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Relative effects of environmental variation and fishing on the demography and ecology of tropical wrasses

Thesis submitted by

Jake R. Lowe BSc, GCertResMeth

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and the ARC Centre of Excellence for Coral Reef Studies,

James Cook University

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I performed Chapters 2 and 3 of this thesis in collaboration with colleagues David Williamson, Daniela Ceccarelli, and Richard Evans. The long-term data used in these chapters were collected through David Williamson's long-term monitoring program "Assessing the ecological effects of management zoning on inshore reefs of the Great Barrier Reef Marine Park". I assisted this monitoring program as a benthic observer from 2016 – 2018. Data from 2006 – 2014 used in chapters 2 and 3 were collected without my assistance. David, Daniela, and Richard all appear as co-authors on published versions of Chapter 2 and 3 which appear in the Journals *Marine Biology* and *Environmental Biology of Fishes*, respectively. Funding for monitoring field work that contributed to chapters 2 and 3 of this thesis was provided via grants to David Williamson by the Australian Research Council (ARC); the CRC Reef Research Centre; and the Australian Government Department of Environment and Energy through the Marine and Tropical Sciences Research Facility (MTSRF), the National Environmental Research Program (NERP), the National Environmental Science Program (NESP), and the Reef 2050 Integrated Monitoring and Reporting Program (RIMReP).

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Publications Arising from this Thesis

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2. Lowe JR, Williamson DH, Ceccarelli DM, Evans RD & Russ GR (2020) Environmental disturbance events drive declines in juvenile wrasse biomass on inshore coral reefs of the Great Barrier Reef, Australia. *Environmental Biology of Fishes* 103, 1279-1293. doi:10.1007/s10641-020-01022-2.
3. Lowe JR, Russ GR, Bucol AA, Abesamis RA & Choat JH (in prep.) Spatial variability in the early gonadal development and sexual ontogeny of *Hemigymnus*, *Cheilinus*, and *Oxycheilinus* wrasses among Indo-Pacific coral reefs. *Journal of Fish Biology*.
4. Lowe JR, Russ GR, Bucol AA, Abesamis RA & Choat JH (in prep.) Spatial variation in the demography of fished and unfished *Hemigymnus, Cheilinus,* and *Oxycheilinus* wrasse populations among Indo-Pacific coral reefs. *Journal of Animal Ecology*.

Abstract

One of the greatest challenges faced by fishery managers and ecologists is determining the degree to which natural variation in population dynamics (i.e., species abundance and life history traits) are modified by fishing. Multiscale sampling that encompasses temporal and spatial variation in anthropogenic and environmental factors are key to understanding mechanisms that drive population dynamics. To date, our understanding of these processes has been hindered by a lack of spatially explicit demographic information for many fishery-targeted species. This is particularly true for multi-species, Indo-Pacific coral reef fisheries that are under increasing levels of exploitation. For example, across Indo-Pacific reefs, large-bodied wrasses are common components of reef fish assemblages and are exposed to increasing levels of exploitation, yet little is known regarding their life histories or drivers of population variability. This thesis was designed to assess the relative effects of environmental variation and fishery exploitation on the demography and ecology of tropical wrasses both spatially and temporally, to determine patterns of demographic variation and population drivers among and within species.

To assess the relative importance of fishing and environmental factors influencing population dynamics, here I combine data from long-term monitoring of wrasse populations across marine reserve networks of the Great Barrier Reef (GBR), Australia with multiscale, age-based comparisons of sexual ontogenies and age-based demography of the fishery-targeted wrasses *Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus,* and *Oxycheilinus digramma* collected from low-latitude Philippine fish markets and from two unfished populations on the Great Barrier Reef.

Firstly, in **Chapter 2**, I analyse a long-term (2006 – 2018), spatially extensive (≈ 700 km) ‘natural experiment’ quantifying the responses of 11 wrasse taxa to acute environmental disturbance events, predator density, and no-take marine reserve (NTMR) protection on fringing coral reefs in the Palm (18°34′ S, 146°29′ E), Whitsunday (20°08′ S, 148°56′ E), and Keppel Island (23°10′ S, 150°57′ E) groups, Great Barrier Reef, Australia. The responses of wrasse densities to benthic habitat change were taxa-specific and temporally consistent. Disturbance-mediated reductions in live hard coral cover and/or habitat complexity resulted in density

declines for *Hemigymnus melapterus*, *Hemigymnus fasciatus*, *Cheilinus fasciatus*, *Labroides* spp., *Oxycheilinus digramma*, and *Thalassoma* spp. Conversely, *Halichoeres* spp. densities correlated positively with increased relative cover of sand and rubble, while *Stethojulis* spp., *Anampses* spp., *Epibulus insidiator*, and *Bodianus* spp. displayed variable responses to habitat changes. No wrasses exhibited a direct NTMR effect (i.e., higher density inside NTMRs relative to fished controls over time), nor a predator density effect inside NTMRs (lower wrasse density inside reserves where predator density was higher over time). Moreover, predator density, irrespective of NTMR status, only influenced five taxa across all island groups. The lack of NTMR effects and variable top-down predator effects suggested that taxa-specific benthic habitat associations were the predominant drivers of wrasse densities on inshore GBR reefs.

In **Chapter 3** I investigate further the population dynamics of *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* wrasses studied in Chapter 2 to determine whether the effects of NTMR protection, predator density, or environmental disturbance events impacted immature and mature wrasses differently, which could have major implications for population persistence. To do this, I used detailed reproductive data to separate juvenile and adult components of wrasse populations and quantified the influences of benthic composition, predator density, and NTMR protection on the biomass of *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* populations at the Palm and Whitsunday Island groups, GBR. This study included multiple cycles of benthic disturbance and recovery during the period 2007 – 2018. The biomass of juvenile and adult wrasses on inshore GBR reefs were driven predominantly by benthic habitat associations, rather than by NTMR protection or density of a major wrasse predator (*Plectropomus* spp.). Despite similar species-specific associations of juvenile and adult wrasses with benthic cover, juvenile wrasse biomass consistently declined following coral bleaching and cyclone events. Conversely, biomass of adult wrasses had variable responses to disturbance events, including some increases in biomass. Disturbance-mediated declines in the biomass of juvenile wrasses are likely to generate ongoing reductions in the abundance of these species on inshore GBR reefs. My findings provide further evidence that habitat loss impacts a range of coral reef fishes beyond those that are directly reliant upon live coral for food and shelter. Shifts in assemblage structure, loss of biodiversity, and reductions in fishery productivity will become increasingly apparent in coral reef ecosystems if anthropogenic global warming, and its effects on coral cover, continues unabated.

Differential responses to environmental disturbances of sexually immature and sexually mature wrasses identified in Chapter 3 stressed the importance of understanding life histories when determining drivers of population dynamics. To determine effects of fishing and environmental variation on wrasse life histories **Chapter 4** compared patterns of reproductive ontogeny in four large-bodied, fishery-targeted coral reef wrasses (Labridae) *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma*. Populations of each species were sampled from two unfished island groups of the central Great Barrier Reef (GBR), Australia and from heavily fished coral reefs in the central Philippines. These three sampling locations span 30° of latitude. The GBR and Philippine reefs have distinct differences in water temperature, geography, and human activity. Gonad histology and demographic information were obtained across the entire size and age range of *H. melapterus*, *C. fasciatus*, and *O. digramma* from the GBR and the Philippine reefs. Analysis identified three methods of male recruitment into wrasse populations; functional gonochorism and both forms of protogynous hermaphroditism, monandry and diandry. The expression of these different sexual ontogenies was locality dependent. Populations of the four species (the three indicated above, plus *H. fasciatus*) on the GBR showed consistently simple patterns of sexual ontogeny, with all species being exclusively monandric, as all males were recruited by transition from mature females. The three species investigated in the Philippines displayed complex sexual ontogenies, with all species displaying histological evidence of both diandry and functional gonochorism. Reproductive investment in gonadal tissue, and population sexual structure, also differed between GBR and Philippine coral reefs. Philippine populations had substantially lower gonadosomatic indices than populations on the GBR. However, Philippine populations matured more rapidly and displayed a protracted timing of sex change over a large size and age range. Thus, mature females appeared earlier and persisted later into ontogeny in the Philippines than on GBR reefs. Protracted timing of sex change on Philippine reefs is likely linked to the presence of primary males in the population, which likely reduced the strength of selection for mature females to undergo sex change and become male. Hypotheses based on social structure of fish populations, environmental factors, and evolutionary history were developed to account for the frequent appearances of functional gonochorism in the focal wrasses in the Philippines.

Chapter 5 quantified the age-based demographic parameters of large-bodied wrasses *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus,* and *Oxycheilinus digramma* from fished populations in the Philippines and multiple unfished populations on the Great Barrier Reef (GBR), Australia to investigate drivers of demography across regional and biogeographic scales. Histological analysis and age-based demographic assessments indicated distinct differences in growth patterns, sexual ontogenies, and estimates of longevity, mortality, maturity, sex change, body condition, and maximum body size across both small- and large-latitudinal distances (2° and 30° latitude). Wrasses sampled from Philippine reef fisheries (9.0 – 11.0 °N), exhibited significantly faster growth rates, rapid maturation, shorter lifespans, and greater mortality rates than conspecifics on GBR reefs. Despite this, Philippine populations obtained a similar asymptotic and maximum length, and had better relative body condition than GBR populations. Significant differences in demography were also evident at regional spatial scales between sampled inshore GBR reefs separated by 2° of latitude. *Oxycheilinus digramma* and *C. fasciatus* grew slower, matured later, and lived longer on higher-latitude reefs (Whitsunday Islands: 20.05-20.21° S) compared to those to the north (Palm Islands: 18.53 – 18.70° S and the Philippines). Conversely, *H. melapterus* and *H. fasciatus* populations on Whitsunday reefs reached lower asymptotic sizes than those on Palm reefs, exhibited reduced longevities, and *H. melapterus* matured earlier on Whitsunday reefs. Across locations, demographic variation was species-specific and across taxa was largely inconsistent with predictions of the Temperature-Size Rule for ectotherms, the metabolic theory of ecology, and the expected effects of fishing on size structures. These unexpected relationships suggest localised sources of demographic variation are affecting life histories of the focal wrasses across various spatial scales.

Across these four chapters, effects of fishing were observed, but results largely suggested that life histories and population dynamics of tropical wrasses were more strongly driven by environmental variation at both regional and biogeographic scales. Therefore, despite significant fishing pressure on large-bodied labrids in the Philippines, it appears that the life histories and population dynamics of tropical wrasses studied here are primarily dependent on the surrounding environment, particularly benthic habitat and food resources. Across locations, wrasses will respond differently to varying environments and thus models predicting the effects of fishery

exploitation on wrasse populations should incorporate benthic habitat and other relevant environmental conditions (e.g., food availability and quality) into analyses.

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Chapter 1: General Introduction

1.1 Reef Fish Populations, Fishery Exploitation, and Disturbance Events on Coral Reefs

Coral reefs support high biodiversity and provide nutrition and economic security to hundreds of millions of people, most of whom reside in developing nations (Dalzell *et al.*, 1996; Teh *et al.*, 2013; Hicks *et al.*, 2019). However, increasing fishing pressure and climatic warming have the potential to reduce biodiversity and the future sustainability of coral reef fisheries (Cheung *et al.*, 2010; Knutson *et al.*, 2010; Hughes *et al.*, 2018a).

Over the past three decades, there has been considerable discussion surrounding how to best manage coral reefs and the fisheries they sustain (Roberts and Polunin 1991; Pauly *et al.*, 2002; Russ, 2002; Hilborn *et al.*, 2004; Green *et al.*, 2014; MacNeil *et al.*, 2015; Cinner *et al.*, 2016; Bruno *et al.*, 2018; Graham *et al.*, 2020; Roberts *et al.*, 2020). One of the most effective management tools has been the implementation of spatial closures to fishing, known as no-take marine reserves (NTMRs), which have proven successful for conserving biodiversity and fisheries production (Russ *et al.*, 2004; Sale *et al.*, 2005; Harrison *et al.*, 2012). Evidence demonstrates that NTMRs can result in increased species richness, body-size, abundance, and reproductive potential of target species within their boundaries (Halpern, 2003; Lester *et al.*, 2009; Molloy *et al.*, 2009). When well-designed and enforced, NTMRs can also replenish local fisheries via larval export and adult spill over to surrounding fished areas (Roberts *et al.*, 2001; Russ *et al.*, 2004; Harrison *et al.*, 2012). Most studies demonstrate positive NTMR effects on high-trophic level target species (Russ, 2002; Halpern, 2003; Lester *et al.*, 2009). However, some studies show that NTMR’s have no effect of reef fish abundance, and only provide benefits to reef fishes intermittently, or even negatively impact reef fish density (Ferreira and Russ, 1995; Russ and Alcala, 1998; Russ *et al.*, 2015b; Emslie *et al.*, 2015). Different results between studies can often be attributed to the ecological and life history traits of the study organism, particularly when focal species are not heavily targeted or are of a low trophic level and thus are more strongly affected by indirect ecological processes that can occur years to decades after NTMR establishment (Russ and Alcala, 1998; Babcock *et al.*, 2010). Additionally, the intensity of the surrounding fishing pressure, the NTMR size, level of NTMR enforcement, and geographic location will all contribute to an NTMRs effectiveness in sustaining local fisheries and biodiversity (Lubchenco *et al.*, 2003; Russ *et al.*, 2008). For example, fishers in developing nations of the Indo-Pacific, such as the Philippines, heavily target a broad array of fishes using destructive fishing techniques, and in these regions NTMR protection would be expected to promote broader ecosystem services in addition to boosting the populations of target species (Russ and Alcala, 1989; Bohnsack and Ault, 1996; McClure *et al.*, 2020). In contrast, NTMRs may only provide benefits for fishery target species in developed nations, which do not use destructive fishing practices and only target a small number of species, such as Australia (Emslie *et al.*, 2015). Irrespective of location, overfishing of high trophic level target species has far-reaching effects on coral reef ecosystems, initiating major changes in species abundances and ecosystem structure (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003; Pinca *et al.*, 2012). Evidence suggests in some cases that NTMRs can restore trophic structure of reef fish assemblages (Graham *et al.*, 2003; Edgar, 2011) and increase ecosystem resilience to climate-driven disturbance events in temperate marine ecosystems (Ling *et al.*, 2009). However, in systems with many trophic links this is not always the case and thus whether NTMRs on coral reefs can attenuate predicted effects of global warming and increasing disturbance frequency remains equivocal (Côté and Darling, 2010; Bruno *et al.*, 2019; Graham *et al.*, 2020, but see Roberts *et al.*, 2020).

Many of the environmental stressors degrading coral reefs extend well beyond the boundaries of NTMR protection (Jones *et al.*, 2004; Emslie *et al.*, 2015; Russ *et al.*, 2015b). Over the past 30 – 40 years the average live coral cover on reefs globally has declined by 50 – 75% due to a combination of coral bleaching events, sedimentation, eutrophication, outbreaks of crown of thorn starfish (COTS), destructive fishing, and coastal development (Gardner *et al.*, 2003; Bruno and Selig, 2007; Hughes *et al.*, 2018a). But the primary global factor of concern is ocean warming and its subsequent effects on the frequency of coral bleaching events and severe tropical storms (Hoegh-Guldberg, 1999, 2007; Knutson *et al.*, 2010; Hughes *et al.*, 2017a, b, 2018a, b). As the majority of reef fishes depend on coral cover or the structural complexity of coral reefs for food, shelter, or recruitment, reef fish abundance and diversity generally decline following coral loss (Wilson *et al.*, 2006; Pratchett *et al.*, 2008; Coker *et al.*, 2014). Negative impacts on reef fishes are particularly pronounced when coral cover declines below 10% (Wilson *et al.*, 2006; Holbrook *et al.*, 2008), suggesting that at least 10% coral cover is required to support diverse assemblages of coral reef fishes. However, not all reef fish species are negatively impacted by disturbance-mediated coral loss. Species of parrotfish, wrasse, surgeonfish, and goatfish have all been shown to increase in density following acute disturbance events to the benthos that reduced coral cover and habitat complexity (Russ *et al.*, 2015a, c, 2017, 2018). Determining which species are ‘winners’ and ‘losers’ following disturbances is fundamental to predicting future reef community structure, biodiversity, and productivity. Yet, environmental processes driving increases in abundance of some species and declines of others are not well understood. A need exists to better understand the links between reef fish life histories and population dynamics.

1.2 Life History Traits and Their Effects on Population Growth and Vulnerability

Coral reef fishes respond to fishery harvest and benthic habitat changes in different ways, dictated by ecological and life history traits (Adams, 1980; Winemiller, 2005; Pratchett *et al.*, 2008). The most obvious trait that differentiates individuals and species is body-size, which influences habitat selection, diet, energetics, and predation risk (Wainwright, 1988; Hixon and Beets, 1993; Caley and St John, 1996; Robertson, 1998). In addition, larger body-size has been shown to correlate positively with longevity, age of maturity, fecundity, population turnover rate, and increased species abundance (Stearns, 1983; Roff, 1986; Calder, 1996). Basically, trade-offs between demographic traits, in particular mortality, growth, and reproduction, determine local population dynamics (Jones, 1990; Sale, 2002; Kritzer and Sale, 2010). For example, smaller-bodied species are commonly early-maturing, short-lived, and less fecund than larger-bodied reef fishes, but early maturation and short generation times increase the chances of reproductive success in these species and lessens their vulnerability to habitat loss and fishing pressure (Jennings *et al.*, 1998; Reynolds *et al.*, 2005). Conversely, most large bodied species are slow-growing, late maturing, have long generation times, and are thus more vulnerable to the effects of fishing and habitat loss, but these species are capable of persisting, despite intermittent population replenishment events (Jennings *et al.*, 1998; Reynolds *et al.*, 2005). Yet, spurious correlations between body size and longevity complicate the use of body-size as a life history proxy (Choat and Robertson, 2002). For example, contrary to general body size correlations, some small groupers live in excess of 40 years, while some large-bodied groupers rarely survive beyond 15 years (Ferreira, 1994; Mosse, 2002). Moreover, some long-lived reef fishes are known to grow rapidly, mature early, and reach their asymptotic body size in only a few years, allowing for early and concentrated reproductive investments typical of high-turnover species, but over an extended life span (e.g., acanthurids) (Choat and Axe, 1996; Hart and Russ, 1996; Choat and Robertson, 2002; Trip *et al.*, 2008). Other fishes are comparatively short lived, exhibit indeterminate somatic growth, and often mature later in life to species with a pronounced asymptote in their growth trajectory (e.g., labrids) (Choat *et al.*, 1996; Choat and Robertson

2002; Taylor *et al.*, 2018). Consequently, reliable estimates of age structure, as well as body-size, are critical for understanding life history evolution, population dynamics, and the capacity of reef fishes to respond to environmental change and fishing pressure. Despite this, age-based demographic information is lacking or non-existent for many coral reef fishes, and to date most assessments of reef fish vulnerability to fishing and habitat loss have been based on inferred characteristics rather than measured life history traits (Abesamis *et al.,* 2014; Taylor *et al.*, 2014a).

A paucity of age-based life history data for tropical reef fish stems from two key sources; 1) a lack of suitably trained scientists and funding for research in many tropical nations and 2) delays in the collection of age-based life history data from tropical fishes due to prior notions that tropical fishes did not deposit annual increments in sagittal otoliths because of a lack of seasonal variation in water temperature (Longhurst and Pauly, 1987; Fowler, 2009). Initial age-based studies of reef fish life history traits dispelled this misconception and showed that the majority of coral reef fishes deposit regular annual increments and have substantially different life histories within and among taxonomic groups (Choat, 1969; Robertson and Choat, 1974; Victor, 1986; 1987; Choat and Axe, 1996; Hart and Russ, 1996; Sponaugle and Cowen, 1997; Choat and Robertson, 2002; Robertson *et al.,* 2005; Choat *et al.*, 2009). The evolution of life history characteristics can be explained from a Darwinian perspective, whereby organisms adapt to their surrounding environments (Fisher, 1930; Charnov, 1982; Conover *et al.*, 2005). Coral reefs are extremely heterogeneous environments and intra- and inter-specific trait variation in coral-reef fishes can occur within habitats on the same reef, as well as across regional or biogeographic scales (Choat and Robertson, 2002; Gust *et al.*, 2002; Taylor *et al.*, 2018). Therefore, understanding the inherent age-based demographic plasticity of a species to differing environments is critical to properly assess species vulnerability to fishery exploitation and habitat loss.

1.3 Demographic Trade-offs in Variable Environments

All organisms have limited amounts of energy that must be allocated to different body functions (Fisher, 1930; Charnov, 1982; Brown *et al.*, 2018). For example, provisioning more energy towards reproduction takes energy away from somatic growth, and vice versa. In order to persist, organisms exposed to environmental variability or intense selective regimes are forced to adapt their pattern of energy allocation to new conditions through changes in behaviour (e.g., change in distributions), phenotypic plasticity, and/or ongoing evolution (Hoffmann and Sgro, 2011; Price *et al.*, 2011; Audzijonyte *et al.,* 2013). These adaptive responses are strongly manifested through changes in growth and reproduction, or life-histories. The relative importance of demographic plasticity, genetic inheritance, and the respective drivers of life history variation in teleosts, have been intensely debated (e.g., Olsen *et al.*, 2004; Kraak, 2007; Rogers *et al.*, 2011; Baudron *et al.*, 2014). Central to this debate is the fact that genetic and phenotypic evolution of life history traits are not discrete and therefore evaluating the relative importance of each component remains difficult (Lacey, 1998; Munday *et al.*, 2013; Todd *et al.*, 2016).

