidae. GBR, Great Barrier Reef

^a *SL* standard length, *FL* fork length

^b Diet was calculated as (1) percent frequency of stomachs with prey present, (2) percent dry weight of stomach contents, (3) percent frequency of prey items in pooled diet, or (4) percent volume of prey items

patterns of adult *Plectropomus* are temporally predictable, occur at multiple spatial scales, and arise in response to a variety of stimuli.

Diet

Diet of *P. leopardus* has been well studied, but only limited data are available for other *Plectropomus* species (e.g. *P. maculatus*: Wen et al. 2012). Nonetheless, all adult *Plectropomus* have similar dentition, mouth morphology and feeding behaviour, suggesting that all species are likely to have a similar diet. Therefore, diet of *P. leopardus* serves as a useful proxy of diet in other *Plectropomus* species.

Juvenile (<12 cm TL) *P. leopardus* consume a high proportion (44 %) of benthic crustaceans but consume an increasing proportion of fish as they grow, such that adult individuals are almost entirely (95 %) piscivorous (St John 1999). Diet of adult *P. leopardus* is diverse and consists of at least 27 families of teleosts, including many obligate reef dwellers (e.g. Gobiidae, Scaridae, Pomacentridae) (Table 4). Adult *Plectropomus* also consume substantial quantities of pelagic and demersal planktivorous fishes such as Clupeidae,

Engraulidae and Pomacentridae, suggesting that they derive a large proportion of their primary production (carbon) from planktonic sources rather than from benthic sources such as coral or algae (Frisch et al. 2014). It should also be noted that *P. leopardus*' diet is spatially and temporally variable (Kingsford 1992; St. John et al. 2001), reflecting their generalist nature.

Mutualism, parasitism and disease

Plectropomus closely associate with numerous other organisms for a range of reasons. The most conspicuous inter-specific interaction is with ectoparasite predators such as *Labroides dimidiatus* (cleaner wrasse) and *Lysmata* sp. (cleaner shrimp). Cooperative relationships with cleaner wrasse are presumably highly beneficial for *Plectropomus*, because some individuals spend long periods 'posing' at cleaning stations (Goeden 1978). At least two species of *Plectropomus* also engage in cooperative hunting: individuals of *P. pessuliferus marisrubri* and *P. leopardus* use rapid head-shakes to communicate the location of hidden prey to hunting partners such as *Gymnothorax javanicus* (moray eel) and *Octopus*

Table 5 Occurrence of parasites on *Plectropomus*

Host	Parasite taxa	Number of species	References
<i>P. leopardus</i>	Protozoa	1	Lester and Sewell (1989)
	Myxozoa	1	Gunter and Adlard (2009)
	Nematoda	4	Lester and Sewell (1989), Justine (2011), Moravec and Justine (2014)
	Trematoda	9	Cribb et al. (2002), Bray et al. (2007), Ho et al. (2014)
	Monogenea	5	Lester and Sewell (1989), Justine and Euzet (2006), Deveney and Wittington (2010)
	Cestoda	3	Lester and Sewell (1989)
	Copepoda	3	Lester and Sewell (1989), Bennett and Bennett (2001)
	Isopoda	2	Lester and Sewell (1989)
<i>P. maculatus</i>	Nematoda	3	Lester and Sewell (1989)
	Trematoda	6	Cribb et al. (2002), Bott et al. (2013)
	Monogenea	2	Lester and Sewell (1989)
	Copepoda	2	Lester and Sewell (1989)
<i>P. laevis</i>	Trematoda	9	Bott et al. (2013)
	Monogenea	2	Justine and Euzet (2006)
<i>P. areolatus</i>	Trematoda	2	Bott et al. (2013)

cynea (octopus) (Bshary et al. 2006; Vail et al. 2013). In addition, juveniles of four species of *Plectropomus* resemble one or more species of poisonous pufferfish (*Canthigaster*) and/or wrasse (*Cheilinus*, *Coris*, *Hali-choeres*), presumably because the resemblance affords mimetic benefits such as predator avoidance (Batesian mimicry) and/or prey acquisition (aggressive mimicry) (Kuiter 1995; Frisch 2006). The affinity and highly evolved nature of these associations implies they are ecologically important to *Plectropomus* and potentially capable of enhancing its survival.

Plectropomus are susceptible to numerous microbial diseases and are host to many species of internal and external parasites. In particular, *P. leopardus*, *P. maculatus* and *P. laevis* are host to at least 28, 13 and 11 species of parasite, respectively (Table 5). *Plectropomus* typically carry a heavy parasite load relative to other piscivorous reef fishes (Bott et al. 2013), which may compromise their capacity to cope with other stressors such as increased temperature. As in other groupers (Cheng et al. 2009), captive *Plectropomus* experience higher rates of disease at elevated temperatures (A.D. Reynolds, pers. obs.), but the ecological consequences of this are not known. Recently, evidence of melanoma (a type of skin cancer) was discovered in 15 % of *P. leopardus* individuals in the southern GBR (Sweet et al. 2012). If affected individuals have higher mortality rates and

thus generate fewer offspring (e.g. Setlow et al. 1989), there may be negative consequences for population replenishment.

Ciguatoxins are a group of potent marine toxins that originate in unicellular algae (*Gambierdiscus toxicus*) and bioaccumulate up marine food chains. Due to the high trophic position of *Plectropomus* (Frisch et al. 2014), they are potential carriers of ciguatoxins and often the proximate cause of ciguatera poisoning in humans (Wong et al. 2005). Ingestion of ciguatoxins may be physiologically harmful to *Plectropomus* as it can depolarize nerve fibres and adversely alter fish behaviour (Capra et al. 1988; Davin et al. 1988). At present, the prevalence of ciguatoxins in *Plectropomus* is generally low and site-specific, but may be increasing given that the distribution and abundance of *G. toxicus* is likely to be expanding (Skinner et al. 2011).

Coral grouper fisheries

Fisheries characteristics

Plectropomus support important subsistence, artisanal, commercial and recreational fisheries throughout their distributions, and are captured using a range of gears including hook-and-line, spear, traps, and occasionally gillnets and trawls. More controversial

methods such as cyanide fishing are also used in parts of the Indo-Pacific, mainly to supply the LRFFT (Sadovy et al. 2003). In Australia, most fishing for *Plectropomus* occurs in shallow water (<30 m depth) during daylight, when individuals actively take baited hooks or are easily seen by spearfishers (Frisch et al. 2008). In Micronesia and Melanesia, however, spearfishers usually target *Plectropomus* at night, particularly aggregations of *P. areolatus* (Rhodes and Tupper 2008; Hamilton et al. 2012).

The largest commercial fisheries for *Plectropomus* are located in Indonesia, Philippines, Malaysia and Australia, which are the major exporting countries in the LRFFT (Sadovy et al. 2003). Smaller-scale artisanal fisheries for *Plectropomus* occur throughout developing Indo-Pacific and Red Sea countries. In these locations, fishers use a range of gears (hook-and-line, spear, traps) and small boats (outriggers, bancas) to exploit relatively small areas of shallow coral reef within close proximity to coastal communities (Sadovy et al. 2003; Fabinyi and Dalabajan 2011). On the GBR, commercial fishing is undertaken by hook-and-line, usually from outboard-powered dories (4–6 m long) that are tendered to larger (15 m) primary vessels (Thebaud et al. 2014). Recreational fisheries for *Plectropomus* are well developed across northern Australia and typically involve small outboard-powered boats or larger charter vessels, and use hook-and-line and/or spears (Frisch et al. 2008). Due to their high value, export of *Plectropomus* occurs almost entirely by air, although large vessels are occasionally used to transport fish from remote areas directly to Hong Kong.