The evolutionary potential of populations can be assessed in several ways. Genetic approaches often focus on a small number of laboratory-controlled populations in a highly simplified artificial environment and/or focus on a single mutation which can have many phenotypic effects. Because of this, studies performed in aquaria can partition the relative strength of genetic selection and phenotypic plasticity on reef fishes but results of these studies are difficult to extrapolate to wild populations that are subject to the simultaneous influence of a number of dynamic factors (Stearns, 1992; Roff, 1993; Flatt and Heyland, 2011). Conversely, field-based approaches involve documenting phenotypic trait variation across spatial scales ranging from hundreds of meters to thousands of kilometres, encompassing the combined effects of genetic selection and demographic plasticity (e.g., Choat and Robertson, 2002). Because realised life-histories depend on both genetic inheritance and phenotypic plasticity, studies of wild populations more accurately reflect life history trade-offs within and among species. But, disentangling the strength of genetic evolution from phenotypic plasticity, and the respective drivers of life history variation in wild populations, is notoriously difficult (Gienapp *et al.*, 2008; Hansen *et al.*, 2012). While understanding mechanistically life history variation within and among taxa remains difficult, demographic variation has important implications for marine ecosystem management (Audzijonyte *et al.*, 2016).

Some of the most rapid life history responses have been documented for species subject to fishery exploitation (Jørgensen *et al.*, 2007; Audzijonyte *et al.*, 2013). When fishers or fishing gears target larger individuals disproportionately it often initiates changes to local population size and age structure (Ricker, 1981; Hutchings, 1996). Consequently, fishery harvest may favour genotypes that mature rapidly at small body-sizes or may cause phenotypic plasticity alone (Jennings *et al.*, 1999; Law, 2000; Hutchings and Fraser, 2008). Thus, in addition to describing the evolutionary history of a species, temporal and spatial monitoring of life histories can help to elucidate the effects of fishing on populations and determine the spatial scale at which fishery exploitation affects life histories (Jennings *et al.*, 1998; Alonzo and Mangel, 2004 ; Munday *et al.*, 2008). For example, studies across gradients of latitude often report that life history traits respond to differences in water temperature (Atkinson, 1994; Robertson *et al.*, 2005; Trip *et al.*, 2008), while on smaller spatial scales, fishing, reef size, and the degree of social control in the local population have all been shown to play important roles in driving demographic traits (Warner *et al.*, 1975; Warner and Hoffman, 1980a; Gust, 2004; Taylor *et al.*, 2014b). However, the relative importance of growth, reproduction, and survival in determining fitness will differ among and within species across a range of environments (Brown *et al.*, 2018). As such, identifying the best suite of traits that determine organism fitness across various environments remains an important empirical challenge (Laughlin *et al.*, 2020).

As evidenced by the persistence of thousands of reef fish species that vary widely in body-size and form across diverse environments, species will respond differently to environmental variation across space and time. Life history theories were developed to understand trade-offs arising from energetic, physiological, developmental, or genetic constraints across species or taxa (Stearns, 1992; Roff, 1993). Classical life history theory, which assumes that natural selection selects for the most optimal group of demographic traits (i.e., optimality theory), has been used extensively to describe intra- and interspecific variation in growth, survival, and reproduction (Stearns, 1992; Roff, 1993). The successful application of classical life history theory across taxa suggested that age and size specific impacts on mortality and reproduction were more important than often overlooked factors, such as genetics, explicit population dynamics, and frequency dependence (Reznick *et al.*, 1990; Stearns, 2000). Yet, when studies began reporting that individuals within heavily exploited fish stocks were maturing earlier at smaller sizes (Pauly, 1979; Ricker, 1981), fisheries scientists were motivated to proceed toward more accurate and complex life history theories which included effects of natural genetic selection (Stearns, 2000). This began a paradigm shift, from the traditional view that evolution unfolded too slowly to be observed in real time, to the incorporation of ongoing evolution into life history studies (Reznick *et al.*, 2019). Indeed, data are accumulating which show that natural populations of reef fish generally have considerable genetic variation in life-history traits, and some species can respond quickly to changing environments and mortality regimes via changes in behaviour, phenotypic plasticity, and/or ongoing evolution (Hoffmann and Sgro, 2011; Price *et al.*, 2011; Audzijonyte *et al.*, 2013). Therefore, to understand the demographic trade-offs evident in natural reef fish populations, hierarchical sampling designs that incorporate both habitat and latitudinal environmental variation, in addition to anthropogenic stressors (e.g., fishing pressure), are required (Taylor *et al.*, 2014b). Accounting for these trade-offs across various spatial scales will have significant impacts on the outcomes of models aiming to predict population level consequences of life-history changes and concomitantly the effective management of reef fish populations in the face of increasing global fishing pressure and climate change.

Studies of life history traits in reef fishes have long focused on the family Labridae, which are one of the most abundant, specious, and widely distributed families of fishes on coral reefs (Choat, 1969; Choat and Robertson, 1975; Dipper and Pullin, 1979; Jones, 1980; Charnov, 1982; Warner, 1984). High inter-specific variability of life history traits has enabled labrids to exploit a broad range of environmental conditions, and as such labrids are highly suitable study species for determining the drivers of population dynamics. Furthermore, diverse mating systems and complex sexual ontogenies have evolved many times within the Labridae, allowing the drivers of gonochorism, both forms of protogyny (monandry and diandry), bisexuality, and multidirectional sex change to be investigated both temporally and spatially (Robertson and Choat, 1974; Todd *et al.*, 2016; Hodge *et al.*, 2020). Large-bodied labrids are also increasingly important fishery targets throughout the Central and Eastern Indo-pacific (Dalzell *et al.*, 1996; Houk *et al.*, 2012), yet we know little regarding effects of fishing on life history variation. To date, a disproportionate amount of life history data on tropical labrids has been obtained for parrotfishes and small-bodied wrasses (Choat and Robertson, 1975; Warner *et al.*, 1975; Robertson and Warner, 1978; Warner and Robertson, 1978; Warner and Hoffman, 1980a; Warner, 1982; Choat *et al.*, 1996; Sponaugle and Cowen, 1997; Ackerman, 2004; Choat *et al.*, 2006; Hamilton *et al.*, 2008; Taylor *et al.*, 2018). Spatial sampling of demographic variation in large-bodied tropical wrasses has been comparatively limited, despite the perceived vulnerability of these fish to fishing (Fairclough, 2005; Choat *et al.*, 2006; Morton *et al.*, 2008; Caselle *et al.*, 2011). As such, it is unclear whether demographic patterns identified in large-bodied parrotfishes can be applied to large-bodied wrasses that have different ecological characteristics, evolutionary histories, and rates of evolutionary diversification.

1.4 Aims of Thesis

This thesis was designed to investigate the relative influence of environmental variation and fishing pressure in driving the ecology and demography of tropical wrasses. This included the analysis of a long term (12 year), spatially extensive (≈ 700 km) 'natural experiment' on the Great Barrier Reef (GBR), Australia in which the responses of 11 wrasse taxa to acute environmental disturbance events, predator density, and no-take marine reserve (NTMR) protection were quantified. In addition, multiscale age-based demographic comparisons of growth, longevity, mortality, body condition, and the timing of maturity and sex change from fishery targeted large-bodied wrasses *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus* and *Oxycheilinus digramma* were made between populations on heavily fished Philippine coral reefs and multiple unfished populations on the GBR.

Specific objectives were to:

1. Quantify the effects of benthic habitat change, environmental disturbance events, predator density, and long-term no-take marine reserve (NTMR) protection on the density of 11 tropical wrasse taxa over a significant temporal and spatial scale (Chapter 2).
2. Determine the relative effects of NTMR protection, predator density, and multiple environmental disturbance events on biomass of juvenile and adult *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* by using detailed reproductive data to separate sexually immature juveniles from mature adults (Chapter 3).
3. Determine pathways of sexual development and reproductive ontogeny in *Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus,* and *Oxycheilinus digramma* between the central GBR, Australia and the central Philippines, a geographic region spanning 30° of latitude, covering gradients of temperature, geography, and human activity (Chapter 4)
4. Partition the relative effects on environmental variation and fishing pressure on the age-based demography of four Indo-Pacific fishery targeted, large-bodied wrasses (*Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma)* in a multiscale analysis spanning 30 degrees of latitude, between multiple unfished Australian wrasse populations and fished populations of the Philippines (Chapter 5).

Chapter 2: Responses of Coral Reef Wrasse Assemblages to Disturbance and Marine Reserve Protection on the Great Barrier Reef

Lowe JR, Williamson DH, Ceccarelli DM, Evans RD & Russ GR (2019) Responses of coral reef wrasse assemblages to disturbance and marine reserve protection on the Great Barrier Reef. *Marine Biology*. 166, 119. doi:10.1007/s00227-019-3566-5

2.1 Abstract

Coral reefs are periodically impacted by disturbance events that reduce live coral cover and habitat complexity, with concomitant effects on fish assemblage structure. While the density of some fish species may increase following coral loss, most species decline. Determining which species are ‘winners’ and ‘losers’ following disturbances is fundamental to inform projections of future reef community structure, biodiversity, and productivity. Here I analyse a long-term (2006-2018), spatially extensive (≈ 700 km) ‘natural experiment’ in which the responses of 11 wrasse taxa to acute disturbance events and no-take marine reserve (NTMR) protection were quantified on fringing coral reefs in the Palm (18°34’ S, 146°29’ E), Whitsunday (20°08’ S, 148°56’ E), and Keppel (23°10' S, 150°57' E) Island groups, Great Barrier Reef, Australia. The responses of wrasse densities to benthic habitat change were taxa-specific and temporally consistent. Disturbance-mediated reductions in live hard coral cover and/or habitat complexity resulted in density declines for *Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus, Labroides* spp.*, Oxycheilinus digramma,* and *Thalassoma* spp. Conversely, *Halichoeres* spp. densities correlated positively with increased relative cover of sand and rubble, while *Stethojulis* spp.*, Anampses* spp.*, Epibulus insidiator,* and *Bodianus* spp. displayed variable responses to habitat changes. No wrasses exhibited an NTMR effect and predator density, irrespective of NTMR status, only influenced five taxa across all island groups. The lack of NTMR effects and variable top-down predator effects, suggest that taxa-specific benthic habitat associations were the predominant drivers of wrasse densities on inshore GBR reefs.

2.2 Introduction

Environmental disturbances such as coral bleaching, cyclones, floods, and crown of thorn starfish (COTS) outbreaks on coral reefs periodically result in reductions of live hard coral cover and habitat complexity at local to regional scales (Hoegh-Guldberg *et al.*, 2007; De'ath *et al.*, 2012; Hughes *et al.*, 2018a). Since the majority of coral reef fishes have a positive association with either live hard coral cover or the structural complexity of coral reefs, reef fish densities are often negatively affected by environmental disturbances that cause coral loss (Wilson *et al.*, 2006; Pratchett *et al.*, 2011; Coker *et al.*, 2014). For example, cumulative disturbance events and chronic pressures on Caribbean coral reefs have resulted in shifts from live coral to macroalgal-dominated reefs with a simultaneous decline of reef fish populations (Jackson *et al.*, 2001; Hughes *et al.*, 2013). Conversely, some species of reef fishes appear to respond positively to benthic changes common after environmental disturbances, such as increasing cover of sand (McCormick 1995; Russ *et al.*, 2015a), rubble (Russ *et al.*, 2015a, b, 2017), hard dead substrate (Russ *et al.*, 2015a, b), dead coral skeletons (Pratchett *et al.*, 2008; Wilson *et al.*, 2010a), turf algae (Williams and Polunin 2001), macroalgae (Wilson *et al.*, 2010a), and detritus (Wilson *et al.*, 2003).

Reef fishes that are not directly dependent on live coral for food or shelter can exhibit short-term increases in density following disturbances (Wilson *et al.*, 2006; Russ *et al.*, 2015a, b, 2017), but such effects may be region-specific and highly influenced by the nature of the disturbance event, post-disturbance habitat structure, and prey availability. Disturbances such as coral bleaching, sedimentation, and outbreaks of coral predators (e.g., COTS), generally have lower short-term impacts on reef habitat complexity and thus effects on reef fish assemblages may be less severe or temporally lagged (Graham *et al.*, 2007; Wilson *et al.*, 2009; Emslie *et al.*, 2014). Changes to benthic and fish assemblages can persist for years to decades depending upon the ecosystem, site history, existing fish assemblage structure, the severity of disturbance events, and ecological processes such as competition, mortality, recruitment, immigration, and emigration (Cheal *et al.*, 2007; Graham *et al.*, 2007; Emslie *et al.*, 2014). Recovery to pre-disturbance states may also take decades (Halford *et al.*, 2004; Berumen and Pratchett 2006; Babcock *et al.*, 2010), and few studies have documented the impact of multiple disturbance events and long-term post-disturbance recovery of coral and fish assemblages (Babcock *et al.*, 2010; Russ *et al.*, 2015c).

Australia’s Great Barrier Reef (GBR) has been affected sixty-six times by major environmental disturbances in the past few decades (Emslie *et al.*, 2017), recently losing an estimated 29% of live shallow water hard corals due to bleaching-related mortality (GBRMPA 2017; Hughes *et al.*, 2018b). While several studies have addressed the effects of disturbance on the dynamics of coral reef benthic and fish assemblages in the GBR no-take marine reserve (NTMR) network, the majority of these studies have focused on fishery-target species (Miller *et al.*, 2012; Emslie *et al.*, 2014; Williamson *et al.*, 2014). However, the degree to which environmental disturbances and long-term NTMR protection affect lightly-targeted and non-target species, such as tropical wrasses, remains an open question (Emslie *et al.*, 2015). As the frequency of severe disturbance events increases with ongoing atmospheric and ocean warming, identifying which fish species are ‘winners’ and which are ‘losers’ is important for informing current and future management strategies for coral reef ecosystems.

In response to increasing human impacts and increased frequency of severe climatic disturbances, no-take marine reserve (NTMR) networks are now widely advocated for coral reef conservation and fisheries management (Jackson *et al.*, 2001; Graham *et al.*, 2011a). Evidence demonstrates that effective NTMR protection can have positive effects on the density, biomass, body-size, fecundity, and diversity of fishery-targeted species within reserve boundaries (Lester *et al.*, 2009; Molloy *et al.*, 2009; Edgar *et al.*, 2014). NTMRs can also supplement surrounding fished stocks via larval export and recruitment subsidies (Harrison *et al.*, 2012; Williamson *et al.*, 2016; Abesamis *et al.*, 2017), and adult spill-over (Abesamis and Russ 2005). In contrast, the effects of NTMRs on lightly-targeted and non-target reef fish species are more variable (Lester *et al.*, 2009; Edgar *et al.*, 2014) and remain to be fully understood (Molloy *et al.*, 2009). While non-target reef fish species may not directly benefit from decreased fishing pressure within NTMRs, they may respond to changes in benthic community structure (Babcock *et al.*, 2010; McCook *et al.*, 2010; Miller *et al.*, 2012), or the relative abundance of other fish taxa (e.g., predators or prey) within reserves (Graham *et al.*, 2003; Wen *et al.*, 2012; Boaden and Kingsford 2015). One previous study partitioned the effects of benthic habitat and NTMR protection on the density of wrasses on Philippine coral reefs and found no direct NTMR effect, but a strong effect of changes in benthic habitat due to environmental disturbances inside and outside NTMRs (Russ *et al.*, 2017). A similar result is expected for wrasses on the GBR due to the light fishing pressure on large-bodied wrasses (i.e., *Hemigymnus melapterus* and *Cheilinus fasciatus*). Yet, given that small-bodied wrasses are common prey items of predatory fishes (Wen *et al.*, 2016), their densities may be affected by secondary NTMR effects such as higher densities of predators within NTMRs (Graham *et al.*, 2003; Evans and Russ 2004; Williamson *et al.*, 2004). For example, NTMR reefs in the Palm and Whitsunday Islands of the GBR can support 3 – 4 times higher biomass of coral trout (*Plectropomus leopardus*) than fished reefs, and reduced densities of some prey species (Graham *et al.*, 2003). Reserve effects on fish communities can take years to accrue and it is important to partition the effects of predatory fishes and benthic habitat on non-target fish species over extended time periods (Babcock *et al.*, 2010; Miller and Russ, 2014).

To date, many studies that have attempted to partition the effects of benthic habitat changes and fishing pressure on tropical wrasse assemblages have been temporally or spatially limited and lack taxonomic resolution (McClanahan *et al.*, 2002; Graham *et al.*, 2007; Sandin *et al.*, 2008; but see Russ *et al.*, 2017; Emslie *et al.*, 2017). Consequently, wrasses have often been reported as habitat generalists that are largely de-coupled from benthic assemblages (Green 1996; Fulton and Bellwood 2002; Kramer *et al.*, 2016). However, recent decadal-scale and species-specific partitioning of NTMR and benthic habitat effects on tropical wrasses has revealed strong effects of certain benthic habitats on the density and assemblage structure of wrasse populations on Philippine (Russ *et al.*, 2017) and GBR reefs (Emslie *et al.*, 2017). There remains a need to partition the effects of benthic habitat change and NTMR protection at reefal scales on the GBR, particularly for inshore coral reefs where anthropogenic stressors are greatest (Williamson *et al.*, 2014).

Here I employ a multispecies approach to better understand how long-term NTMR protection and changes to benthic habitat affect the density of 11 tropical wrasse taxa at three inshore island groups of the GBR; the Palm, Whitsunday, and Keppel Island groups. Specifically, I aim to address four questions:

(1) What are the major benthic drivers of the density of wrasses on inshore GBR reefs?
(2) How have severe disturbance events affected the density of wrasses on inshore reefs?
(3) Does the density of wrasses or taxa-specific benthic drivers vary regionally among island groups?
(4) What are the effects of long-term NTMR protection and predatory fish density on wrasse assemblages?

2.3 Materials and Methods

2.3.1 Study Area, Marine Park Zoning, and Environmental Disturbance History

Wrasse densities and benthic cover were surveyed biennially from 2006 to 2018 at ninety-three sites on fringing coral reefs in the Palm (30 sites), Whitsunday (41 sites), and Keppel (22 sites) Island groups, Great Barrier Reef Marine Park (GBRMP) (Fig. 2.1). At each island group monitoring sites were approximately distributed evenly among NTMR and fished reefs. No-take marine reserves were first implemented across 5% of the Great Barrier Reef Marine Park (GBRMP) in 1987. In 2004, the GBRMP was rezoned to enhance biodiversity protection and ecosystem resilience, and the NTMR network was expanded to protect approximately 33% of the GBRMP (Fernandes *et al.*, 2005). At all three island groups, long-term monitoring sites are positioned in both ‘old’ (protected since 1987) and ‘new’ (protected since 2004) NTMRs, as well as adjacent areas that have remained open to fishing (General Use, Habitat Protection and Conservation Park zones) (Fig. 2.1).

The Palm Island group (18°34’ S, 146°29’ E), Whitsunday Island group (20°08’ S, 148°56’ E) and Keppel Island group (23°10' S, 150°57' E) are located within 30km of the Queensland coastline in the central and southern GBRMP regions (Fig. 2.1). Several disturbance events that varied in severity damaged fringing reefs of all three island groups during the study period (2006 – 2018). Specific effects of disturbance events on benthic and fish assemblages of each island group are provided in the Results.

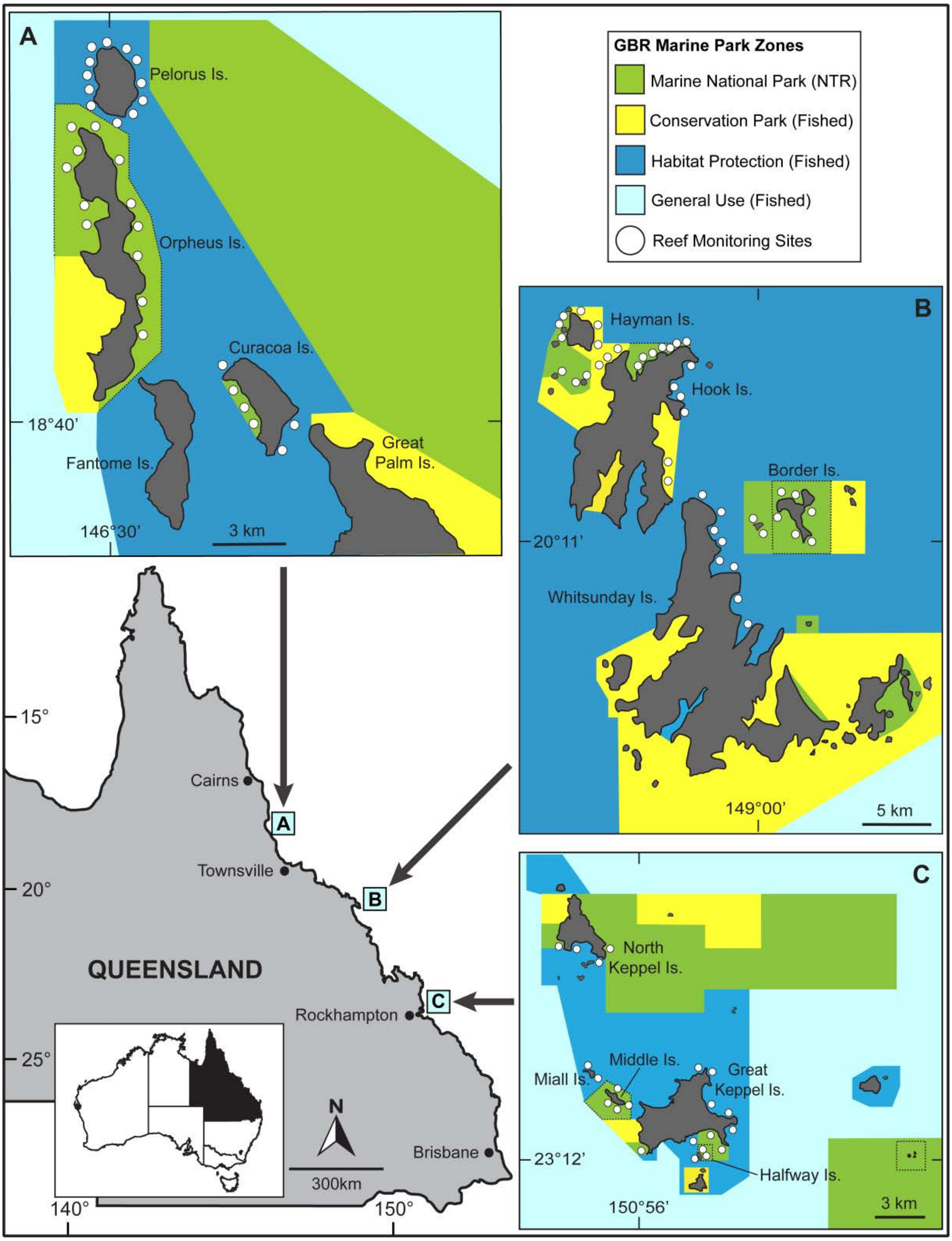


Figure 2. 1: Map of Queensland, Australia, and inset maps of the Palm (A), Whitsunday (B), and Keppel (C) Island groups within the Great Barrier Reef Marine Park. Inset maps illustrate the approximate location of long-term coral reef monitoring sites (white markers) and GBRMP zoning. No-take marine reserves (NTMRs) are shaded green. All other zones are open to fishing. ‘Old’ (protected since 1987) NTMRs have black, dashed borders. ‘New’ (protected since 2004) NTMRs have no border.

2.3.2 Study Taxa

Tropical wrasses (F: Labridae) are a diverse, conspicuous family of fishes that are common on coral reefs (Kuiter 2002; Westneat and Alvaro 2005). Species investigated here are major components of inshore wrasse assemblages of the GBR. In order of increasing maximum total body length (TL), they are: *Labroides* spp., *Stethojulis* spp., *Halichoeres* spp., *Thalassoma* spp., *Bodianus* spp., *Oxycheilinus digramma*, *Epibulus insidiator*, *Cheilinus fasciatus*, *Anampses* spp., *Hemigymnus fasciatus* and *H. melapterus.* Genera and species were chosen based on abundance at study sites and ecological role (Table 2.1).

Table 2. 1: Characteristics of study taxa on inshore GBR reefs. Ecological role and primary dietary components derived from Kramer *et al.*, (2015); (2016), Kuiter (2002), Westneat (1991; 1994) and Wainwright *et al.*, (2004). Maximum total body-length derived from Randall *et al.*, (1998). Macro-crustacea are defined as >3mm length.

Taxa	**Species most common on inshore GBR reefs**	**Maximum total body-length**	**Ecological role**	**Primary dietary components**
Labroides spp.	*L. bicolor* *L. dimidiatus*	14cm	cleaner wrasse	ectoparasites of other fishes (i.e., gnathiids), fish mucous.
Stethojulis spp.	*S. bandanensis* *S. strigiventer*	14cm	micro-invertivore	micro-crustacea, primarily Amphipoda.
Halichoeres spp.	*H. hortulanus* *H. melanurus*	20cm	micro-invertivore	micro-crustacea, e.g., Harpacticoida.
Thalassoma spp.	*T. hardwicke* *T. lunare*	25cm	invertivore/ piscivore	micro and macro-crustacea, fish eggs, small fish.
Bodianus spp.	*B. axillaris* *B. mesothorax*	20cm	invertivore	molluscs, macro-crustacea (primarily Brachyura).
Oxycheilinus digramma		30cm	invertivore/ piscivore	molluscs, macro-crustacea (primarily Brachyura), small fish.
Epibulus insidiator		35cm	invertivore/ piscivore	macro-crustacea (primarily Brachyura), small fish.
Anampses spp.	*A. caeruleopunctatus* *A. geographicus* *A. melanurus*	35cm	micro-invertivore	micro-crustacea (Amphipoda & Harpacticoida), small invertebrates.
Cheilinus fasciatus		35cm	invertivore	macro-crustacea (primarily Brachyura), molluscs.
Hemigymnus fasciatus		45cm	invertivore	micro and macro-crustacea, molluscs, polychaete worms, brittle stars.
Hemigymnus melapterus		50cm	invertivore	micro and macro-crustacea, molluscs, polychaete worms, brittle stars.

2.3.3 Surveys of Benthic and Wrasse Assemblages

Underwater visual censuses (UVC) were conducted biennially between 2006 and 2018. Five replicate 50m * 6m (300 m^2) transects were conducted on reef slopes (4–12m in depth) at each of the 93 long-term monitoring sites in the Palm, Whitsunday, and Keppel Island groups. Two observers on scuba counted individuals of approximately 190 species of coral reef fishes from 15 families, including Labridae, on each transect (Williamson *et al.*, 2014). A third observer followed the two fish observers, deploying the transect tape and recording benthic composition at 1m intervals using a standard point intercept survey method. At each interval the observer classified benthic biota into the following categories: morphology of live and dead corals (including branching, plate, digitate, massive, foliose), soft corals, solitary corals, sponges, clams (*Tridacna* spp.), other invertebrates (e.g., ascidians, anemones), macroalgae, pavement (dead coral substratum covered in epilithic algal matrix), rock, rubble, and sand. An index of structural complexity was also obtained at each site by ranking (1-5) the angle of the reef slope and multiplying it by the average rugosity (also ranked 1-5) at each ten-meter section of each transect (Williamson *et al.*, 2014).

2.3.4 Data Analyses

Boosted regression trees (BRTs) were used to determine taxa-specific benthic drivers of wrasse density on reefs at each island group. Once major benthic drivers from each taxa-specific BRT were determined, the relative contribution of each benthic variate was averaged across species at each island group to indicate the major drivers of wrasse assemblages at the Palm, Whitsunday, and Keppel island groups, respectively. Benthic predictors that contributed more than 5% on average were deemed ‘important’ in driving wrasse density and subsequently used in Generalised Additive Mixed Models (GAMMs) to determine whether NTMR protection, benthic habitat, predator density or interactions between these variables, were most important in determining long-term wrasse densities at each island group. BRTs are a machine-learning technique that can handle extreme outliers, missing values, nonlinear relationships, and account for synergistic effects between predictor variables (Friedman 2001; Elith *et al.*, 2008). BRTs compute many (often hundreds to thousands) simple decision trees where each successive tree is built from the prediction residuals of the previous decision tree (Elith *et al.*, 2008). These decision trees are then combined via the technique of boosting to produce an aggregate model with high predictive performance (Friedman 2001; Elith *et al.*, 2008). BRTs are widely acknowledged as excellent predictors of complex relationships and thus are commonly used to assess the relative influence of different benthic components on species richness and density of reef fish (Parravicini *et al.*, 2013; Russ *et al.*, 2015a).

Benthic predictor variables included in BRTs included live and dead growth morphologies of hard corals (branching, massive, plating, foliose, digitate, encrusting), soft corals, sand, rubble, pavement, a site exposure rating to prevailing wind and waves (exposed, semi-exposed or sheltered), and an index of structural complexity (rugosity * slope). For ecological reasons separate BRTs were performed for each species at each island group (Palm, Whitsunday, and Keppel). While BRTs are considered fairly robust to collinearity, collinearity was assessed using Pearson correlation coefficients (Appendix 2.1). No variables returned a correlation coefficient above the recommended cut-off of $|r| > 0.7$ and thus all predictor variables were retained for analysis (Dormann *et al.*, 2012). All BRTs were fitted in R using the 'gbm' package (R Development Core Team, 2016; Ridgeway, 2006). BRTs require the specification of four main parameters; learning rate (*lr*) - the contribution of each tree to the final model; bag fraction (*bf*) - the proportion of data used at each step; tree complexity (*tc*) - the maximum number of nodes in each fitted tree, and number of trees (*nt*) - the number of boosting iterations (number of trees). To calibrate the optimal parameters for each BRT, combinations of *bf* (0.5), *tc* (1, 2, 5) , *lr (0.005, 0.001),* and *nt* (every 50 trees from 1000-3000 trees) were tested using the '*caret:train'* function in R (Kuhn 2008). Testing values for *lr, tc,* and *nt* were derived from Elith *et al.*, (2008). Top performing BRT parameter combinations were selected using repeated 10-fold cross-validation (CV) which was repeated 5 times to account for stochasticity across BRT models. For each combination of parameters, the root-mean-square error (RMSE) and mean-absolute error (MAE) were calculated over samples that were held-out from 10-fold CV. Each set of optimal model parameters identified via this method were subsequently passed to the gbm package and one BRT per species, per island group was run (Appendix 2.2). To indicate where major changes to benthic substrata led to changes in wrasse density at a reefal-scale, the top benthic predictor identified for each species from BRTs was plotted with long-term wrasse density at each island group.

GAMMS employing a full-subset multiple regression approach were used to determine whether benthic habitat, NTMR protection, predator density, or interactions between these factors, best explained changes in inshore wrasse densities over time. Separate GAMMs, with a Poisson error distribution, were fitted for each wrasse species at each island group using code provided by Fisher *et al.*, (2018) and a call to the *gamm4* package in R

(Wood and Scheipl 2017; Fisher *et al.*, 2018). Global model predictor variables at each location included NTMR status (Fished, NTMR2004, or NTMR1987), time (duration of protection since NTMR implementation), predator density (combined density of selected Lutjanidae, Lethrinidae, and Epinephelidae; for predatory species included see Appendix 2.3), a site exposure rating to prevailing wind and waves (exposed, semi-exposed, or sheltered) and benthic habitat variables deemed important from BRTs. NTMR status, time, site exposure, benthic variables, and predator density were treated as fixed effects, while replicate transects nested within sites were treated as a random effect. Due to the complexity of the null model a maximum of three predictors were selected to be used in each of the final GAMMs. Model selection, based on the minimisation of Akaike Information Criterion corrected for small sample sizes (AICc), was performed inside the full-subset multiple regression function (Fisher *et al.*, 2018). The smallest AICc value identified the model with the greatest support, yet all GAMMs within ΔAICc ≤ 2 of the 'top model' (smallest AICc) were deemed 'important' because models within this threshold can have similar explanatory power (Burnham and Anderson, 2002)(Appendix 2.4). Variable importance scores from GAMMs were subsequently plotted into a heatmap (Fisher *et al.*, 2018) that represents the importance of predictor variables in determining the density of each species at each island group. In this heatmap blank squares represent benthic variates that did not appear in top models (ΔAICc ≤ 2). Variates that did appear in taxa-specific 'important' models are shown as columns and were colour coded according to summed AICc weights of all 'important' models for that species. NTMR protection was classified as important if there was a Time*Status interaction or a Predator density*Status interaction present in the top models (within ΔAICc ≤ 2) and there was an appropriate change in NTMR wrasse density relative to the fished control sites over time.

2.4 Results

2.4.1 Major Drivers of Wrasse Densities

A total of 26,393 individual wrasses were recorded at long-term reef monitoring sites in the Palm, Whitsunday, and Keppel Island groups between 2006 and 2018. All 11 taxa studied were recorded at all three island groups. However, *C. fasciatus*, *Bodianus* spp., *H. fasciatus*, and *O. digramma* were rare in the Keppel Islands, and thus these taxa were not included in subsequent analyses for this locality. The density of most wrasses was highest on Whitsunday reefs (Fig. 2.3, 2.4, 2.5), however *H. melapterus* and *Stethojulis* spp. were found at higher average densities on Keppel reefs (Fig. 2.5). At all island groups, BRTs and long-term density plots indicated consistent benthic drivers that resulted in clear density responses of most taxa (Table 2.2; Fig. 2.2, 2.3, 2.4, 2.5). Moreover, GAMMs confirmed that benthic habitat was consistently a more important driver of wrasse density than NTMR status or predator density (Fig. 2.6; Appendix 2.4).

BRTs indicated that structural complexity of the benthos (SCI) was the most consistent driver of wrasse density across island groups, with approximately 60% of wrasse taxa having SCI as one of their top two benthic predictors of density (Table 2.2). *Hemigymnus melapterus, H. fasciatus, Thalassoma* spp., *C. fasciatus,* and *Labroides* spp. all had positive relationships with SCI, while *Stethojulis* spp. had a negative relationship with SCI (Table 2.2; Appendix 2.2). Live branching coral (LBC) cover, which contributes to structural complexity, was a poor predictor of wrasse density at the Palm and Keppel island groups, influencing only *Thalassoma* spp. density strongly in the Keppels (Table 2.2). Conversely, in the Whitsundays, densities of *H. melapterus, H. fasciatus, C. fasciatus,* and *O. digramma* had positive relationships with cover of LBC (Table 2.2; Fig. 2.2, 2.3, 2.4, 2.5). When taxa-specific benthic drivers differed spatially, taxa often associated with similar substrata (Table 2.2; Appendix 2.2; Fig. 2.3, 2.4, 2.5). Wrasse density at each island group responded to both SCI and some island-group-specific benthic components (Table 2.2; Fig. 2.2). In the Palms, along with SCI, the cover of disturbed benthos (i.e., sand, pavement, and rubble) was either the top or secondary driver of density of all 11 wrasse taxa (Table 2.2). In the Whitsundays, BRTs showed that either LBC and/or SCI were the top two predictors for approximately 80% of taxa, and in the Keppels SCI and/or the cover of macroalgae (MA) were the top predictors of density for approximately 70% of taxa (Table 2.2).

BRTs indicated that the cover of live branching coral (LBC), rubble (RUB), and sand (SA) were also important predictors of wrasse density at all locations (Fig. 2.2). Conversely, the cover of dead massive corals (DMC), live plating corals (LPC), dead plating corals (DPC), sponges (SP), and rock (R) did not influence density of wrasses strongly at any island group (Fig. 2.2). Exposure of sites to prevailing wind and waves did not exhibit consistent relationships with wrasse density among taxa or locations (Table 2.2; Fig. 2.6). However, at the Palms, GAMMs indicated that site exposure was an important driver of density of wrasse populations for 9 of 11 taxa (Fig. 2.6). In the Palms, increased exposure to prevailing wind and waves increased density of *Anampses* spp. and *Bodianus* spp., while density of *Halichoeres* spp., *Labroides* spp., *C. fasciatus, H. melapterus,* and *Stethojulis* spp. was higher in semi-exposed and sheltered habitats (Fig. 2.6). At the Whitsunday and Keppel Islands, site exposure was less important in driving wrasse densities, and instead GAMMs identified various benthic habitats nested within NTMR zones as important drivers (Fig. 2.6; Appendix 2.4). Despite density responses of tropical wrasses to alternate benthic substrata nested within NTMRs, no taxa displayed an NTMR Status*Time interaction or a change in fish density over time consistent with an NTMR effect.

Table 2. 2: Relative influence (%) of most important taxa-specific predictor variables on wrasse density from boosted regression tree analyses.

	Palm Island Group				**Whitsunday Island Group**				**Keppel Island Group**			
	Top Predictor		2nd most important predictor		Top Predictor		2nd most important predictor		Top Predictor		2nd most important predictor	
Species	Variate	% relative influence (direction of relationship)	Variate	% relative influence (direction of relationship)	Variate	% relative influence (direction of relationship)	Variate	% relative influence (direction of relationship)	Variate	% relative influence (direction of relationship)	Variate	% relative influence (direction of relationship)
Anampses spp.	E	27.7 (v)	PAV	27 (-)	F	25.2 (+)	LBC	22.1 (+)	SA	16.4 (+)	DDC	16.4 (+)
Bodianus spp.	SCI	18.2 (+)	SA	13.7 (-)	E	16.4 (+)	SCI	15.4 (+)				
C. fasciatus	SCI	14.9 (+)	EX	12.8 (-)	SCI	14.9 (w)	LBC	12.8 (+)				
E. insidiator	SCI	19 (+)	SC	16.9 (+)	SC	11 (+)	SCI	10.6 (+)	F	14.3 (+)	LPC	9.6 (v)
H. fasciatus	SA	20.1 (-)	RUB	15.2 (-)	LBC	19.1 (+)	E	13.5 (+)				
H. melapterus	SCI	18 (+)	SA	13.6 (-)	LBC	20.3 (+)	RUB	20 (+)	SCI	13.9 (^)	MAC	11(-)
Halichoeres spp.	SA	23.7 (+)	SCI	12.7 (w)	SA	19.4 (+)	SCI	17.4 (-)	RUB	15.6 (+)	SCI	13.2 (-)
Labroides spp.	SC	11.6 (+)	SCI	11.3 (+)	SC	15.9 (+)	LMC	14.7 (w)	SCI	23.1 (+)	EX	9.6 (-)
O. digramma	SC	27 (+)	SCI	14.3 (+)	LBC	17.2 (+)	SCI	14.1 (-)				
Stethojulis spp.	PAV	14.9 (+)	LPC	13.4 (-)	MAC	32 (w)	EX	14.1 (+)	MAC	34 (+)	SCI	17.8 (-)
Thalassoma spp.	SCI	20.7 (+)	RUB	14.8 (-)	SCI	13.4 (+)	PAV	10.8 (w)	LBC	15.9 (^)	MAC	13.7 (v)

LBC = live branching corals, DBC = dead branching corals, LMC = live massive corals, DDC = dead digitate corals, LPC = live plating corals, E = encrusting corals, F = foliose corals, SC = soft corals, RUB = rubble, SA = sand, PAV = pavement, MAC = macroalgae, SCI = structural complexity index, EX = site exposure to prevailing wind & waves. Direction of relationship between response and predictor variables are indicated in parenthesis: (+) = increasing, (-) = decreasing, (^) = increase followed by decline, (v) = decline followed by increase, (w) = multiple increases and declines. For site exposure, direction of trend is from to “sheltered” to “exposed” (i.e., sheltered, semi-exposed, exposed). Grey squares represent rare taxa excluded from analysis.

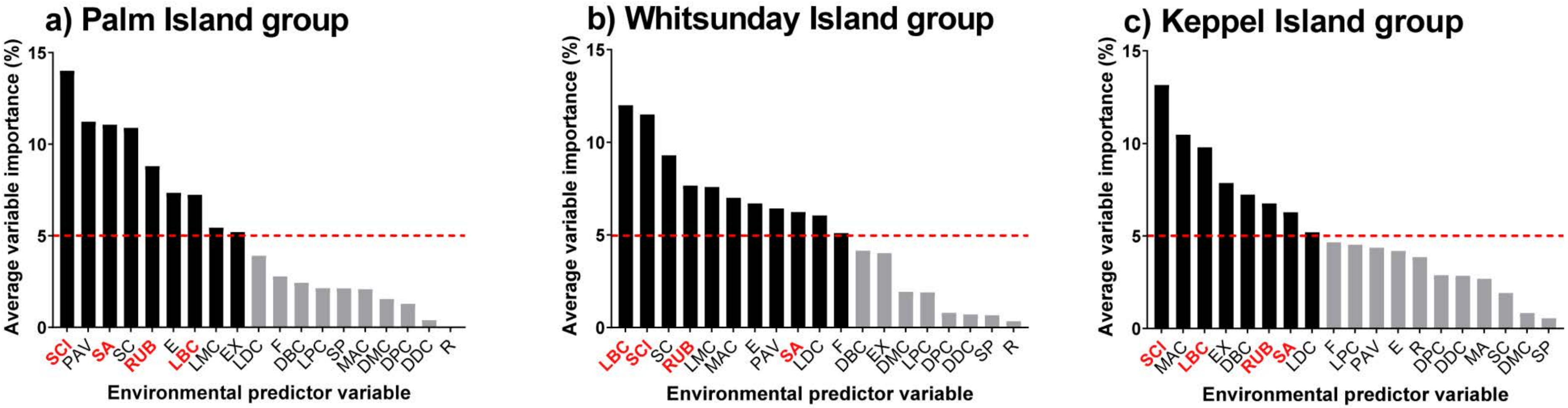


Figure 2. 2: BRT-derived average relative importance of benthic drivers as predictors of long-term wrasse density at the Palm (a), Whitsunday (b), and Keppel (c) Islands. LBC = live branching corals, DBC = dead branching corals, LMC = live massive corals, DMC = dead massive corals, DDC = dead digitate corals, LDC = live digitate corals, LPC = live plating corals, DPC = dead plating corals, E = encrusting corals, F = foliose corals, SC = soft corals, RUB = rubble, SA = sand, PAV = pavement, R = rock, SP = sponges, MAC = macroalgae, SCI = structural complexity index, EX = site exposure to prevailing wind & waves. 5% importance cut-off indicated by dotted red line. Variables deemed important and subsequently included in GAMMs are shown in black. Four benthic variables that were consistently important drivers of wrasse density across island groups displayed in red.