Catch and effort

Reporting of catch statistics for *Plectropomus* is poor or absent in most countries, particularly for artisanal and recreational fisheries, which likely account for a considerable portion of the global catch. The most recent estimate of global annual catch of *Plectropomus* reported by the Food and Agriculture Organization (FAO) is 21,449 t (Anon. 2012), but since catch data are limited to just three species (*P. leopardus*, *P. areolatus* and *P. pessuliferus*) and just two countries (Indonesia and Saudi Arabia), this is certainly a gross underestimate. Indeed, approximately 75 % of the total weight of live *P. leopardus* imported into Hong

Kong comes from countries other than Indonesia and Saudi Arabia (Anon. 2013). Although not included in the FAO's catch statistic, total annual commercial catch of *Plectropomus* in Australia for the years 2000–2013 was 800–2200 t (mostly sourced from the GBR) and has been declining since 2002 (Keag et al. 2014) due to reduced fishing effort caused by declining profitability and changes in fishery regulations (Leigh et al. 2014; Thebaud et al. 2014). The lack of spatial, temporal and species coverage in FAO statistics renders it impossible to formulate meaningful generalisations about global catch trends of *Plectropomus*. To overcome this problem, developed countries are urged to assist with catch reporting in developing countries, particularly those linked to export fisheries such as the LRFFT.

Catches of *P. areolatus* tend to be highest during the spawning season, whereas those of *P. leopardus* are more consistent across seasons, potentially reflecting the differential propensity of these two species to form spawning aggregations (Hamilton et al. 2012; Tobin et al. 2013). Catches of *Plectropomus* are also influenced by monsoonal weather and tropical cyclones (Sadovy et al. 2003; Leigh et al. 2014). Together, these two factors (spawning aggregations and weather) weaken the relationship between catch and fishing effort and thus reduce the utility of fishery-dependent indices of abundance such as catch-per-unit-effort (CPUE) as indicators of stock status (e.g. Rhodes and Tupper 2008; Leigh et al. 2014).

The size of harvested *Plectropomus* is highly variable and depends on management regulations (Welch et al. 2008), fishing gear (Frisch et al. 2008), relative value, and location of fishing grounds (Sadovy et al. 2003). In areas of the Indo-Pacific where management and/or compliance are minimal, all sizes of *Plectropomus* are harvested. In the Maldives for example, juvenile fish are retained for export or grow-out in sea-cages and comprise over 70 % of harvested *Plectropomus* (Sattar et al. 2012). In the LRFFT, the demand is for 'plate-size' fish (35–42 cm TL; Sadovy et al. 2003), which is close to (or below) the size at first maturity for most species of *Plectropomus* (Table 2). On the GBR, 12–47 % of captured *Plectropomus* are discarded due to regulatory size limits (Welch et al. 2008) and ~20 % of these subsequently die from barotrauma or hook-related injury (Sumpton et al. 2010). Importantly, this type of incidental fishing mortality is likely to increase if fishing effort moves

into deeper water due to degradation of shallow coral reefs and/or overfishing of traditional fishing grounds.

Effects of fishing

Fishing can have rapid and substantial negative effects on *Plectropomus* populations, particularly when fishers target spawning aggregations, as this practice is highly efficient and can rapidly deplete reproductively active fish (Sadovy and Domeier 2005; Hamilton et al. 2012). In general, fished reefs have fewer, smaller and younger *Plectropomus* than unfished reefs (Williamson et al. 2004; Pet et al. 2005; Frisch et al. 2012; Miller et al. 2012; Shedrawi et al. 2014; Emslie et al. 2015), although poaching and/or high spatio-temporal variability in *Plectropomus* populations may mask the effects of fishing in some instances (Mapstone et al. 2004; Mclean et al. 2011). Conversely, reduced fishing pressure can have rapid, positive effects on the abundance of *Plectropomus*: newly established NTMRs led to a 68 % increase in density of *Plectropomus* within 2 year on the GBR (Russ et al. 2008) and a 600 % increase within 8 year at the Abrolhos Islands, Western Australia (Nardi et al. 2004). These results suggest that many *Plectropomus* populations are suppressed by fishing, but also that they respond well to a reduction in fishing pressure. However, rates of population recovery will depend on spawning stock biomass (SSB) and interacting environmental factors such as coral bleaching and extreme weather events (Karkarey et al. 2014; Williamson et al. 2014).