2.4.2 Effects of Environmental Disturbances on Benthos

Fringing reefs in the Palm, Whitsunday and Keppel Islands experienced numerous disturbances that ranged in severity throughout the 11-year study period. Palm Islands reefs were affected by coral bleaching in 2002 and benthic communities were recovering when surveys of wrasse density began in 2007. In 2011, benthic communities of the Palm Islands were damaged significantly by cyclone Yasi, particularly north and east-facing exposed sites on Pelorus and Orpheus Islands, resulting in an approximate 50% decline in live hard coral cover and significant increases in the cover of sand, macroalgae and pavement between 2009 and 2012 (Fig. 2.3a). Removal of hard and soft corals by cyclone Yasi exposed the high rugosity reef-matrix at the Palm Islands monitoring sites, which consequently resulted in an initial increase but then decline of SCI post cyclone Yasi (Fig. 2.3a). Following cyclone Yasi, hard coral cover had partly recovered at impacted reefs at Pelorus and Orpheus Islands (Fig. 2.3a). In 2014, a flood plume that originated from cyclone Ita engulfed fringing reefs of the Palm Island group, however this flood plume had little detectable effect on coral assemblages at the monitoring sites, and live hard coral cover continued to increase reef-wide (Fig. 2.3a). A coral bleaching event in early 2016 (Hughes *et al.*, 2018b) had little discernible effect on benthic assemblages of the Palm Islands. Cover of live hard corals continued to increase on fringing reefs of the Palm Islands and a shift in benthic composition from pavement and macroalgal dominated substratum back to hard coral dominated reefs was evident (Fig. 2.3a). In 2017, the GBR was again affected by a severe and broad-scale coral bleaching event, including the Palm Islands (Hughes *et al.*, 2018c). While moderate mortality of *Pocillopora* spp. and some *Acropora* spp. colonies located in shallow reef crests were noted following this event, surveys undertaken in August of 2018 indicated a relative increase in live hard-coral cover of approximately 4% between 2016 and 2018. (Fig. 2.3a).

Despite cyclone Ului (category 5) crossing the Whitsunday Islands from the southeast in 2010, benthic assemblages on monitored Whitsunday reefs were not subject to any major disturbance events from 2007 to 2016 and maintained average live hard coral cover of approximately 42% during this period (Fig. 2.4a). The lack of impact on benthic assemblages from cyclone Ului was, presumably, due to the approach direction of this cyclone (the majority of monitoring sites were protected from prevailing winds) and its high tracking speed (only taking a few hours to cross the Whitsunday Island group). Whitsunday reefs bleached during the widespread bleaching event in early 2016 (Hughes *et al.*, 2018b), however, no coral mortality was subsequently recorded on monitored reef slopes in late 2016. In March 2017, severe (category 4) tropical cyclone Debbie crossed directly over the Whitsunday Islands from the northeast, causing major destruction of benthic communities and severe coral loss at the majority of monitoring sites (Fig. 2.4a). Hard coral cover declined sharply from approximately 42% in 2016 to 19% post-cyclone Debbie and the cover of dead substratum (sand, rubble, and pavement) increased from approximately 28% to 59% (Fig. 2.4a). Counterintuitively, SCI estimates continued to increase following-cyclone Debbie due to the removal of hard and soft corals which exposed a complex underlying reef matrix with numerous holes and crevices at monitoring sites (Fig. 2.4a). In early 2017, coral bleaching was reported in the Whitsunday Island group (Hughes *et al.*, 2018b), however little evidence of loss of live coral cover due to bleaching was recorded at monitoring sites in late 2017 (Fig. 2.4a). It is likely that any dead standing coral colonies that were killed during the 2017 coral bleaching were dislodged from the reefs during cyclone Debbie and converted to rubble. Thus, it is not possible to determine the true effects of the 2017 coral bleaching event on Whitsunday reefs from this dataset.

Reefs in the Keppel Islands were subjected to significant declines in live hard coral cover from 2006 to 2017, largely due to the impact of four major environmental disturbance events (Fig. 2.5a). In March 2006, a coral bleaching event caused by an extended period of elevated sea surface temperature resulted in a significant short-term reduction (reduction not evident in this study but see Williamson *et al.*, 2014) in live hard coral cover at the majority of reef monitoring sites (Fig. 2.5a). However, the cover of live hard coral had returned to pre-disturbance levels at most sites by 2009, due to remnant *Acropora* tissue regrowing over dead coral skeletons (Diaz-Pulido *et al.*, 2009). Successive major flood events of the nearby Fitzroy River during 2011 and 2013 caused flood plumes to engulf reefs in the Keppel Islands, reducing coral cover at almost all sites and resulting in severe coral-mortality at shallow, heavily exposed reefs (Jones and Berkelmans 2014; Williamson *et al.*, 2014) (Fig. 2.5a). These flood plumes caused live hard coral cover to decline from approximately 62% in 2009 to 26% in 2013 and the cover of macroalgae to increase, reaching a peak cover of approximately 48% in 2015 (Fig. 2.5a). Category 5 cyclone Marcia passed over the Keppel Islands in 2015, yet impact on benthic assemblages was restricted to several north-east facing sites which were directly exposed to the full force of cyclone-generated swells (Fig. 2.5a). Due to the spatial patchiness of the cyclone impacts, many sites remained undisturbed and live hard coral cover more than doubled from

2013 to 2015 across the Keppel Islands (Fig. 2.5a). In 2017 the Keppel Islands were again inundated by a Fitzroy River flood plume that originated from cyclone Debbie. Despite this, live-hard coral cover at monitored reefs continued to increase from 2015 to 2017, as did the relative cover of dead substratum (Fig. 2.5a).

2.4.3 Effects of Disturbance Events and Benthic Habitat Changes on Density of Wrasses

Changes in benthic habitat often resulted in consistent and clear changes in the density of most taxa of tropical wrasses (Fig. 2.3, 2.4, 2.5). Density of *H. melapterus*, *C. fasciatus* and *Thalassoma* spp. had positive relationships with SCI or LBC at the Palm, Whitsunday, and Keppel Islands (Appendix 2.2; Fig. 2.3b, d, e, 2.4b, d, e, 2.5b, c). *Hemigymnus fasciatus* also correlated positively with SCI and cover of LBC at the Palm and Whitsunday Island groups (Appendix 2.2; Fig. 2.4c), however, the cover of sand was a more prominent driver for this species at the Palm Island group (Fig. 2.3c).

Densities of *H. melapterus, Thalassoma* spp. and *C. fasciatus* increased at the Palm Islands from 2007 to 2012 as SCI increased, largely due to increased cover of LBC (Fig. 2.3b, d, e, h, i). Density of *H. melapterus* and *Thalassoma* spp. then declined from 2012 to 2016 as SCI decreased (Fig. 2.3b, d). Density of *C. fasciatus* had a similar downward trajectory to SCI over the same period, but remained stable for unknown reasons while SCI declined from 2012 to 2014 (Fig. 2.3e). In 2011 cyclone Yasi resulted in major declines in live hard coral cover on Palm Island group reefs and this led to varying degrees of density increase for *H. melapterus*, *Thalassoma* spp., and *C. fasciatus* (Fig. 2.3a, b, d, e). In contrast, the cyclone Ita flood plume event in 2014, and successive bleaching events in 2016 and 2017, had little effect on SCI or the density of *H. melapterus* and *C. fasciatus* (Fig. 2.3b, d). Density of *Thalassoma* spp. declined 2.5–fold from 2012 to 2014, presumably due to the impact of cyclone Yasi on SCI rather than due to the impact of Cyclone Ita runoff (Fig. 2.3d). Subsequent bleaching events in the Palm Islands in 2016 and 2017 did not affect density of *Thalassoma* spp. significantly (Fig. 2.3d). Positive relationships with SCI and negative relationships to site exposure (EX) were indicated in GAMMs as important predictors of density of *H. melapterus* and *C. fasciatus* (Fig. 6, Appendix 2.4). *Hemigymnus fasciatus* and *Thalassoma* spp. also had positive relationships with SCI at the Palm Islands and with the cover of LBC and SCI at the Whitsunday Islands, respectively (Table 2.2; Appendix 2.2; Fig. 2.4c, d). However, at the Palm Islands a negative relationship with sand (SA) was identified as a stronger driver of *H. fasciatus* density in BRTs and GAMMs (Table 2.2; Fig. 2.3c). Density of *H. fasciatus* increased at the Palm Islands from 2007 to 2009 as the cover of sand declined and SCI increased (Fig. 2.3c). From 2009-2012, density of *H. fasciatus* declined substantially as the cover of sand increased due to the impact of cyclone Yasi (Fig. 2.3c). From 2012 to 2014 the cover of sand declined and *H. fasciatus* densities increased before density declined in 2016, possibly due to the lagged increase in the cover of sand on reef slopes following cyclone Ita in 2014 (Fig. 2.3c). In 2018 *H. fasciatus* returned to a density of approximately 1 fish per 1000 m^2 as the cover of sand declined from over 15% to 10% (Fig. 2.3c).

In the Whitsunday Islands, the density of *Thalassoma* spp. increased from 2007 until 2012 as SCI increased and cover of LBC declined (Fig. 2.4d). Density of *Thalassoma* spp. declined until 2017 for unknown reasons, then increased in 2018, possibly due to disturbance-mediated increases in dead pavement (Table 2.2; Fig. 2.4d). Densities of *H. melapterus* and *H. fasciatus* in the Whitsunday Islands declined as cover of LBC declined between 2007 and 2009, then increased substantially in 2012, peaking at 4 fish 1000 m^{-2} and 2 fish 1000 m^{-2}, respectively (Fig. 2.4b, c). Densities of *H. melapterus* and *H. fasciatus* declined post-2012 as cover of LBC also declined (Fig. 2.4a, b, c). Density of *H. fasciatus* declined substantially from 2012-2018 (Fig. 2.4c), while the density of *H. melapterus* remained stable during this period, despite changes in the cover of LBC (Fig. 2.4b). The lack of a change in density of *H. melapterus* in the 2 years following cyclone Debbie may have been due to SCI remaining high (Table 2, Fig, 3b, 5b). Density of *C. fasciatus* in the Whitsunday Islands remained stable from 2007-2018, despite SCI continually increasing over the same period (Fig. 2.4e). Minor density responses of *C. fasciatus* were seen a year after cyclone Debbie, yet surveys in 2018 showed recovery to undisturbed densities (Fig. 2.4e).

In the Keppel Islands, *H. melapterus* correlated positively to SCI, while *Thalassoma* spp. correlated positively to the cover of LBC (Fig. 2.5b, c). Densities of *H. melapterus* and *Thalassoma* spp. increased substantially between 2006 and 2007, despite SCI only increasing marginally over the same period (Fig. 2.5b, c). Densities of *H. melapterus* and *Thalassoma* spp. then declined from 2007-2013, as did SCI and cover of LBC (Fig. 2.5b, c). Densities of *Thalassoma* increased from 2013 to 2017, as did the cover of LBC (Fig. 2.5c). *H. melapterus* densities remained stable from 2013-2015 despite increases in SCI, before increasing in density in 2017 (Fig. 2.5b). Positive relationships with SCI and live branching corals were detected in BRTs and GAMMs for density of *H. melapterus* and *Thalassoma* spp. in the Keppel Islands (Table 2.2; Fig. 2.5b, c; Appendix 2.2, 2.4).

Density of *Halichoeres* spp. was positively associated with dead substratum (i.e., sand (SA) and rubble (RUB)) (Table 2.2, Fig. 2.3g, 4g, 5d). The relationships between the cover of sand and density of *Halichoeres* spp.at the Palm and Whitsunday Islands are clear and consistent across 11-years (Table 2.2; Fig. 2.3g, 2.4g). In the Palm Islands, density of *Halichoeres* spp. had strong disturbance-mediated responses, particularly following cyclone Yasi in 2011, which resulted in more than double the cover of sand (increase of over 258%) and almost a 3-fold increase in density of *Halichoeres* spp. (nearly 290% increase) (Fig. 2.3g). Similarly, in the Whitsunday Islands, density of *Halichoeres* spp. correlated strongly with the cover of sand for 12 years (Fig. 2.4g). The density response of *Halichoeres* spp. to the impact of cyclone Debbie at the Whitsundays (Fig. 2.4g) was surprisingly weak compared to responses to cyclone Yasi in the Palm Island group (Fig. 2.3g), despite the cover of sand almost doubling from 2016 to 2017 in the Whitsundays (Fig. 2.4g). Positive relationships of density of *Halichoeres* spp.to cover of rubble (RUB) were clear in the Keppel Islands for 12 years (Fig. 2.5d). One minor deviation from this relationship was evident from 2006 to 2007, where *Halichoeres* spp. densities declined substantially despite the cover of rubble remaining stable over the same period (Fig. 2.5d). Successive river flood plume events in 2011 and 2013 resulted in a 2.5–fold decline in the cover of rubble and significant increases in the cover of macroalgae (Fig. 2.5a, d). Consequently, density of *Halichoeres* spp. declined 3-fold between 2011 and 2015 in the Keppels (Fig. 2.5d). Density of *Halichoeres* spp. displayed only minor change in density following a flood event in 2017 which substantially increased the cover of rubble and decreased macroalgal cover at long-term monitoring sites (Fig. 2.5a, d).

Density of *O. digramma* negatively correlated with the long-term (12 year) decline of cover of soft corals (SC) at the Palm Islands and to the long-term decline of cover of live branching corals (LBC) at the Whitsunday Islands (Table 2.2; Fig. 2.3f, 4f). *Oxycheilinus digramma* were rarely seen in the Keppel Islands. Similarly, density of *Labroides* spp. negatively correlated with the long-term (12 year) decline of cover of soft corals at the Palm and

Whitsunday Islands (Fig. 2.3j, 2.4j) and the long-term decline of SCI in the Keppel Islands (Fig. 2.5f).

Density of *Bodianus* spp., *E. insidiator*, *Anampses* spp. and *Stethojulis* spp. did not display consistent relationships with benthic habitat (Table 2.2; Fig. 2.3h-i, k-l, 2.4h-i, 2.4k-l, 2.5e, 2.5g-h). However, the density of *Bodianus* spp. and *E. insidiator* correlated positively with SCI at the Palm Islands for 12 years (Fig. 2.3h, i). Both *Bodianus* spp. and *E. insidiator* exhibited negative density responses to the impact of cyclone Yasi in 2011 despite an initial increase in SCI (Fig. 2.3h, i). Density of *E. insidiator* negatively correlated with the long-term (12 year) decline of cover of soft corals at the Whitsunday Islands and exhibited moderate negative density-responses to cyclone Debbie in 2017 which reduced soft coral cover at long-term monitoring sites (Fig. 2.4i). For *Anampses* spp. and *Stethojulis* spp., the importance of benthic components in driving density differed among island groups and was particularly weak for *Stethojulis* spp. (Table 2.2; Fig. 2.3k-l, 2.4k-l, 2.5g-h; Appendix 2.4). Density of *Anampses* spp. declined over the long-term as cover of encrusting coral at the Palm Islands (Fig. 2.3k) and foliose coral at the Whitsunday Islands (Fig. 2.4k) declined. BRTs indicated *Stethojulis* spp. had a positive, complex relationship with cover of macroalgae at the Whitsunday Islands and the Keppel Islands (Table 2.2), yet long-term density plots showed that this relationship was not consistent through time (Fig. 2.4l, 2.5j). *Stethojulis* spp. results at the Palm Island group should be interpreted cautiously due to the presence of the null model within 2 AICc of the lowest AIC score (Appendix 2.4). Environmental disturbances did not have clear effects on density of *Anampses* spp. and *Stethojulis* spp. (Fig. 2.3, 2.4, 2.5).

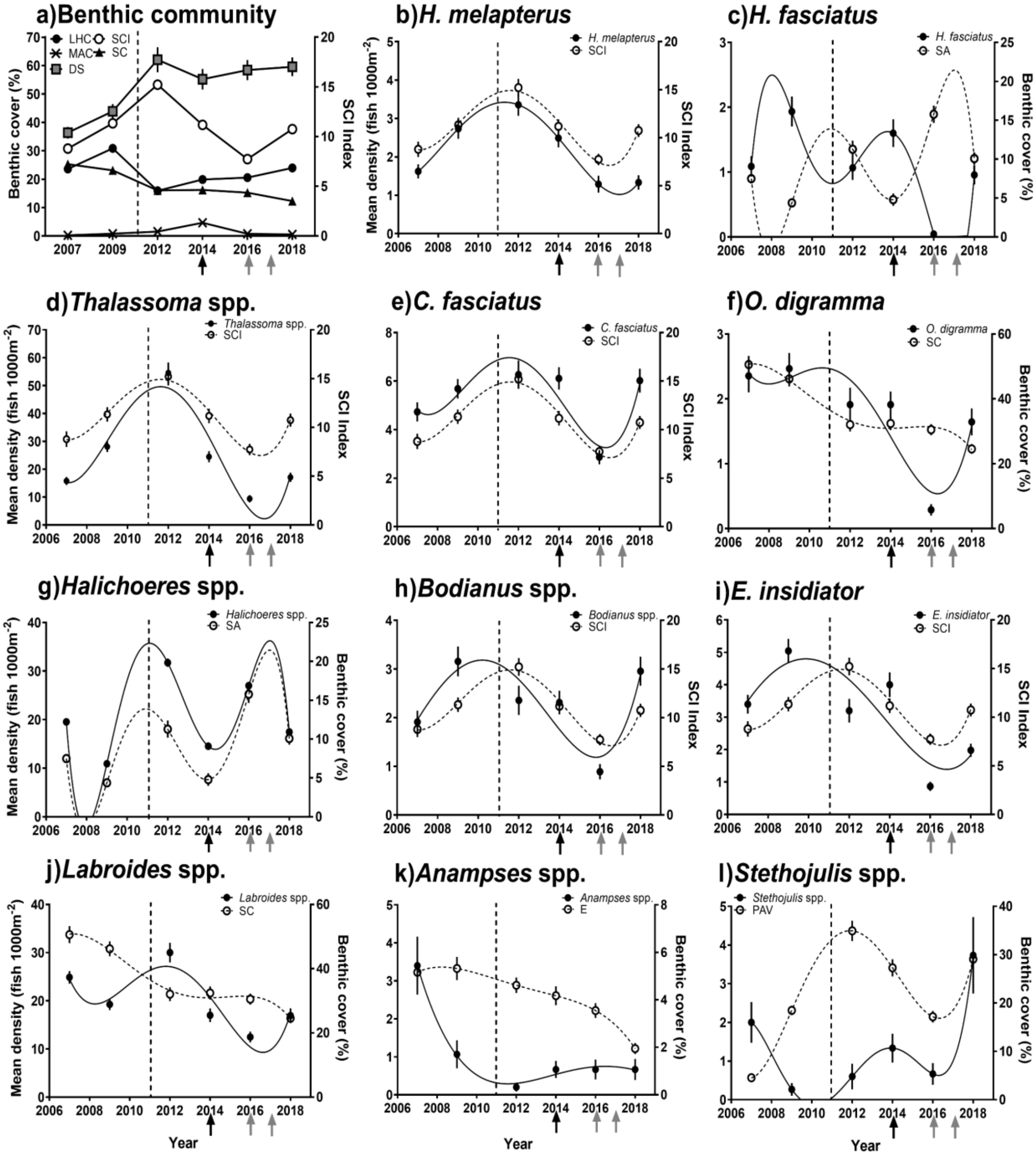


Figure 2. 3: Long-term temporal trends of (a) benthic cover and the density of (b) *H. melapterus*, (c) *H. fasciatus*, (d) *Thalassoma* spp., (e) *C. fasciatus*, (f) *O. digramma*, (g) *Halichoeres* spp., (h) *Bodianus* spp., (i) *E. insidiator*, (j) *Labroides* spp., (k) *Anampses* spp., (l) *Stethojulis* spp., and temporal trends in cover of their respective top benthic predictor identified from BRTs (Table 2.2) at the Palm Island group. LHC = live hard coral, DS = dead substratum (combined cover of sand, rubble, and pavement), MAC = macroalgae, SC = soft corals, SCI = structural complexity, LBC = live branching coral, E = encrusting corals, F = foliose corals, SA = sand, PAV= pavement. Wrasse density shown by black, solid data points and continuous polynomial trend

lines. Top benthic predictor from taxa-specific BRTs shown by white, open data points and dotted polynomial trend lines. Environmental disturbance events indicated by arrows and dotted lines: 2014 runoff event – black arrow, 2016 and 2017 coral bleaching events – grey arrow, cyclone Yasi in 2011 – dotted line. Standard errors (SE) displayed for benthic cover and wrasse density, n =150 transects per sampled year.

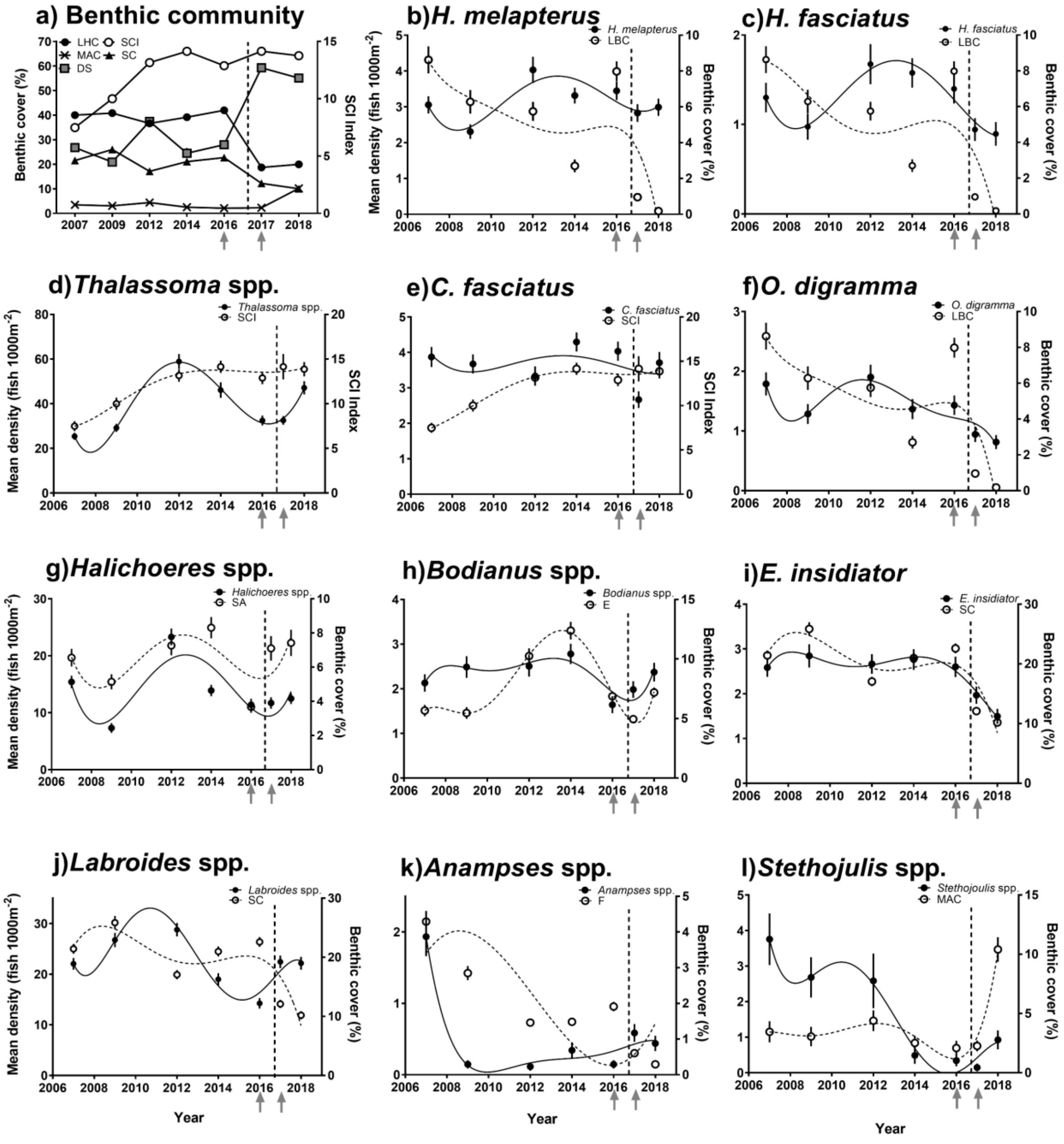


Figure 2. 4: Long-term temporal trends of (a) benthic cover and the density of (b) *H. melapterus*, (c) *H. fasciatus*, (d) *Thalassoma* spp., (e) *C. fasciatus*, (f) *O. digramma*, (g) *Halichoeres spp.*, (h) *Bodianus spp.*, (i) *E. insidiator*, (j) *Labroides spp.*, (k) *Anampses* spp., (l) *Stethojulis* spp., and temporal trends in cover of their respective top benthic predictor identified from BRTs (Table 2.2) at the Whitsunday Island group. LHC = live hard coral, DS = dead substratum (combined cover of sand, rubble, and pavement), MAC = macroalgae, SC = soft corals, SCI= structural complexity, LBC = live branching coral, E = encrusting corals, F = foliose corals, SA = sand. Wrasse density shown by black, solid data points and continuous polynomial trend lines. Top benthic predictor from taxa-specific BRTs shown by white, open data points and dotted

polynomial trend lines. Environmental disturbance events indicated by arrows and dotted lines: 2016 and 2017 coral bleaching events – grey arrow, cyclone Debbie in 2017 – dotted line. Standard errors (SE) displayed for benthic cover and wrasse density, n = 205 transects per sampled year.

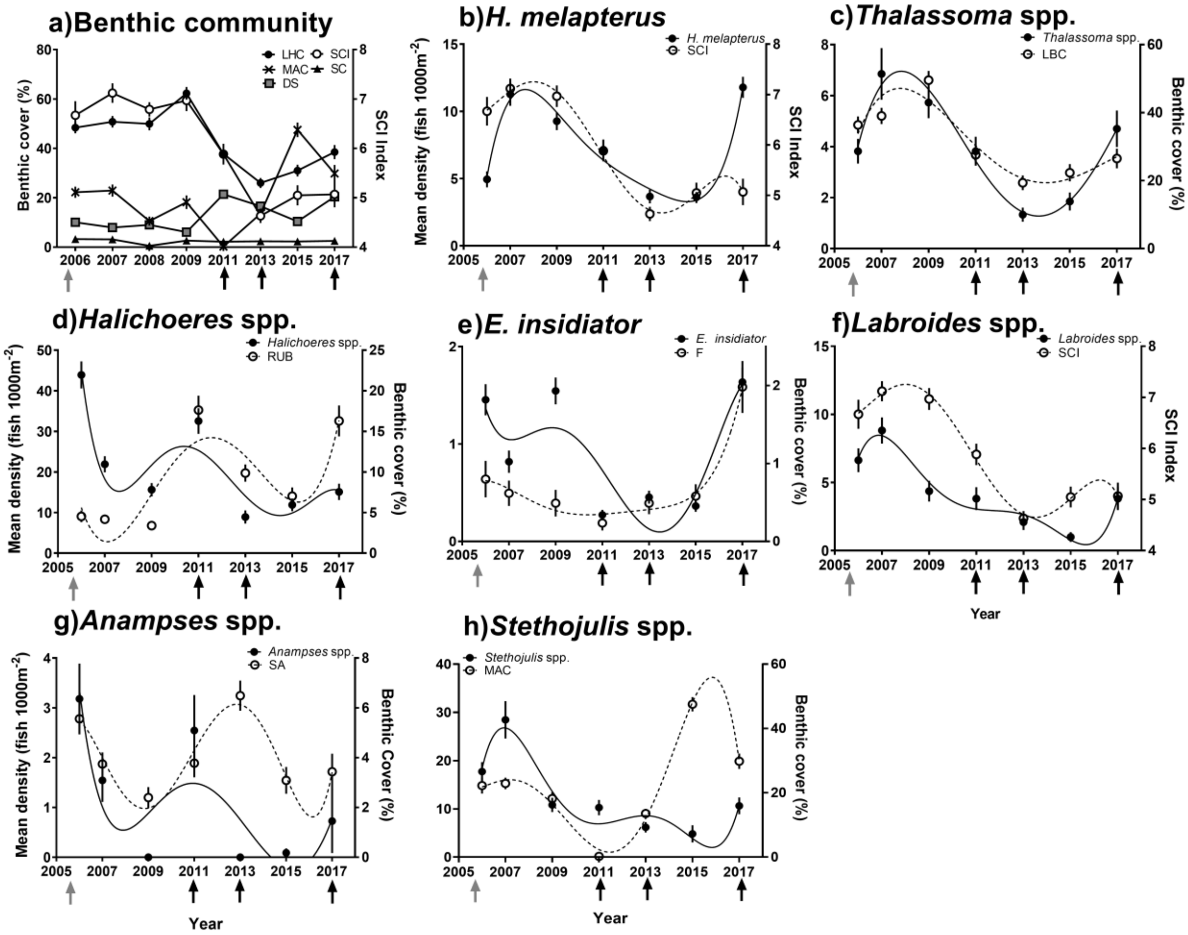


Figure 2. 5: Long-term temporal trends of (a) benthic cover and the density of (b) *H. melapterus*, (c*) Thalassoma* spp., (d) *Halichoeres* spp., (e) *E. insidiator*, (f) *Labroides* spp., (g) *Anampses* spp., (h) *Stethojulis* spp., and temporal trends in cover of their respective top benthic predictor identified from BRTs (Table 2.2) at the Keppel Island group. LHC = live hard coral, DS = dead substratum (combined cover of sand, rubble, and pavement), MAC = macroalgae, SC = soft corals, SCI = structural complexity, LBC = live branching coral, RUB = rubble, F = foliose corals, SA = sand. Wrasse density shown by black, solid data points and continuous polynomial trend lines. Top benthic predictor from taxa-specific BRTs shown by white, open data points and dotted polynomial trend lines. Environmental disturbance events indicated by arrows: 2006 coral bleaching event – grey arrow and 2011, 2013, 2017 runoff events – black arrows. Standard errors (SE) displayed for benthic cover and wrasse density, n =110 transects per sampled year.

2.4.4 Effects of NTMR Protection and Predators on Density of Wrasses

No NTMR Status*Time interactions nor Predator density*NTMR Status interactions were detected in GAMMs (Fig. 2.6; Appendix 2.4). In addition, plots of wrasse density over time in NTMR and fished control sites were not consistent with NTMR effects for any taxa at any island group. Instead, GAMMs identified various benthic habitats nested within NTMR zones as important drivers of wrasse density (Fig. 2.6; Appendix 2.4). GAMMs identified higher densities of *C. fasciatus* and *Thalassoma* spp. in new (2004) NTMRs than in old (1987) NTMRs and fished sites in the Palm Island Group, associated with differences in SCI and sand cover among management zones (Appendix 2.4). Higher densities of *Labroides* spp. and *E. insidiator* were found in new NTMRs than in fished sites of the Whitsunday Islands, and higher densities of *Bodianus* spp., *O. digramma,* and *Hemigymnus* (both species) in old NTMRs than in fished sites of the Whitsundays, associated with differences in various benthic components nested within NTMR zones (Fig. 2.6; Appendix 2.4). Similarly, in the Keppel Islands GAMMs indicated differences in the cover of macroalgae and rubble between NTMR zones. This correlated with lower densities of *E. insidator* and *Labroides* spp. in new NTMRs (Fig. 2.6; Appendix 2.4). There were no significant interactions between predator densities and NTMR status on wrasse densities. However, predator density independent of NTMR status was a significant determinant of the density of *H. melapterus* in the Palm Islands, density of *C. fasciatus* in the Whitsunday Islands and density of *H. melapterus*, *E. insidiator*, *Thalassoma* spp., and *Stethojulis* spp. in the Keppel Islands (Fig. 2.6; Appendix 2.3). Negative relationships between wrasse density and predator density were evident for *C. fasciatus* in the Whitsunday Islands and for *Thalassoma* spp., *E. insidiator,* and *Stethojulis* spp. in the Keppel Islands. In contrast, density of *Stethojulis* spp. and *H. melapterus* in the Keppel Islands was positively related to predator density. Density of *H. melapterus* in the Palm Islands had a complex relationship with predator density, being negatively related to predator density at sheltered sites, but positively related to predator density at exposed sites.

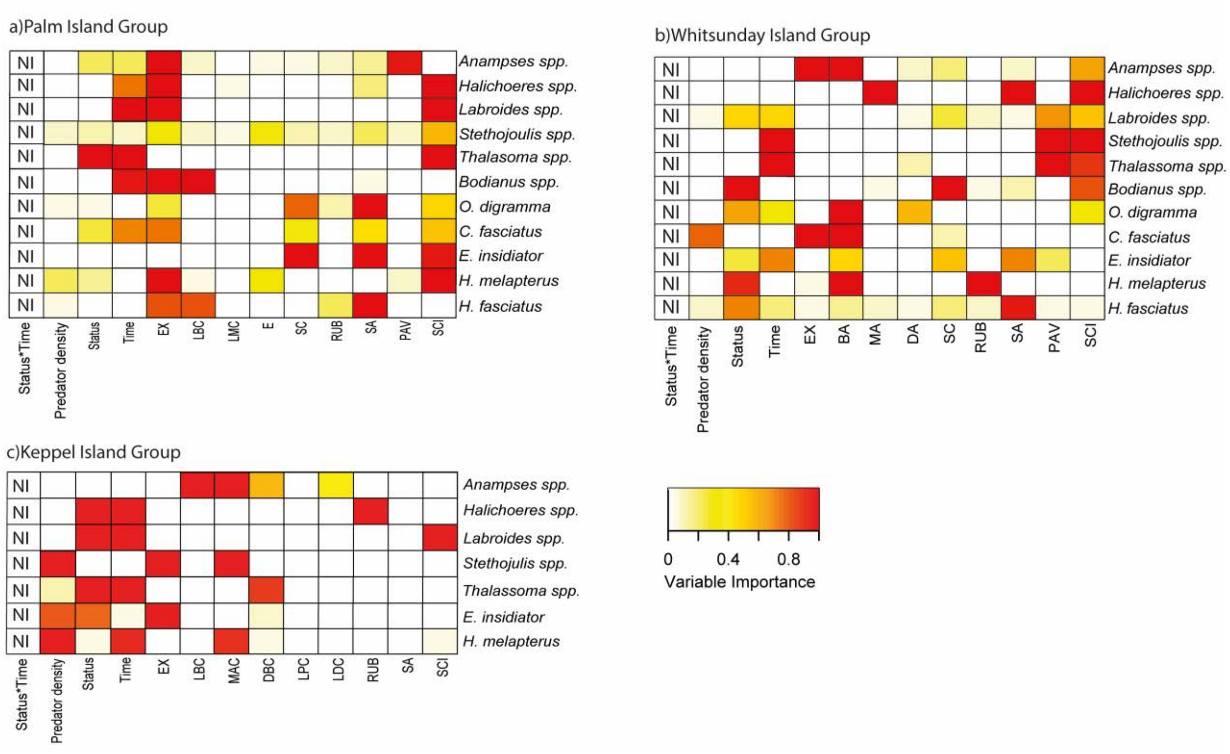


Figure 2. 6: Generalised Additive Mixed Model (GAMM) heatmaps that display the importance of environmental drivers on wrasse density at the Palm (a), Whitsunday (b), and Keppel (c) Island groups. LBC = live branching corals, DBC = dead branching corals, LMC = live massive corals, LDC = live digitate corals, LPC = live plating corals, E = encrusting corals, SC = soft corals, RUB = rubble, SA = sand, PAV = pavement, MAC = macroalgae, SCI = structural complexity index, EX = site exposure to prevailing wind & waves. Blank squares represent benthic variates that did not appear in top models (ΔAICc ≤ 2). Variates that did appear in taxa-specific 'important' models are represented as columns and were colour coded according to summed AICc weights of all 'important' models for that species. NI = no interaction within top models (ΔAICc ≤ 2).

2.5 Discussion

The density of tropical wrasses on inshore GBR coral reefs appears to be driven predominantly by taxa-specific benthic habitat associations, rather than NTMR protection or the density of wrasse predators. Previous studies have also suggested strong relationships between benthic cover and the density of wrasses (Wilson *et al.*, 2008; Russ *et al.*, 2017; Emslie *et al.*, 2017). However, this investigation is the first to partition the effects of benthic habitat, NTMR protection, and predator density over a large spatial (≈ 700 km) and temporal scale (2006-2018) in the GBRMP.

2.5.1 Effects of NTMRs and Density of Predators on Density of Wrasses

Long-term partitioning of benthic habitat and NTMR effects on wrasses on Philippine coral reefs failed to detect a direct NTMR effect on wrasse density over a 31-year period, despite targeted fishing of these fishes (Russ *et al.*, 2017). The low harvest rate of wrasses on the GBR likely accounts for the lack of a direct NTMR effect on both large- and small-bodied wrasses in this study. This result supports previous studies, which reported no NTMR effect on the density of other non-target species on the GBR (Williamson *et al.*, 2004; Ayling and Choat 2008; Emslie *et al.*, 2015). While direct NTMR effects were absent, particular benthic habitats nested within NTMRs were important drivers of wrasse density. This suggests that while the focal wrasses do not benefit directly from decreased fishing pressure alone, NTMRs that include favoured benthos can support higher wrasse densities. Variable benthic assemblages inside and outside NTMRs also affected wrasse density in the Philippines (Russ *et al.*, 2017). In the present study, the lack of clear top-down predator effects on the density of wrasses within NTMRs was somewhat unexpected. NTMRs on inshore reefs of the GBRMP often support higher densities of large predatory fishes, such as coral trout (*Plectropomus* spp.), than surrounding fished reefs (Williamson *et al.*, 2004; McCook *et al.*, 2010; Emslie *et al.*, 2015). This suggests that any build-up of predators within NTMRs relative to fished areas did not affect wrasse density differentially due to NTMR establishment. However, predator density irrespective of NTMR status, influenced the density of some species of wrasses at some locations. Examples include negative relationships between predator density and the density of *C. fasciatus* in the Whitsunday Islands; and *Thalassoma* spp., *E. insidiator*, *Stethojulis* spp. in the Keppel Islands. However, given the high rates of predation on coral reefs (Hixon and Beets 1993), the complexity of coral reef ecosystems, the diversity of prey species and opportunistic feeding by predatory fishes, this is likely a conservative list of wrasses negatively affected by predator density. The lack of NTMR effects, and weak predator effects, further suggests that benthic habitat attributes were the most important drivers of wrasse densities on inshore GBRMP reefs.

2.5.2 Habitat Associations of Wrasses on Inshore Reefs

Taxa-specific benthic habitat associations of inshore wrasse assemblages were generally consistent through time, irrespective of diet or vulnerability to fishing. Yet, this study also found taxa-specific benthic drivers differed spatially, suggesting some taxa may change benthic preferences according to differences in prey availability or species-specific interactions at each island group. As such, I suggest the influence of changing benthic condition on wrasse taxa is best monitored by separately assessing ecosystems at reefal scales, rather than relying on broad-scale assessments which may confound ecosystem-specific drivers. On inshore GBR reefs, increases in structural complexity or the cover of live branching corals generally led to density increases of *Hemigymnus* spp., *Thalassoma* spp., *C. fasciatus*, *O. digramma* and *Labroides* spp., while increases in the cover of sand and rubble resulted in increased densities of *Halichoeres* spp.

Positive habitat associations of *H. melapterus* and *H. fasciatus* with SCI and live branching corals were consistent with findings in the Philippines, where increased cover of live branching and tabular corals resulted in increased density of *H. melapterus* and *H. fasciatus* (Russ *et al.*, 2017). Similarly, studies from Japan indicate that SCI and live coral cover were major drivers of *Hemigymnus* spp. density (Sano *et al.*, 1987; Nanami *et al.*, 2005). It is important to recognise that population density is buffered via inter-reefal larval connectivity at larger spatial scales, thus, while wrasses may show strong patterns of microhabitat use at restricted spatial scales, the organism-habitat relationship may or may not be important in structuring populations at broader scales (Almany *et al.*, 2009; Green *et al.*, 2015). For example, results of the present study differ from those of Kramer *et al.*, (2016), which reported that *H. fasciatus* and *H. melapterus* associate positively with dead coral habitats in spatially restricted studies on the GBR, yet the present study conducted on a much larger temporal and spatial scale indicated positive density relationships of *Hemigymnus* spp. with live hard coral cover and structural complexity over 12 years on inshore GBR reefs. Results presented here also differ from Emslie *et al.*, (2017), which reported that cover of massive corals and sand were major drivers of density of *H. fasciatus* and *H. melapterus* on a GBR-wide scale (inner-, mid-, and outer-shelf coral reefs spanning 9 degrees of latitude). Disparity between my results and those of Emslie *et al.*, (2017) likely stem from specific differences in sampling design, but may suggest that key benthic drivers of *Hemigymnus* spp. density differ between mid- and outer-shelf GBR reefs, and inner-shelf reefs (Emslie *et al.*, 2017).

The positive relationship between SCI, the cover of branching corals and density of *Thalassoma* spp. was unexpected. This result differs from that reported in the Philippines, where the density of *T. lunare* and *T. hardwicke* increased as the cover of sand, rubble and hard-dead substratum increased (Russ *et al.*, 2017). However, the result here is consistent with short-term studies of benthos and *Thalassoma* spp. density in Fiji (Wilson *et al.*, 2008), Papua New Guinea (Berkström *et al.*, 2012) and Japan (Sano *et al.*, 1987; Nanami *et al.*, 2005). Responses of density of *Hemigymnus* spp. and *Thalassoma* spp. to environmental disturbances were modest and consistent across space and time in the present study. Results thus suggest substantial persistence of *Hemigymnus* spp. and *Thalassoma* spp. populations to changes in benthos on inshore GBR reefs.