Harvest of juvenile *Plectropomus*, which is common in many developing countries (see above), reduces yield per recruit and increases risk of growth overfishing. In addition, harvest of large adult *Plectropomus* disproportionately removes male fish because larger *Plectropomus* are predominantly male. If sex change is ontogenetically inflexible, then fishing is expected to bias sex ratios, potentially limiting the availability of sperm. Alternatively, if sex change is socially mediated, then earlier transition of female fish is expected to compensate for the loss of male fish, leading to a smaller mean size of female fish and reduced egg production. In either case, theoretical modelling suggests that protogynous *Plectropomus* are more vulnerable to overfishing than equivalent gonochoristic (separate sex) fishes (Armsworth 2001).

To date, however, empirical studies have yielded equivocal results, with sex ratios and size structures being regionally variable and independent of fishing pressure (Adams et al. 2000; Carter et al. 2014).

Given that *Plectropomus* feed at a high trophic level and are numerically dominant predators throughout much of their ranges, theory predicts that they are ecologically important and capable of influencing the structure of coral reef communities (Goeden 1982). Indeed, field studies indicate that adult *Plectropomus* influence the distribution and feeding activity of herbivorous fishes (Rizzari et al. 2014) as well as the size and abundance of small prey fishes (Graham et al. 2003; Watson et al. 2007; Shedrawi et al. 2014; Boaden and Kingsford 2015; but see also Emslie et al. 2015). The ecological significance of these findings is poorly understood and it remains unclear as to whether the flow-on effects of fishing for *Plectropomus* have serious consequences in terms of reduced biodiversity, compromised ecosystem function, and/or reduced fisheries productivity. This uncertainty, combined with the recognized role of top predators in maintaining biodiversity (Estes et al. 2011), suggests that a precautionary approach to management of *Plectropomus* is warranted.

Aquaculture

Compared to other grouper species, *Plectropomus* are difficult to culture and production is limited, but high demand and depletion of wild stocks ensures that research and development is ongoing. Using techniques developed for other groupers, small-scale production of *P. leopardus*, *P. maculatus* and *P. areolatus* has been achieved in parts of Southeast Asia (Liao and Leano 2008). Typically, broodstock are obtained from wild populations and subsequently housed in either sea-cages or onshore tanks. Exposure to natural photoperiod and temperature is usually sufficient to stimulate natural spawning on a seasonal basis (3–4 mo year⁻¹), although indoor tanks with full photo-thermal control can be used to extend spawning periods (up to 8 mo year⁻¹) and increase the supply of juvenile fish for grow-out (Liao and Leano 2008).

In comparison to other cultured marine fish, larvae of *Plectropomus* are small, fragile and have low

feeding capacity. The transition from endogenous to exogenous feeding (3–4 days post-hatch) is critical for larval survival as their small gape (0.24 mm) necessitates timely provision of suitably sized live prey such as copepod nauplii and ‘ss-strain’ rotifers (Masuma et al. 1993; Qu et al. 2012). Short (<24 h) delays in first feeding due to lack of suitable prey or suboptimal environmental conditions are sufficient to cause mass mortality of larvae, such that survival to metamorphosis is commonly less than 5 % (Liao and Leano 2008; Yoseda et al. 2008). Fewer problems are encountered after metamorphosis, when survival rates increase substantially. High mortality of early-stage larvae therefore constitutes the greatest obstacle, and highest research priority, for expansion of *Plectropomus* aquaculture.

Socio-economics

Plectropomus are a high-value commodity, not only because of their exceptional eating qualities, but also because of their often bright red colour, which symbolises good fortune in many Southeast Asian countries (Fabinyi and Liu 2014). Consumer markets and demand for *Plectropomus* in Southeast Asia have expanded substantially in recent decades due to increasing human population and rising affluence (Sadovy et al. 2003; Fabinyi and Liu 2014). At restaurants in Hong Kong, mainland China, Taiwan and Singapore, which are the major importing destinations, live *Plectropomus* retail for US\$100–316 kg⁻¹ (Sadovy et al. 2003; Fabinyi and Liu 2014; Yin 2014). The global economic value of *Plectropomus* is not known, but is estimated to be US\$35 million year⁻¹ in Australia alone (Keag et al. 2014). At the source, *Plectropomus* fisheries contribute significantly to the food and livelihood needs of many coastal communities throughout the Indo-Pacific, but often occur in contexts of poverty, lack of alternative livelihood options, high fishing pressure and destructive fishing practices (Sadovy et al. 2003; Fabinyi and Dalabajan 2011). Finding the right balance between economic opportunity, food security, productive fisheries and healthy ecosystems is clearly a difficult task and highlights the social-ecological challenges faced by users, managers and policy-makers of *Plectropomus* fisheries specifically and coral reefs generally.

Management of Coral grouper

Key challenges

Despite the social, economic and ecological importance of *Plectropomus*, few populations are adequately managed, which puts them at risk of being overfished. A key challenge is that *Plectropomus* fisheries are mostly distributed across developing nations where (a) human populations are increasing rapidly and many fishers are desperate for food and/or income, (b) the resource is considered ‘open access’ and short-term economic gains are often prioritized over long-term fishery sustainability and biodiversity conservation, and (c) institutional capacity for management and enforcement is limited and the high market demand overwhelms any local regulatory mechanisms that may exist. For example, in the Philippines and Indonesia, which are major exporting countries, many management policies have been promulgated at national and provincial levels, but on-ground implementation of (and compliance with) these policies has been poor and thus has failed to reduce fishing effort or halt destructive fishing practices (Fabinyi and Dalabajan 2011; Campbell et al. 2012b). This mismatch between policy, implementation and compliance indicates that ecologically sustainable management of *Plectropomus* in developing countries is unlikely to succeed without cooperation from fishers, and highlights the need for a deeper understanding of the social and economic contexts in which *Plectropomus* fisheries are often embedded.

Plectropomus are often primary target species within complex multi-species, multi-gear and multi-sector reef fisheries that often generate substantial quantities of byproduct (retained) and, in developed countries, bycatch (discarded). Due to differential life-history characteristics, optimal management arrangements for *Plectropomus* may be suboptimal or even inappropriate for byproduct or bycatch species, with unexpected and potentially detrimental ecological consequences (Mangel and Levin 2005). Control of primary and incidental catch and fishing effort is therefore regarded as a fundamental component of ecosystem-based management of *Plectropomus* fisheries. Another key challenge for management is that *Plectropomus* populations are often heavily impacted by indirect phenomena such as coral bleaching, severe weather events, and declining water quality from

coastal development (Karkarey et al. 2014; Leigh et al. 2014; Williamson et al. 2014; Emslie et al. 2015). A holistic, precautionary approach to management that seeks to maintain relatively high SSB as insurance against unpredictable, indirect threats is therefore important.

Stock assessment

Estimates of stock size are limited or non-existent for almost all *Plectropomus* fisheries and, with few exceptions, formal stock assessments are lacking. However, a broad range of information sources (e.g. fisher interviews, trade data) and indirect indicators (e.g. declining fish sizes at markets, disappearance of spawning aggregations, ‘boom and bust’ business cycles) provide strong evidence that many major stocks of *Plectropomus* are over-exploited and/or in decline, due primarily to heavy fishing pressure and habitat degradation (Scales et al. 2007; Fabinyi and Dalabajan 2011; Sadovy de Mitcheson et al. 2013). Potential exceptions are the *Plectropomus* stocks harvested by small-scale subsistence fisheries at remote Pacific islands (e.g. Marshall Islands) and those on Australia’s GBR, which have formed the foundation of commercial and recreational fisheries for at least 60 years.