Density of *C. fasciatus* was positively associated with western-facing-sites, sheltered from wind and wave energy with high SCI. This consistent relationship provides the first long-term evidence that supports short-term studies that document *C. fasciatus* preference for sheltered sites (Fulton *et al.*, 2013) and preference for sites with high structural complexity (Nanami *et al.*, 2005).

Density of *Labroides* spp. also correlated positively with increases in SCI. Yet, based on the positive effect SCI has on predator densities on the GBR (Emslie *et al.*, 2017), I presume density fluctuations of *Labroides* spp. are due to fluctuating food availability (availability of fish to clean), rather than due to changes in benthic complexity *per se*. Previous studies that document benthic habitat associations of *Labroides* spp. are inconsistent, with some studies sharing my interpretation (Triki *et al.*, 2018), while others suggest that structurally complex live coral cover provides a refuge for juvenile *Labroides* (Berkström *et al.*, 2012).

As an ambush predator of small fishes, *O. digramma* is known to hide among soft corals and the branches of *Acropora* corals (Kuiter 2002). Thus, the positive relationship between density of *O. digramma* and the cover of soft corals at the Palm Islands, and with the cover of live-branching corals at the Whitsunday Islands, was not surprising. While such relationships have been reported previously in short-term studies, this is the first time that these habitat effects have been documented on a decadal scale (12 years), spanning multiple cycles of environmental disturbance and recovery.

Positive responses of *Halichoeres* spp. density to increases in sand and rubble are consistent with previous studies on the GBR. Halford, *et al.*, (2004) reported a negative relationship between *Halichoeres* density and hard coral cover. In PNG, positive responses of *Halichoeres hortulanus* and *H. melanurus* recruits to increased cover of sand and rubble have been reported by Berkström *et al.*, (2014). Moreover, many species of *Halichoeres* are known to use sand-diving to evade predation, explaining their preference for sandy substrata (Tatom-Naecker and Westneat, 2018). *Halichoeres* spp. density increased significantly following cyclone Yasi in the Palm Islands and cyclone Debbie in the Whitsunday Islands. If the frequency and severity of disturbance events increases as predicted (Hoegh-Guldberg *et al.*, 2007; Mendelsohn *et al.*, 2012; Hughes *et al.*, 2017a), then density of *Halichoeres* spp. may increase with increased cover of disturbed reef environments, while *Hemigymnus* spp., *Thalassoma* spp., *C. fasciatus*, *O. digramma*, and *Labroides* spp. would be expected to decline in density as the impact of more numerous disturbance events is likely to result in lower coral cover and structural complexity.

The relationships of density of *Anampses* spp., *Bodianus* spp., *Stethojulis* spp., and *E. insidiator* to benthos were inconsistent through time and across island groups, yet, in most cases density of these taxa still correlated with shifts in benthic substratum. The lack of clear responses of these taxa to benthic change could be due to the fact that many of these taxa contain multiple species that may have preferences for different benthic habitats or could be due to temporal fluctuations in larval supply and juvenile recruitment rates. Moreover, while it is not always feasible to consider numerous species-specific responses or all possible environmental drivers in a single study, my findings indicate that other factors could be important in driving density of *Anampses* spp., *Bodianus* spp., *Stethojulis* spp., and *E. insidiator* on inshore GBR reefs.

Despite the spatial and temporal consistency of many benthic drivers of wrasse density and the high correlation of wrasse density with particular benthic types, BRTs based on transect-level data only reported weak to moderate habitat associations for most species. Low relative importance of benthic components in BRT models may support previous studies that suggest that wrasses are habitat generalists at small spatial scales (Green 1996; Fulton and Bellwood 2002; Kramer *et al.*, 2016). Furthermore, such results could be a product of the extreme patchiness of benthic assemblages that were averaged to a transect level for analyses. My results support those presented from the Philippines (Russ *et al.*, 2017) and suggest that wrasse densities may respond strongly to changes in preferred benthic substrata at reefal scales and over extended timeframes, and thus are most suitably monitored at this resolution. Yet, whether temporal changes in wrasse density due to benthic change caused by disturbances, or changes in fish density as benthos recovers after disturbance, are a result of adult mortality due to declining food and shelter, changes in larval supply, or due to habitat selection at recruitment, requires further investigation.

2.5.3 Responses of Wrasses and Benthos to Disturbance Events

Wrasse density on inshore GBR coral reefs, particularly of large-bodied species, displayed unexpected persistence to severe environmental disturbances (i.e., cyclones and flood plume events) that resulted in significant damage to benthic communities and habitat structure. Despite >50% relative loss of live hard coral cover at the Palm Islands following cyclone Yasi and at the Whitsunday Islands after cyclone Debbie, many wrasses exhibited only minor density changes. This was likely due to the retention of SCI immediately after cyclones on these reefs. In comparison, the 2011 flood plume in the Keppel Islands reduced live hard coral cover and SCI (at exposed sites) simultaneously, resulting in moderate to strong density responses for 70% of taxa investigated. A number of other studies on the GBR have also identified SCI and live branching coral cover as critical benthic components for structuring reef fish assemblages (Emslie *et al.*, 2014; Williamson *et al.*, 2014). Like other demersal reef fishes, structural complexity likely affects the density of some taxa of wrasses by providing shelter, which mediates competition and predation, enabling increased survivorship and co-existence among species (Kerry and Bellwood 2012; Coker *et al.*, 2014; Emslie *et al.*, 2014). Resilience of wrasse assemblages was also evident following cyclone Yasi in the Palm Islands, where 8 of 12 investigated wrasse taxa either increased in density or returned to pre-disturbance densities within seven years following the cyclone disturbance event.

Inshore reef benthic assemblages also exhibited unexpected resistance and resilience to environmental disturbance events. In 2016, bleaching reportedly caused 29% mortality of shallow-water hard corals on the GBR (GBRMPA 2017; Hughes *et al.*, 2018b). Then in 2017, a subsequent bleaching event was reported to have generated additional coral mortality, particularly in the central GBR region where the Palm and Whitsunday Island groups are located (Hughes et al., 2018c). My findings suggest that despite these events, live hard coral cover increased marginally on fringing reef slopes of the Palm Islands from 2016 to 2018 and wrasse assemblages responded accordingly. Other studies have also reported negligible effects of the 2016 bleaching event on Palm Island coral assemblages (Torda et al., 2018). While results from Hughes *et al.*, (2018b) aerial surveys over large areas of the GBR and long-term monitoring studies based on permanent underwater transects on inshore GBR islands are difficult to compare, it is notable that the two studies do not provide the same result. Perhaps current coral assemblages of the Palm Islands are more resistant to coral bleaching mortality and other stressors than those on offshore reefs (Roff *et al.*, 2013). Moreover, long-term recovery of Palm Islands benthic assemblages following cyclone Yasi, suggests that inshore reefs are capable of returning to pre-disturbance hard coral cover within a decade. However, while recovery trajectories of inshore reefs appear encouraging, it is important to note that coral cover on fringing reefs of the Palm Island group remains lower than pre-1998 bleaching levels (Torda *et al.*, 2018).

The number of publications that document the decline of coral reefs worldwide has increased substantially over the past two decades (Hoegh-Guldberg *et al.*, 2007; Graham *et al.*, 2011; Hughes *et al.*, 2017a, 2018a). Although the GBR has experienced substantial declines in live hard coral and shifts in benthic assemblage structure cover over recent decades (Roff *et al.*, 2013, Hughes *et al.*, 2018b), some authors suggest that the GBR may be more resistant to such declines than coral reef systems elsewhere (Pandolfi *et al.*, 2003; Burke *et al.*, 2011). The GBR's higher resistance to degradation can perhaps be attributed to its size (≈ 3000 individual reefs, spanning 2300 kilometres), connectivity (Ayre and Hughes 2000; Harrison *et al.*, 2012; Williamson *et al.*, 2016), relatively low fishing pressure (Allison *et al.*, 2009), sound fisheries management practices, and a large and effective NTMR network (Fernandes *et al.*, 2005; Emslie *et al.*, 2015). Yet, while this and other studies have indicated coral recovery on the GBR can occur in roughly a decade (Halford *et al.*, 2004; Graham *et al.*, 2014; Johns *et al.*, 2014), predicted increases in the frequency, severity, and scale of coral mortality due to global warming and other disturbance events indicate that the rate of coral recovery will undoubtedly be too slow on the GBR to maintain coral cover (Hoegh-Guldberg *et al.*, 2007; Mendelsohn *et al.*, 2012; Hughes *et al.*, 2017a). Moreover, as the density fluctuations of reef-fishes following environmental disturbance events to the benthos are influenced by climate-mediated factors (Cheal *et al.*, 2007), future effects of global warming, such as increased sea-surface temperatures and changes to oceanographic currents, could alter the nature of wrasse-benthic habitat associations reported here.

This study of tropical wrasse assemblages of the inshore GBR provides a useful contribution to knowledge of the drivers of wrasse assemblages for managers and ecologists in the face of potential increases in environmental disturbances (e.g., storms, terrestrial runoff, coral bleaching, cyclones etc.). While I suggest similar density responses of tropical wrasses to disturbance events can be expected on other coral reef systems, caution must be taken when extrapolating results from this study to more isolated reefs, heavily degraded reefs, or those positioned in areas of higher human use and fishing pressure. Ultimately, in order to effectively manage the effects of persistent environmental disturbance events on coral reefs, it is necessary to better understand links between reef organisms and ecosystem persistence via the use of long-term, robust sampling programs, and to reduce anthropogenic stressors that contribute to the degradation of coral reefs.

Chapter 3: Environmental Disturbance Events Drive Declines in Juvenile Wrasse Biomass on Inshore Coral Reefs of the Great Barrier Reef

Lowe JR, Williamson DH, Ceccarelli DM, Evans RD & Russ GR (2019) Environmental disturbance events drive declines in juvenile wrasse biomass on inshore coral reefs of the Great Barrier Reef. *Environmental Biology of Fishes* 103, 1279-1293. doi: 10.1007/s10641-020-01022-2

3.1 Abstract

Environmental disturbances and fishing are well known drivers of coral reef fish population size, length-frequency, and assemblage structure. However, few studies have partitioned the spatial and temporal impacts of multiple disturbance events and long-term no-take marine reserve (NTMR) protection on the biomass of juvenile and adult reef-fishes based on the known size of sexual maturity. Here, I document responses in the biomass of juvenile and adult wrasses (F: Labridae) *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma*, to environmental disturbance events, NTMR protection, and predator density on inshore fringing coral reefs at the Palm and Whitsunday Island groups, Great Barrier Reef (GBR), Australia from 2007 to 2018 (12 years). The biomass of juvenile and adult wrasses on inshore GBR reefs were driven predominantly by benthic habitat associations, rather than by NTMR protection or density of wrasse predators (*Plectropomus* spp.). Despite similar species-specific associations of juvenile and adult wrasses with benthic cover, juvenile wrasse biomass consistently declined following coral bleaching and cyclone events. Conversely, adult wrasses had variable responses to disturbance events, including some increases in biomass. Disturbance-mediated declines in the biomass of juvenile wrasses are likely to generate ongoing reductions in the abundance of these species on inshore GBR reefs. My findings provide further evidence that habitat loss impacts a range of coral reef fishes beyond those that are directly reliant upon live coral. Shifts in assemblage structure, loss of biodiversity, and reductions in fishery productivity will become increasingly apparent in coral reef ecosystems if anthropogenic global warming continues unabated.

3.2 Introduction

Coral reefs are often modified by environmental disturbance events, and current projections indicate that the frequency of severe impacts will increase as global warming progresses (Knutson *et al.*, 2010; De'ath *et al.*, 2012; Hughes *et al.*, 2018a; Ceccarelli *et al.*, 2019). Whilst severe environmental disturbances typically result in acute mortality of corals and other benthic invertebrates, effects on reef fishes are often less apparent, and may take years to accrue (Graham *et al.*, 2007; Emslie *et al.*, 2014; Hughes *et al.*, 2018b). Environmental disturbance events on coral reefs rarely result in fish mortality at the time of impact (Harmelin-Vivien 1994), rather, fish communities respond to changing benthic condition (Wilson *et al.*, 2006; Emslie *et al.*, 2014; Russ *et al.*, 2015c). As most coral reef fishes are dependent on live corals or the three-dimensional reef matrix for food, shelter, or recruitment, most species decline in density following environmental disturbances that reduce coral cover and habitat complexity (e.g., cyclones) (Jones *et al.*, 2004; Wilson *et al.*, 2006; Coker *et al.*, 2014, Williamson *et al.*, 2014). However, species not directly dependent on coral cover, such as goatfishes (Mullidae), parrotfishes (Scarinae), and small-bodied wrasses (Labridae) often increase in density with disturbance-mediated increases in cover of abiotic substratum, such as sand, rubble, or dead coral pavement (Russ *et al.*, 2015a, 2015b, 2017). While many studies have documented the short-term effects of environmental disturbance events on reef fish abundance and assemblage structure, few have investigated longer-term implications for the demographic structure of affected fish communities. Consequently, few data exist that demonstrate how environmental disturbance events may differentially affect the biomass of large-bodied sexually mature individuals as opposed to small-bodied immature juveniles, or how these two demographic groups are affected as coral and fish assemblages recover post-disturbance. Understanding the effects of environmental disturbance events on the demographic structure of reef fishes provides an important link between prevailing environmental conditions and the ecological mechanisms driving reef-fish population dynamics.

Disturbance-mediated changes in coral reef fish assemblages are well documented and are driven by a number of factors, including; the intensity and frequency of disturbance, changes in resource availability (e.g., degree of loss of benthic habitat), the initial size of the fish population, metapopulation structure, larval connectivity and recruitment, environmental stochasticity, fishing pressure, and site history (Caley *et al.*, 1996; Almany *et al.*, 2009;

McClanahan *et al.*, 2011; Russ *et al.*, 2015c). Most of these factors relate to the demographic structure of reef-fish populations, suggesting that population recovery post-disturbance is a cumulative process that is linked to environmental factors, particularly benthic habitat structure and diversity (Cheal *et al.*, 2007; Graham *et al.*, 2007; Emslie *et al.*, 2014). Population turnover and recovery rates are also a function of species-specific life-history traits, such as body-size and the age of sexual maturity, as they directly influence mobility, home range size, diet, resource allocation, and generation times (Adams 1980; Roff 1993; Hutchings 2000; Jennings 2000). Previous studies also demonstrate the importance of considering fish size when quantifying the effects of environmental drivers on the demographic structure of fish assemblages, as "… a single 2-kg fish produces many more eggs than do two 1-kg fish" (Bohnsack 1990; Hixon *et al.*, 2013; Barneche *et al.*, 2018; Marshall *et al.*, 2019). However, despite these clear links between body size and the recovery potential of coral reef fishes following disturbances, few studies have documented the temporal and spatial impacts of multiple disturbance events on the demographic structure of fish populations, where the size of sexual maturity is known.

Long-term monitoring of benthic and fish communities on no-take marine reserve (NTMR) and fished reefs fringing inshore islands of the Great Barrier Reef (GBR), Australia, provides a perfect opportunity to partition effects of NTMR protection, predator density, and multiple environmental disturbance events on the biomass of sexually-mature (hereafter adult) and sexually-immature (hereafter juvenile) wrasses. Previous studies have shown that long-term NTMR protection did not significantly increase the density of wrasses, both in the Philippines (Russ *et al.*, 2017) and on inshore GBR reefs (Lowe *et al.*, 2019). Furthermore, increased predator density within NTMRs on inshore GBR reefs did not significantly affect the total density of wrasses compared to fished control sites (Lowe *et al.*, 2019). However, as densities of large-bodied predators (e.g., *Plectropomus* spp.) continue to increase on NTMR reefs in the GBR Marine Park (Emslie *et al.*, 2015), there remains a need to determine the extent to which increased predation pressure may impact the population dynamics of smaller-bodied prey species and fish assemblage structure. Reduced densities of several small-bodied prey species, including wrasses, have been reported on NTMR reefs in the Palm and Whitsunday Islands that supported significantly increased density of coral trout (*Plectropomus* spp.) (Graham *et al.*, 2003). Moreover, the immediate and sustained impacts of NTMR protection and environmental disturbance events on the biomass of adult and juvenile wrasses remain to be elucidated. Specifically, this study will address the following questions:

1. What are the impacts of long-term NTMR protection, and the build-up of predator density within NTMRs, on the biomass of adult and juvenile wrasses?
2. What are the impacts of multiple environmental disturbance events on the biomass of adult and juvenile wrasses?
3. Do the effects of environmental disturbance events, NTMR protection, or predator density differ spatially among island groups?

3.3 Methods

3.3.1 Study Area

Wrasse populations and benthic cover were surveyed biennially at seventy-one long-term monitoring sites on fringing coral reefs in the Palm and Whitsunday Island groups, Great Barrier Reef, Australia, from 2007 to 2018, as part of a larger long-term monitoring program (Appendix 3.2). There were thirty monitoring sites on reefs at the Palm Island group and forty-one sites at the Whitsunday Island group (Fig. 3.1). At both island groups, monitoring sites were located on ‘old’ (protected since 1987) and ‘new’ (protected since 2004) NTMR reefs, as well as on adjacent reefs that remained open to fishing (General Use, Habitat Protection and Conservation Park zones) (Fig. 3.1).

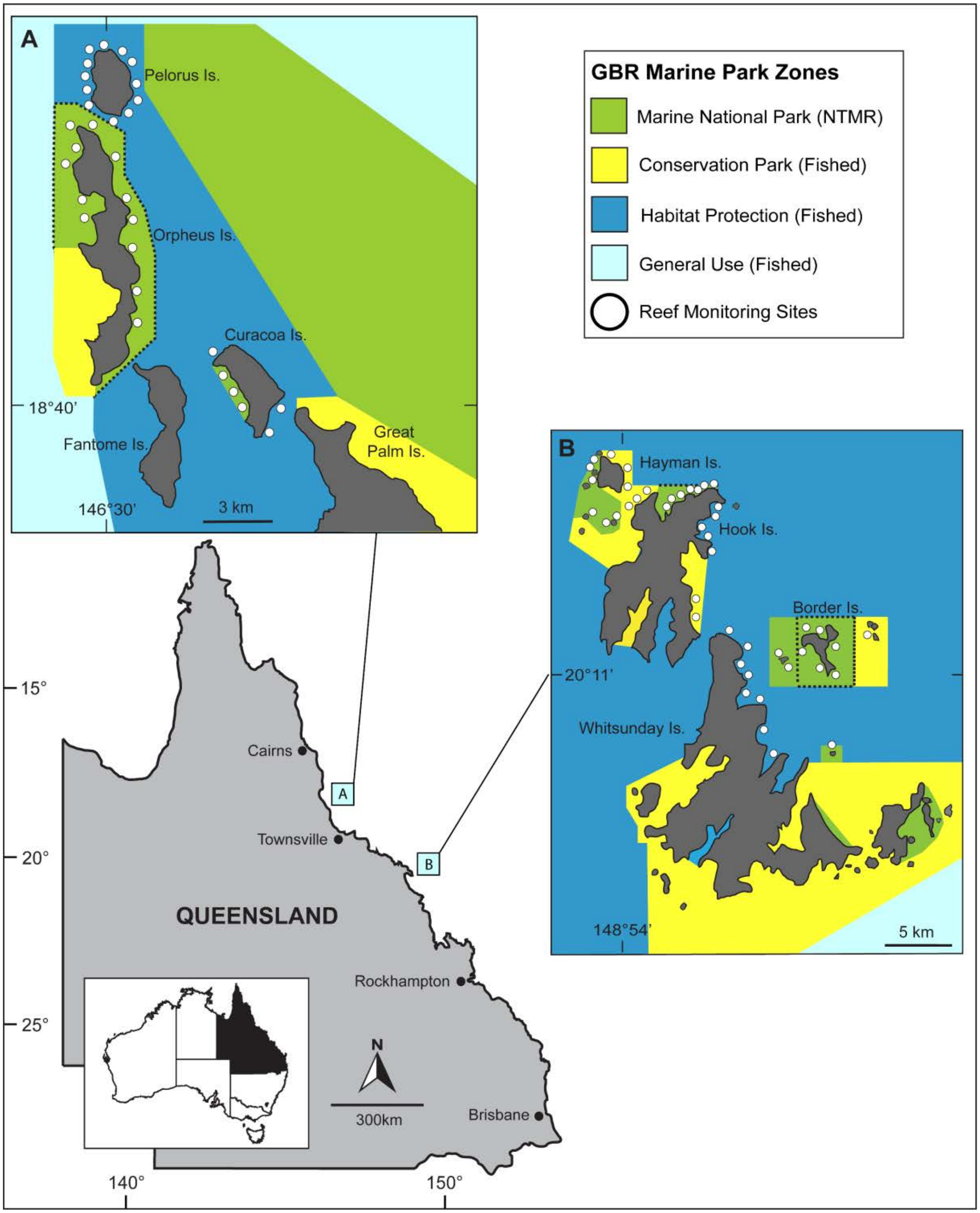


Figure 3. 1: Map of Queensland, Australia, and inset maps of the Palm (A) and Whitsunday (B) Island Groups within the Great Barrier Reef Marine Park. Inset maps illustrate the approximate location of long-term coral reef monitoring sites (white markers) and Great Barrier Reef Marine Park (GBRMP) zoning. No-take marine reserves (NTMRs) are shaded green. All other zones are open to fishing. 'Old' (protected since 1987) NTMRs have black, dashed borders. 'New' (protected since 2004) NTMRs have no border.