Only three stock assessments of *Plectropomus* fisheries have ever been undertaken or reported. Yield-per-recruit (YPR) models were applied to *P. leopardus* and *P. pessuliferus marisrubri* stocks in Palawan (Philippines) and Red Sea (Sudan) respectively, and both were found to be overfished; for the *P. leopardus* stock, SSB was estimated to be 12–24 % of virgin stock biomass (SSB_0) (Elnaem 2012; Yin 2014). An age-structured population dynamic model was applied to the *P. leopardus* stock on the GBR, and SSB was estimated to be 60 % (± 11 %, SE) of SSB_0 in areas open to fishing (~ 70 % of total reef area) (Leigh et al. 2014). For comparison, SSB at maximum sustainable yield is ~ 40 % of SSB_0 for a diverse range of marine fishes (Thorson et al. 2012). Given the longevity (60 year), active management (see below) and moderate exploitation rate of the *Plectropomus* fishery on the GBR relative to other locations (e.g. Palawan), there is reason to be optimistic about its sustainability. However, there are still significant

justified concerns about the status of *Plectropomus* stocks on the GBR due to substantial uncertainty of model inputs (particularly estimates of abundance and recreational catch) and ambiguity of baselines (see Pauly 1995; Keag et al. 2014; Leigh et al. 2014).

Management tools

In developed countries such as Australia, a broad range of management tools have been applied to *Plectropomus* fisheries, including size, catch and effort limits, temporal closures, gear and vessel restrictions, and limited-entry licensing (Thebaud et al. 2014; Leigh et al. 2014). In addition, NTMRs have been used as a conservation management tool in some countries. Given that *Plectropomus* occupy relatively small territories and form spatially predictable spawning aggregations, NTMRs are also potentially useful for managing *Plectropomus* fisheries, provided that compliance is high and any displaced fishing effort is managed effectively (Little et al. 2005). No-take marine reserves enable build-up of larger fish (see above) and a disproportionate increase in reproductive output (Sadovy 1996), which, under particular conditions, lead to export of fish via adult spill-over and larval dispersal to surrounding fished areas (Zeller and Russ 1998; Harrison et al. 2012). At the Keppel Islands (Australia), NTMRs encompass just 28 % of total reef area, yet they have been shown to supply ~ 50 % of total *P. maculatus* recruitment in the region (Harrison et al. 2012). Despite these benefits, evaluations of alternative management strategies for *Plectropomus* on the GBR and in Torres Strait (Australia) indicate that NTMRs are generally less effective at maintaining SSB and improving catches and economic returns than catch and effort limits, primarily because displaced fishing effort becomes concentrated in outlying areas (Little et al. 2005; Mapstone et al. 2008; Williams et al. 2011). However, at certain levels of spatial closure, joint application of NTMRs and catch limits (as rights-based catch shares) can theoretically maximise both SSB and economic returns (Little et al. 2011). Therefore, careful planning and evaluation is required in the application of NTMRs to optimize both fishery and biodiversity objectives (see Green et al. 2015).

In developing countries, NTMRs are often one of few management tools available, but they often fail to meet their objectives because of poor compliance and limited institutional capacity for enforcement (Fabinyi and Dalabajan 2011; Campbell et al. 2012b). Even at relatively low levels, poaching can substantially reduce the ability of NTMRs to conserve *Plectropomus* populations (Little et al. 2005). In these contexts, management initiatives may achieve better outcomes by focusing their limited resources on elimination of undesirable fishing practices such as cyanide fishing and targeting of juvenile fish for grow-out, which contribute to habitat degradation and growth overfishing respectively (Jones and Steven 1997; Pomeroy et al. 2008). In addition, allocation or resurrection of property rights in the form of territorial user rights for fisheries (TURFs) or customary marine tenure systems (CMTs) can increase legitimacy of spatial management tools, improve stewardship, and reduce opportunities for non-resident and foreign exploitation of reefs that would otherwise be regarded as 'open access' (Foale et al. 2011; Afflerbach et al. 2014). Social and ecological benefits of TURFs and CMTs have been demonstrated at local scales (Campbell et al. 2012a; Afflerbach et al. 2014) and thus provide new opportunities for conservation and management of *Plectropomus* in developing countries.