3.3.2 Surveys of Benthic and Wrasse Assemblages

Reef fishes were surveyed using a standardised underwater visual census (UVC) technique. At each monitoring site, five replicate 50m x 6m (300 m^2) transects were deployed on reef slopes (4 – 12 m in depth). On each transect two observers on SCUBA estimated the number and size of approximately 190 species of coral reef fishes from 15 families, including juvenile and adult *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* (Williamson *et al.*, 2014; Lowe *et al.*, 2019).

The four focal species of wrasse were selected for the present study because age-based demographic information was available for these species, at these island groups (Appendix 3.1), and because these species have a range of diets, body sizes, and are common prey of the most abundant piscivore on these reefs (coral grouper - *Plectropomus* spp.) (St John *et al.*, 1999, 2001). *Oxycheilinus digramma* grow to a maximum length of approximately 35 cm, they associate positively with soft corals and live branching corals and they prey upon macro-invertebrates and small fishes (Kuiter 2002; Lowe *et al.*, 2019). *Cheilinus fasciatus* are durophagous feeders that grow to approximately 36 cm in length and associate positively with structural complexity of the benthos (Wainwright *et al.*, 2004; Kramer *et al.*, 2016; Lowe *et al.*, 2019). *Hemigymnus fasciatus* and *H. melapterus* are large-bodied fishes (reaching 45 and 50cm in length, respectively) that prey upon macro-invertebrates and are commonly found in coral-dominated habitats (Kuiter 2002; Russ *et al.*, 2017; Lowe *et al.*, 2019).

For each of the focal species of wrasse, fish observers counted and recorded total length estimates into 10 cm size categories. A third observer followed the two fish observers and recorded benthic composition at 1 m intervals using a standard point intercept survey method. At each interval the observer classified benthos into the following categories; morphology of live and dead coral (including branching, plate, digitate, massive, foliose), soft corals, solitary corals, sponges, clams (*Tridacna spp.)*, other invertebrates (e.g., ascidians, anemones), macroalgae, pavement (dead coral substratum covered in epilithic algal matrix), rock, rubble, and sand. An index of structural complexity was also obtained at each site by ranking (1-5) the angle of the reef slope and multiplying it by the average rugosity (also ranked 1-5) for each ten-meter section of each transect (Williamson *et al.*, 2014).

Length estimates were converted to biomass by applying the taxa-specific mean weight at length (Appendix 3.3). Biomass was estimated for each species from density of wrasses recorded within each 10 cm size category on each transect multiplied by size-specific weight. As 50% of each focal wrasse population at the Palm and Whitsunday Island groups reaches sexual maturity between approximately 12 cm and 20 cm in size (Appendix 3.1), 20 cm was chosen as the cutoff point between juvenile and adult subsets of fish for all species. Species-specific biomass estimates were subsequently split into juvenile (< 20 cm) and adult (≥ 20 cm) subsets at each island group.

3.3.3 Data Analysis

Generalised Additive Mixed Models (GAMMs), with a Gamma distribution, were used to determine whether benthic habitat, NTMR protection, predator density, or interactions between these factors best explained changes in the biomass of juvenile and adult wrasses over the study period. Top benthic predictors of density of the focal species at the Palm and Whitsunday Island groups were derived from Lowe *et al.*, (2019), these were; live branching corals (LBC), sand (SA), rubble (RUB), soft corals (SC), and structural complexity (SCI). However, the combined cover of live hard corals (LHC) was chosen, rather than LBC, to generalise ontogenetic shifts of wrasse taxa between hard coral morphologies present in juvenile and adult habitats. For example, *H. melapterus* are known to recruit to reef flats dominated by rubble substrata with some plating (e.g., *Acropora hyacinthus*) and digitate corals (e.g., *Porities cyclindrica*), before moving onto reef slopes and associating positively with branching corals in later life stages (Kuiter 2002; Coker *et al.*, 2014; Lowe *et al.*, 2019). Thus, benthic categories used for statistical analysis were structural complexity (SCI), the cover of live hard corals (LHC), rubble (RUB), sand (SA), and soft corals (SC). On the GBR *Plectropomus* spp. commonly prey on wrasses (St John *et al.*, 1999, 2001; Wen *et al.*, 2016) and have consistently been shown to be significantly more abundant and larger on NTMR reefs than on fished reefs in the GBRMP (Evans and Russ 2004; Williamson *et al.*, 2004; Emslie *et al.*, 2015). Thus, *Plectropomus* density was included in GAMMs as a proxy for variable predation pressure on NTMR and fished reefs. *Plectropomus* density can be considered an independent variable because the dynamics of these populations are driven by species-specific rates of recruitment, mortality, reproduction, immigration, and emigration. Generally, *Plectropomus* decline following environmental disturbances that reduce coral cover, but population declines are often temporally lagged due to the ability of coral trout to persist in variable habitats and their ability to switch diets following disturbance events (Williamson *et al.*, 2014; Emslie *et al.*, 2015; Wen *et al.*, 2016; Emslie *et al.*, 2017; Hempson *et al.*, 2017).

Separate GAMMs were fitted for juvenile and adult subsets of each species at each island group via code provided by Fisher *et al.*, (2018) and a call to the *gamm4* package in R (Wood and Scheipl 2017). Global model predictor variables at each location included NTMR status (Fished, NTMR-2004 or NTMR-1987), time (duration of protection since NTMR implementation), predator density (density of *Plectropomus* spp.) and benthic variables (SCI, LHC, SA, RUB, SC). NTMR status, time, benthic variables, and predator density were treated as fixed effects, while replicate transects nested within sites were treated as a random effect. Model selection, based on the minimisation of Akaike information criterion corrected for small sample sizes (AICc), was performed inside the full-subset multiple regression function (Fisher *et al.*, 2018). The smallest AICc value identified the model with the greatest support, yet all GAMMs within ΔAICc ≤ 2 of the 'top model' (smallest AICc) were deemed 'important' because models within this threshold can have similar explanatory power (Burnham and Anderson, 2002). Variable importance scores from GAMMs were subsequently plotted into a heatmap that represents the importance of predictor variables in determining the biomass of juvenile and adult subsets for each species, at each island group. In this heatmap, blank squares represent benthic variates that did not appear in top models (ΔAICc ≤ 2). Variates that did appear in taxa-specific 'important' models are shown as columns and were color-coded according to summed AICc weights of all 'important' models for that species. NTMR protection was classified as important if there was a Status x Time interaction or a Predator density x Status interaction present in the top models and there was an appropriate change in NTMR wrasse density relative to the fished control sites over time.

Biomass responses of juvenile and adult wrasses to initial and ongoing impacts of environmental disturbance events were also examined graphically. For disturbance periods of interest, the percent relative annual change in each variable was calculated as:

$$\frac{\frac{End\ value - Start\ value}{Start\ value} X\ 100}{Duration\ of\ change\ (years)}$$

Percent relative annual change was chosen over absolute annual change, as calculations of absolute change require a maximum value which isn’t rational for variables such as wrasse biomass.

3.4 Results

3.4.1 Effects of Environmental Disturbance Events on Palm and Whitsunday Benthic Communities

Wrasse populations were first surveyed on Palm and Whitsunday reefs in 2007. At that time, reefs in the Palm Islands were still recovering from the widespread mass coral bleaching event of 2002. In 2011, Cyclone Yasi severely impacted reefs in the Palm Islands, resulting in approximately 17% annual relative reduction of live hard coral cover between 2009 and 2012 (Fig. 3.2a). By 2014, coral cover had increased on Palm reefs due to the recruitment of new coral colonies to disturbed reef slopes (Fig. 3.2d). In 2016, coral bleaching impacted fringing reefs in the Palm Islands, especially on shallow reef flat and crest habitats , but no discernible impact was recorded on reef slopes (Fig. 3.2c). In 2017 another coral bleaching event was reported on reefs of the central GBR, with moderate mortality of *Pocillopora* spp. and some *Acropora* spp. colonies. However, despite coral bleaching and loss of live coral cover on Palm Islands reef flats, surveys of reef slopes at the Palm Islands long-term monitoring sites in August of 2018 indicated an approximate 8% relative annual increase in live hard coral cover between 2016 and 2018 (Fig. 3.2d).

Although Whitsunday Island reefs were in the path of Cyclone Ului (category 5) in 2010, benthic and fish assemblages on monitored fringing reefs of the Whitsundays were largely undisturbed between 2007 and 2016 (Fig. 3.2e). In early 2016, a coral bleaching event affected reefs in the central GBR region, yet surveys of Whitsunday reef slopes in late 2016 also indicated negligible impacts of the bleaching event on live hard coral cover. In early 2017 a second coral bleaching event impacted Whitsunday reefs, and in March 2017 Cyclone Debbie (category 4) severely impacted the Whitsunday Island group and resulted in an approximate 54% relative decline of live hard coral cover across all monitored (Fig. 3.2b). Cyclone Debbie likely dislodged dead coral colonies that were killed by the 2017 bleaching event and thus it is not possible to quantify the coral loss specifically attributable to the bleaching event from this dataset.

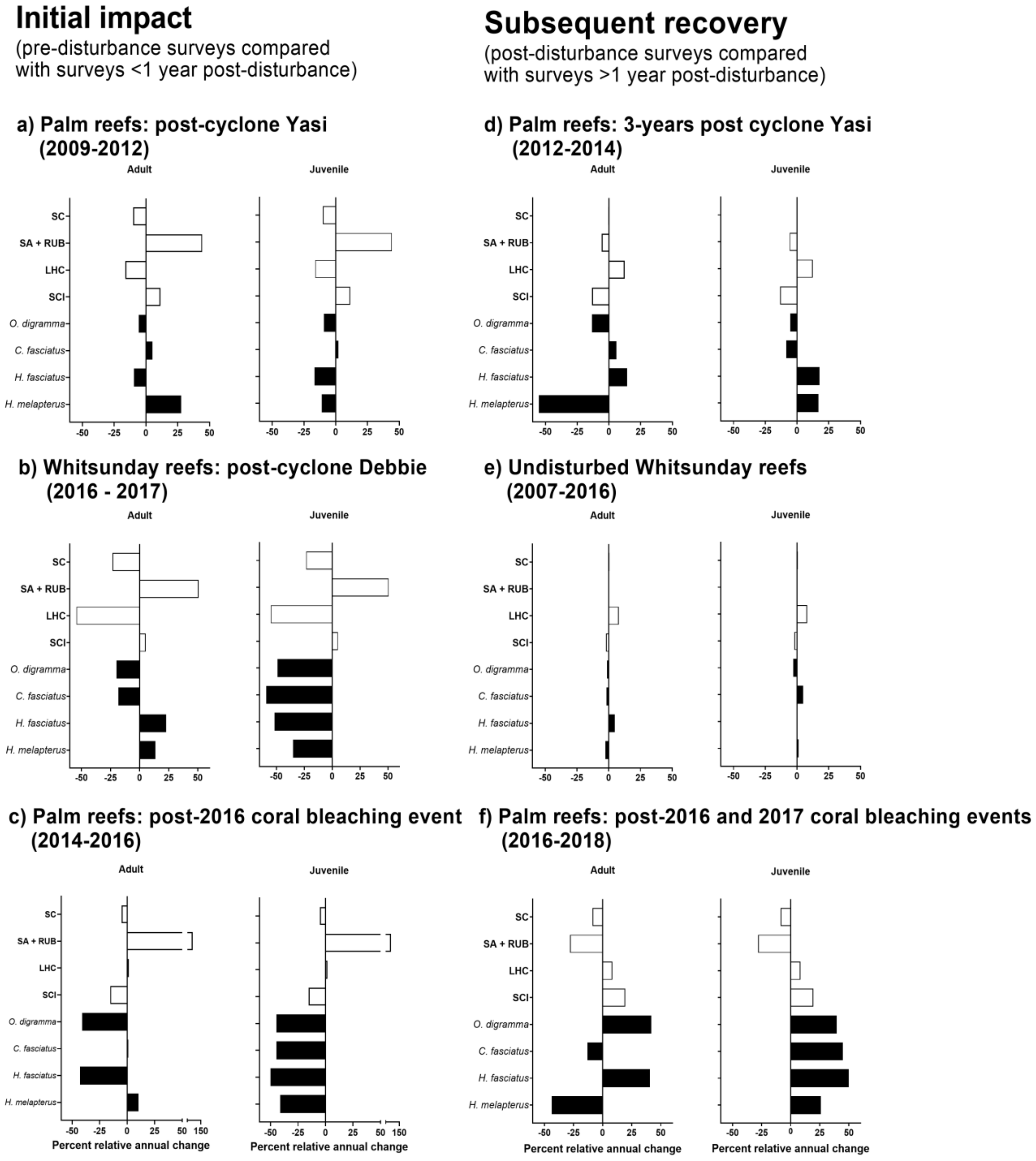


Figure 3. 2: Percent relative annual change in benthos (white bars) and the biomass of *Hemigymnus melapterus*, *Hemigymnus fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* (black bars) in response to environmental disturbances (left hand column) and periods of recovery (right hand column) on Palm and Whitsunday coral reefs between 2007 and 2018.

3.4.2 Effects of Disturbance-mediated Benthic Habitat Change on Juvenile and Adult Wrasse Biomass

Benthic components driving the biomass of juvenile and adult wrasses were largely consistent for each species at each island group (Table 3.1; Fig. 3.3). Yet, despite similar benthic predictors over 12 years, different biomass responses of juvenile and adult wrasses were evident within 1 year following environmental disturbance events at both the Palm and Whitsunday island groups. In almost all cases the biomass of juvenile *Hemigymnus* (both species), *C. fasciatus,* and *O. digramma* declined (Fig. 3.2a, b, c). In contrast, adult wrasses displayed variable biomass responses to disturbance-mediated habitat change, including some increases in biomass (Fig. 3.2a, b, c).

Table 3. 1: Optimal generalised additive mixed models (GAMMs) estimating effects of NTMR status, predator density (*Plectropomus* spp.), time (duration of protection), and cover of benthos on the biomass of juvenile and adult wrasses from 2007 to 2018 at the Palm and Whitsunday Island groups.

Location	**Taxa**	**Top Model**	**df**	**AICc**	**wAICc**
Palm Island group	Juvenile *C. fasciatus*	LHC + Status	2	6940	0.114
	Adult *C. fasciatus*	null	0	9261	0.26
	Juvenile *H. fasciatus*	Status + RUB x Status	8	5967	0.803
	Adult *H. fasciatus*	Time + Status + SA x Status	10	5840	0.777
	Juvenile *H. melapterus*	SCI	5	7082	0.484
	Adult *H. melapterus*	SCI	4	8572	0.221
	Juvenile *O. digramma*	SC + RUB + Predator density	3	5238	0.743
	Adult *O. digramma*	Status + Time x Status + SC x Status	13	6080	0.454
Whitsunday Island group	Juvenile *C. fasciatus*	LHC + RUB + Status	2	11044	0.588
	Adult *C. fasciatus*	LHC + SC	4	14705	0.182
	Juvenile *H. fasciatus*	LHC + SC + Status	4	9446	0.189
	Adult *H. fasciatus*	SA + Status + SCI x Status	5	8776	0.225
	Juvenile *H. melapterus*	LHC + RUB + SCI	3	11075	0.479
	Adult *H. melapterus*	Time + LHC	4	13454	0.202
	Juvenile *O. digramma*	SA + SC + SCI	3	8813	0.73
	Adult *O. digramma*	LHC + Status + SC x Status	8	10088	0.966

LHC = live hard corals, SC = soft corals, SA = sand, RUB = rubble, SCI = structural complexity, Time = duration of protection since NTMR implementation, Status = NTMR status (Fished, NTMR 1987, or NTMR 2004).

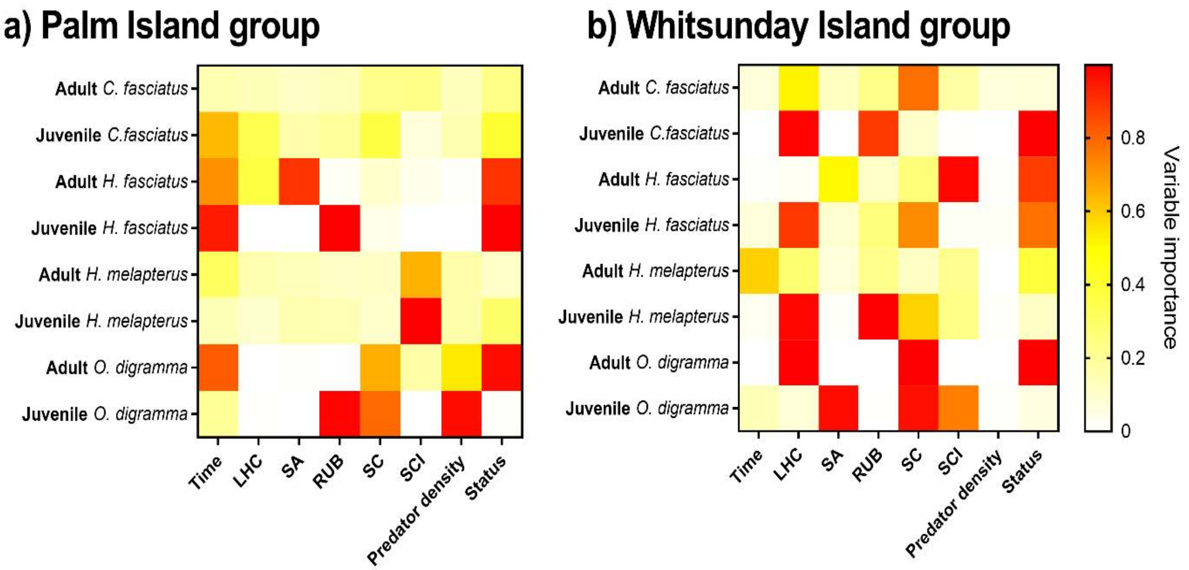


Figure 3. 3: Generalised additive mixed model (GAMM) heatmaps that display the importance of environmental drivers on adult and juvenile wrasse biomass at the Palm (a) and Whitsunday (b) Island groups from 2007 to 2018. LHC = live hard corals, SC = soft corals, RUB = rubble, SA = sand, SCI = structural complexity index, Predator density = density of *Plectropomus* spp. Status = NTMR status (NTMR1987, NTMR2004, or Fished). Blank squares represent variates that did not appear in top models (ΔAICc ≤ 2). Variates that did appear in taxa-specific 'important' models are represented as columns and were color coded according to summed AICc weights of all 'important' models for that species.

There was surprising temporal and spatial consistency in the decline of juvenile biomass at both the Palm and Whitsunday Island groups for most wrasse species following environmental disturbance events. Juvenile biomass often declined following both mechanical (cyclones) and biological (coral bleaching) disturbance events and biomass declines did not show any consistent trend with the magnitude of disturbance-mediated coral loss on reef slopes (Fig. 3.2a, b, c). However, biomass declines of juvenile wrasses on Palm Island reef flats following the spatially patchy impacts of Cyclone Yasi were less severe than following the impact of the 2016 coral bleaching event on reef flats, or Cyclone Debbie in the Whitsunday Islands which impacted a greater proportion of monitoring sites than Cyclone Yasi in the Palm Islands (Fig. 3.2). When undisturbed, juvenile and adult wrasses exhibited negligible biomass responses to benthic habitat change on undisturbed Whitsunday reefs from 2007 to 2016 (Fig. 3.2e).

Of the four species investigated, *O. digramma* appeared to be the most sensitive to coral loss, exhibiting consistent declines in adult and juvenile biomass immediately following (<1 yr) environmental disturbance events on Palm and Whitsunday reefs (Fig. 3.2a, b, c). Moreover, in the 3 years following Cyclone Yasi at the Palm Island group, the biomass of adult *O. digramma* continued to decline as the cover of soft corals remained low on these reefs (Fig. 3.2d, 4a). Similarly, the biomass responses of adult *Hemigymnus spp.* and *C. fasciatus* to habitat change could often be explained by benthic habitat relationships identified by the most parsimonious GAMM for each species at each island group (Table 1; Fig. 3.2a, b, c). Following environmental disturbance events, in most cases, the biomass of adult *Hemigymnus* spp. responded positively to increased structural complexity (Fig. 3.2 a, b, d) and adult *C. fasciatus* biomass often correlated positively with increased live hard coral cover (Fig. 3.2 b, c, d). Adult *O. digramma* biomass correlated positively with the cover of soft corals at the Palm Island group and cover of live hard corals at the Whitsunday Island group (Table 1; Fig. 3.2).