In recent years, new approaches have emerged to bypass the problem of limited management capacity in source countries. Market-based approaches and public information campaigns, for example, aim to reduce demand for overfished species or populations by informing consumers about the geographic origin and sustainability of their seafood choices. In China, these campaigns have had some success for commodities such as shark-fin (Fabinyi and Liu 2014), and could potentially be effective for conservation of *Plectropomus*. Other mechanisms such as trade restrictions on the LRFFT could also be effective, since the majority of export demand for *Plectropomus* is channelled through a single destination (Hong Kong). At present, however, governments of few exporting countries and no importing countries have taken steps to control the trade of *Plectropomus* or other reef fishes (Sadovy and Domeier 2005; Fabinyi and Liu 2014).

Conclusions and recommendations

Relative to other groupers of equivalent body size, *Plectropomus* tend to have shorter life-spans, faster growth and higher rates of natural mortality. Although these 'r-like' characteristics are expected to increase population turnover and reduce innate vulnerability to exploitation and disturbance, a high proportion of *Plectropomus* populations are suffering the same fate as other groupers, i.e. drastically declining abundances (Scales et al. 2007; Sadovy de Mitcheson et al. 2013). This raises two critical issues. Firstly, reduced availability of *Plectropomus* is likely to have significant social and economic consequences for coastal peoples that harvest these fishes as a source of food or income. Secondly, declining abundance is likely to have cascading ecological effects such as altered community structure (Goeden 1982; Graham et al. 2003; Rizzari et al. 2014; Shedrawi et al. 2014; Boaden and Kingsford 2015) and possibly reduced ecosystem resilience. In view of the intensifying global stressors on coral reefs and associated food resources (Hughes et al. 2003), these issues provide strong justification for robust management and conservation of *Plectropomus*.

The two major causes of declining *Plectropomus* abundance are overfishing and habitat degradation. The latter is often caused by large-scale phenomena (e.g. cyclones and coral bleaching) that cannot be managed directly. Fishery managers must therefore focus on effectively controlling fishing effort and eliminating undesirable fishing practices. Clearly, this is not an easy task because many Indo-Pacific countries have limited capacity to apply and enforce adequate management, and because many fishers have limited options for alternative livelihoods. Given the geographic scale and socio-economic complexities of *Plectropomus* fisheries, efforts to restore and conserve *Plectropomus* populations must transcend national and international jurisdictions via regional cooperation and collaboration (e.g. Coral Triangle Initiative for Coral Reefs, Fisheries and Food Security), engage both fishers (e.g. co-management) and consumers (e.g. market-based approaches), and increase public awareness about the social and ecological benefits of management and the severe long-term consequences of maintaining the *status quo*. With fisher participation and buy-in, networks of NTMRs that are adequately enforced and optimally designed to

deliver fishery and conservation benefits would be a useful complementary management tool. If fishing pressure can be reduced to acceptable levels in places where stocks are depleted, then *Plectropomus* populations are likely to be replenished relatively quickly due to their 'r-like' life-history traits, provided that sufficient spawning stocks still exist in the region and that reef habitats remain intact and functional. Aquaculture propagation may also help to bridge the gap between supply and demand, although additional research and development is needed to overcome obstacles associated with broad-scale production, particularly high larval mortality.

This review provides the first synthesis of the biology, fisheries and management of *Plectropomus*. It establishes a sound framework for implementation of knowledge-based management strategies that help to ensure *Plectropomus* are not only harvested on a sustainable basis, but are also maintained at sufficient abundances to fulfil their ecological roles on coral reefs. In addition, this review provides a solid foundation on which to investigate the vulnerability and adaptive capacity of *Plectropomus* to climate change, which will be addressed elsewhere.

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