Surveys conducted in 2014 indicated that the biomass of *H. fasciatus* had begun to recover on Palm Islands reefs within 3 years of Cyclone Yasi (Fig. 3.2d). Conversely, the biomass of *O. digramma* continued to decline, while *C. fasciatus* and *H. melapterus* showed different biomass responses of adults and juveniles (Fig. 3.2d). Following the 2016 and 2017 coral bleaching events on Palm reef flats, which left the structural complexity of juvenile recruitment habitats intact, substantial increases in biomass of all juvenile wrasses investigated were evident within 1-year post-bleaching (Fig. 3.2f). Biomass increases of adult *O. digramma* and *H. fasciatus* were also evident. Conversely, the biomass of adult *H. melapterus* and *C. fasciatus* declined from 2016 to 2018 (Fig. 3.2f). Changes in wrasse biomass within 3 years post-disturbance, were significantly larger than biomass changes recorded on undisturbed Whitsunday reefs subject to natural fluctuations in larval supply from 2007 to 2016 (Fig. 3.2e).

Differential responses of juvenile and adult biomass to disturbance-mediated habitat change were most obvious for *H. melapterus* following cyclone and coral bleaching events on Palm and Whitsunday reefs, where adult biomass increased immediately post-disturbance, while juvenile biomass declined consistently (Fig. 3.2a, b, c, 3.4a, b). *Hemigymnus fasciatus* and *C. fasciatus* also typically exhibited variable biomass changes between adults and juveniles, with the biomass of juvenile wrasses declining substantially following Cyclone Debbie and bleaching events on Palm reefs, while adult biomass exhibited variable responses to disturbance impacts (Fig 3.2a, b, c, 3.4a, b). The biomass of juvenile *O. digramma* also declined strongly and consistently following environmental disturbance events, while adult *O. digramma* biomass declined in the longer-term with declining live hard coral and soft coral cover (Fig 2a, b, c, 3.4a, b). The recovery of wrasse biomass following the spatially patchy impact of cyclone Yasi, which removed live hard corals from exposed reefs in the Palm Islands, was variable across species and demographic stages (Fig. 3.2d, 3.4a). Conversely, the impact of cyclone Debbie on Whitsunday reefs in 2017, which impacted a large proportion of monitoring sites, resulted in consistent declines in the juvenile fish biomass for the four focal wrasses (Fig. 3.2b, 3.4b). Biomass recovery of wrasses on Palm reefs following the 2016 and 2017 coral bleaching events, which retained dead coral structure on reef flats, was consistently positive for all juvenile wrasses investigated (Fig. 3.2f, 3.4a).

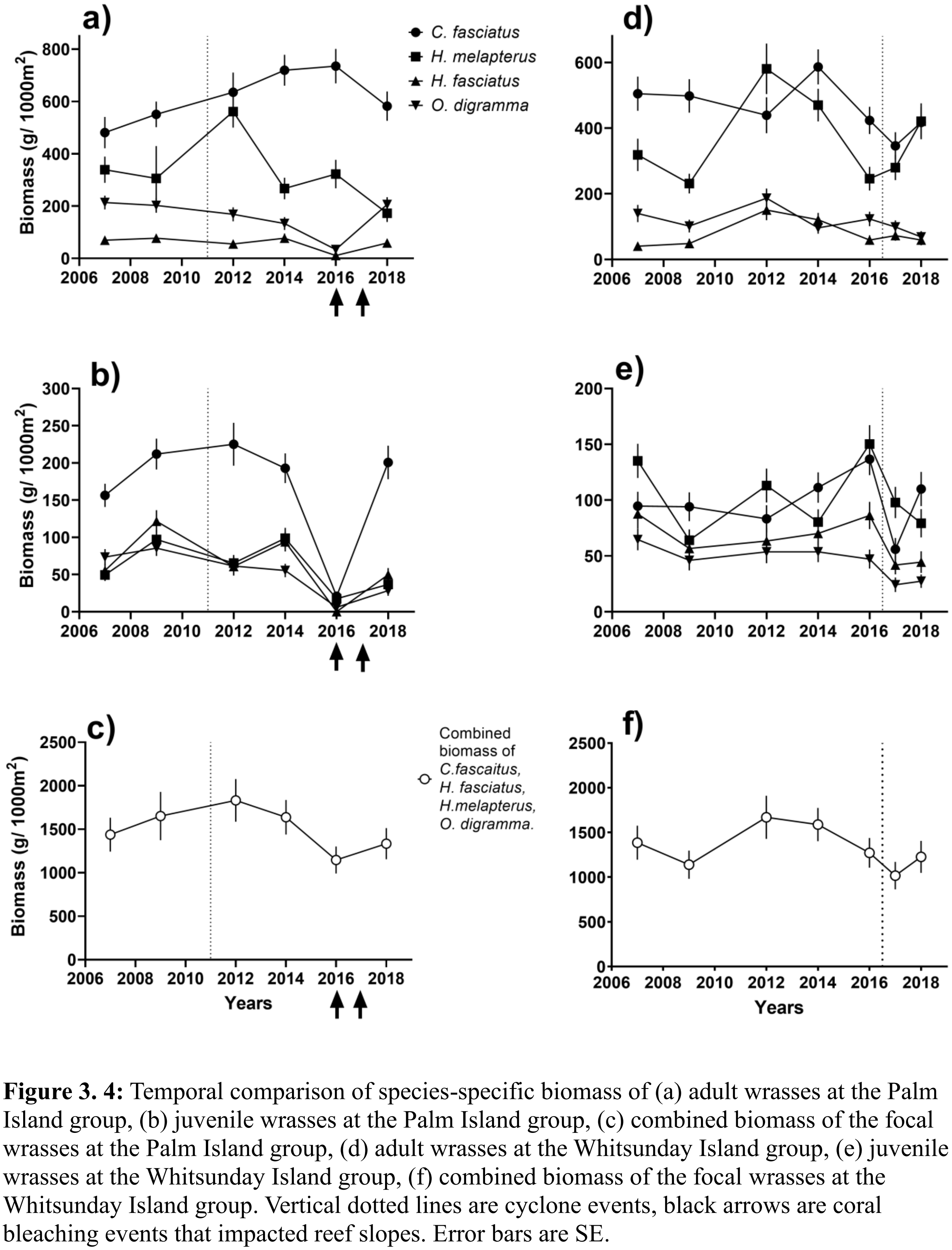


Figure 3. 4: Temporal comparison of species-specific biomass of (a) adult wrasses at the Palm Island group, (b) juvenile wrasses at the Palm Island group, (c) combined biomass of the focal wrasses at the Palm Island group, (d) adult wrasses at the Whitsunday Island group, (e) juvenile wrasses at the Whitsunday Island group, (f) combined biomass of the focal wrasses at the Whitsunday Island group. Vertical dotted lines are cyclone events, black arrows are coral bleaching events that impacted reef slopes. Error bars are SE.

3.4.3 Effects of NTMR Protection and Predator Density on the Biomass of Juvenile and Adult Wrasses

At both the Palm and Whitsunday Island groups, benthic variables were the predominant drivers of juvenile and adult biomass for all focal wrasse species, rather than NTMR protection or the density of *Plectropomus* spp. (Table 3.1; Fig. 3.3). Although GAMMs suggested that NTMR protection was an important predictor of adult *O. digramma* biomass at the Palm Island group (Table 3.1), long-term plots revealed these positive effects were temporary. Juvenile *O. digramma* biomass had a positive relationship with predator density through time at the Palm Islands, however other focal species did not show effects of predator density or NTMR protection within top-ranked models (Table 3.1; Fig. 3.3). Caution must be taken when interpreting drivers of adult *C. fasciatus* biomass on Palm Island reefs due to the presence of a null model (where all terms are zero) within top models ($\Delta \text{AICc} \leq 2$) (Table 3.1; Fig. 3.3). Wrasse biomass on Palm and Whitsunday reefs was generally driven by a species- and size-specific combination of live hard coral, soft coral, rubble, sand, and habitat complexity (Table 3.1; Fig. 3.3).

3.5 Discussion

This study is the first to assess the impacts of multiple environmental disturbance events, predator density and NTMR protection on the demographic structure of wrasse assemblages over a large spatial (≈ 350 km) and temporal scale (2007 – 2018). My findings are consistent with previous partitioning of NTMR and habitat effects on coral reef wrasse populations and suggests that the biomass of wrasses is driven primarily by benthic habitat characteristics, rather than NTMR protection or the density of wrasse predators (Russ *et al.*, 2017; Lowe *et al.*, 2019). Furthermore, while adult wrasses exhibit minor biomass responses to environmental disturbance events, the biomass of juvenile wrasses often declines significantly following disturbance events. This may have profound implications for population persistence as severe climatic disturbances become more frequent in coral reef ecosystems (Hoegh-Guldberg *et al.*, 2007; Knutson *et al.*, 2010; Hughes *et al.*, 2017a).

My findings suggest that environmental disturbance events have significant negative impacts on the biomass of juvenile wrasses on inshore GBR coral reefs, irrespective of species-specific habitat relationships of wrasses or the nature of the disturbance (coral bleaching or cyclone). Juvenile wrasse biomass declines were most obvious following the 2016 coral bleaching event at the Palm Island group, despite only minor levels of bleaching reported on reef flats (Hughes *et al.*, 2017b; Thompson *et al.*, 2018). Interestingly, results from the present study and those from the Australian Intitute of Marine Science Marine Monitoring Program (AIMS MMP) report coral cover increases on reef slopes and reef flats of the Palm Island group following the 2016 coral bleaching event (Thompson *et al.*, 2018). However, the strong and consitent declines in biomass of juvenile *Hemigymnus melapterus*, *H. fasciatus*, and *C. fasciatus* on Palm Islands reefs was possibly due to a direct effect of heat stress on small-bodied wrasses or negative impacts of coral bleaching on the invertebrate community that wrasses prey on, rather than due to habitat changes (Stella *et al.*, 2011; Stuart-Smith *et al.*, 2018). In contrast, the patchy impact of Cyclone Yasi resulted in greater than 50% loss of live hard coral cover, but more moderate declines of juvenile wrasse biomass, possibly due to less dramatic impacts on the invertebrate prey community on inmapcted reefs (Stella *et al.*, 2011; Kramer *et al.*, 2015; Ceccarelli *et al.*, 2019). My findings further support the conclusions of Graham *et al.*, (2011), which suggested that micro-invertivores, such as tropical wrasses, have a low extinction risk from fishing but a moderate extinction risk from environmental disturbances related to climate change. In the absence of annual settlement and recruitment data for the focal wrasses at the monitored reefs it is diffult to ascertain what future effects siginifcant reductions in juvenile wrasse biomass may have on abundance of the larger size classes, population recovery, and long-term persistence. However, environmentally-induced declines in biomass of post-settlement juvenile wrasses documented here will likely result in weak year classes in the age structure of the populations, possibly resulting in a future decline in adult abundance. Both strong and weak age classes are well known to affect population size in commercially exploited teleost fish (Hjort 1914; Hilborn and Walters 1992; Russ *et al.*, 1996).

Differences in biomass responses between juvenile and adult size classes were most likely driven by reduced juvenile recruitment to reef flat habitats following environmental disturbance events on the monitored reefs. Conversely, adults of the wrasses examined here commonly reside on reef crests and slopes rather than reef flats, and only responded moderately to environmental disturbance events. Deeper reef slope habitats were less impacted by cyclone and bleaching disturbances than shallow reef flats and this may largely explain the observed weaker effects of disturbances on adult than juvenile wrasses (Marshall and Baird 2000; Jones and Berkelmans 2014). Previous studies have observed that some degree of live coral cover on reef flats / lagoons is important for the successful recruitment of *Hemigymnus*, *Cheilinus* and *Oxycheilinus* wrasses (Lieske and Myers, 1994; Wilson *et al.*, 2010a; Coker *et al.*, 2014). It is likely that the amount of suitable recruitment habitat for the wrasse species studied here declined on heavily impacted reef flats following cyclones and thermal disturbances at the Palm and Whitsunday Islands, and consequently fewer juvenile wrasses survived to emigrate onto reef slopes within 1 year of the disturbance. It is plausible that biomass changes on reef slopes may reflect changes in recruitment success on the reef flat for the focal wrasses, as all four species are capable of reaching sexual maturity within 1 year of settlement/recruitment (Lowe *unpublished data*) and have been reported to emigrate from shallow lagoons to reef slopes soon after settlement (Eckert, 1987). Other studies of wrasses recruiting to GBR reef flats and lagoons also report density declines for juvenile wrasses following experimental disturbance events that reduced live coral cover and fine-scale rugosity (Syms and Jones 2000). The importance of suitable benthic settlement habitat for the focal wrasses is critical, when one considers that larval settlement and recruitment to reefs is highly variable in time and space, and is often driven by seasonal and oceanographic conditions (Russell *et al.*, 1977; Eckert 1984; Sale *et al.*, 1984). Yet, despite biennial surveys often occurring in different seasons (summer, winter, autumn, spring; Appendix 3.2), the biomass of juvenile wrasses declined strongly and consistently following environmental disturbance events. This suggests that the observed temporally consistent relationships between juvenile wrasse biomass and benthic cover are driven by changes in benthic community composition, rather than fluctuations in wrasse larval supply and recruitment. However, if oceanographic currents of the GBR were impacted by extended periods of elevated sea surface tempratures in 2016 and 2017, as they were in 2004 (DeCarlo and Harrison 2019), changes in larval supply to inshore reefs may have exacerbated declines of juvenile biomass (Cheal *et al.*, 2007; Bode *et al.*, 2019; DeCarlo and Harrison 2019). Excluding reduced recruitment success on disturbed reef flats, other possible drivers of short-term reductions in the biomass of juvenile wrasses following environmental disturbance events include temporary increases in predation on juvenile wrasses due to the rapid decline of other prey taxa following disturbance events (Wen *et al.*, 2016; Hempson *et al.*, 2017), increased predation of juvenile wrasses due to disturbance-mediated declines in fine-scale rugosity (Syms and Jones 2000; Almany 2004; Wilson *et al.*, 2010b), or disturbance-mediated changes in the invertebrate prey community (Stella *et al.*, 2011) and thus food availability for juvenile wrasses (Kramer *et al.*, 2015).

Results presented here are consistent with those of Graham *et al.*, (2007) and Wilson *et al.*, (2010b), who reported consistent density declines of juvenile reef fish smaller than 20cm and 30cm, respectively, following coral bleaching and outbreaks of crown of thorns starfish in Fiji, and following reductions in structural complexity of benthos in the Seychelles. However, the present study builds on these observations and demonstrates that negative effects of environmental disturbance events on the biomass of juvenile wrasses are consistent spatially and temporally, spanning multiple cycles of benthic disturbance and recovery on inshore GBR reefs. Moreover, by splitting biomass estimates for each species according to demographically informed age of sexual maturity (Appendix 3.1, 3.3), rather than at arbitrary lengths as in Graham *et al.*, (2007) and Wilson *et al.*, (2010b), results presented here are suitable for modelling projections of recovery of wrasse populations following environmental disturbance events. Yet, I stress that in order to model projections of wrasse biomass based on results presented here, species-specific demographic information, and studies conducted on reef flats where juvenile wrasses recruit, are required.

My results suggest that temporal changes of *Hemigymnus* spp. (both species) and *C. fasciatus* biomass on inshore reefs over the 12-year monitoring period were primarily driven by changes in the biomass of juvenile wrasses, rather than by biomass fluctuations of adults. Irrespective of the mechanism, environmental disturbance events on inshore GBR reefs consistently resulted in fewer fish in small size classes surviving to replace adults, and a subsequent lagged decline in overall wrasse density seems likely (Graham *et al.*, 2007). Results presented here may explain the observed time lag in the decline of *Hemigymnus* density following environmental disturbances to coral reefs in the Philippines (Russ *et al.*, 2017) and on the GBR (Lowe *et al.*, 2019).

Encouragingly, significant disturbance-mediated biomass declines of juvenile wrasses following cyclones and coral bleaching events appear temporary, with biomass recovery evident within 3 years post-disturbance. Rapid recovery of juvenile biomass on inshore reef slopes of the GBR following environmental disturbance events in the present study suggest that the focal wrasse species remain moderately resilient to the current rate and intensity of impacts from climatic disturbances.

Compared to juvenile wrasses, the biomass responses of large-bodied, adult wrasses to environmental disturbance events on inshore reefs appear much more variable but could often be explained by fish-habitat relationships. Depending on the island group, the biomass of adult *Hemigymnus* spp. often correlated positively with increased structural complexity, adult *C. fasciatus* biomass correlated positively with the cover of live hard corals, and adult *O. digramma* biomass correlated positively with increased cover of soft corals and hard coral cover. Species-specific wrasse-habitat relationships were previously identified by Lowe *et al.*, (2019), however, this study confirms the importance of these benthic components for the focal adult spawning wrasses. Studies from Japan and the Philippines also report positive relationships between abundance of *Hemigymnus* spp. and the cover of live hard corals and structural complexity (Sano *et al.*, 1987; Nanami *et al.*, 2005; Russ *et al.*, 2017). Biomass responses of *C. fasciatus* with hard-coral cover were somewhat expected, as this species is known to prefer sheltered sites (Fulton *et al.*, 2013) with high structural complexity (Nanami *et al.*, 2005), often provided by hard corals on inshore GBR reefs. Moreover, a recent study from the Seychelles reports post-bleaching declines in *H. melapterus* and *C. fasciatus* biomass over 20 years as structural complexity degraded long-term (Robinson *et al.*, 2019). The positive relationship between *O. digramma* biomass and the cover of soft corals and live branching corals was also consistent with previous studies, as *O. digramma* are known to ambush prey from the cover of soft corals and *Acropora* spp. (Kuiter 2002; Lowe *et al.*, 2019).

Due to the low fishing pressure exerted on large-bodied wrasses on GBR reefs, one might expect there to be no direct NTMR effects on the biomass of juvenile or adult wrasses, even after 31 years of NTMR protection on these reefs. My results largely support this, despite GAMMs detecting temporary biomass increases of *O. digramma* in new NTMRs at the Palm Island group, as the cover of soft corals also increased. Moreover, NTMR reefs in the Palm and Whitsunday Island group can support three to four times higher biomass of coral grouper (*Plectropomus* spp.) than fished reefs (Evans and Russ 2004; Williamson *et al.*, 2004), and given that *Plectropomus* spp. regularly prey on labrids (St John *et al.*, 1999, 2001; Wen *et al.*, 2016), a negative relationship between predator and prey biomass may have been expected. Given that Graham *et* *al.*, (2003) found that high biomass of predators in NTMRs reduced the abundance of a suite of small bodied prey species on Palm and Whitsunday reefs, the lack of predator effects on the focal wrasses on NTMR reefs was somewhat unexpected, but consistent with findings of Lowe *et al.*, (2019). Failure to detect predator effects on wrasses within NTMRs that support higher biomass of wrasse predators is likely due to the opportunistic feeding nature of the predators and the high diversity of their potential prey on coral reefs, which dilutes top-down trophic effects (Boaden and Kingsford, 2015). It is possible that top-down predator effects on wrasse densities would be more apparent on reefs with very stable habitat structure over extended time periods (Boaden and Kingsford, 2015). Moreover, in the present study, it is likely that frequent changes in benthic cover and simultanious changes in the abundance of predators and prey made direct and indirect predator effects difficult to detect. Consequently, the temporal span and dynamic nature of the benthic and fish assembalages in the present study,may at least partly explain the disparity between my findings and those of Graham *et al.*, (2003).

In recent decades, many studies have reported the impacts of environmental disturbance events on the abundance of reef fishes, yet few of these have investigated disturbance-mediated impacts on the demographic structure of affected fish populations. Results presented here suggest that juvenile wrasse biomass on inshore reefs of the GBR are quite sensitive to the immediate impacts of environmental disturbance events. These findings, along with those of Lowe *et al.*, (2019), suggest that temporal fluctuations of wrasses on inshore reefs are more strongly driven by juvenile survival following environmental disturbance events than changes in adult mortality or larval supply. However, identifying mechanisms driving disturbance-mediated declines in juvenile wrasse biomass on inshore GBR islands remains a priority, particularly in the face of climate change and changing disturbance regimes (Hoegh-Guldberg *et al.*, 2007; Knutson *et al.*, 2010; Hughes *et al.*, 2017a). The consistent negative effects of environmental disturbance events on juvenile wrasse biomass reported here may suggest wrasse populations are more susceptible to habitat degradation in the long-term than previously thought (Graham *et al.*, 2011b; Russ *et al.*, 2017; Lowe *et al.*, 2019). As the frequency and severity of disturbance events increase as climate change progresses, identifying ecological and demographic drivers of reef fish populations derived from long-term robust sampling programs should be treated as a priority in coral reef ecology and conservation. This is particularly relevant for fishery-targeted species that do not benefit strongly from long-term NTMR protection, such as wrasses on Philippine reefs (Russ *et al.*, 2017), for which NTMRs will be unlikely to provide recruitment subsidies or adult spill over to fished areas. NTMRs are not the only management tool available. It is critically important to minimise other environmental stressors, such as climate change and water quality, to create recovery conditions where population replenishment may be possible if brood stocks are available.

Chapter 4: Spatial Variability in the Early Gonadal Development and Sexual Ontogeny of *Hemigymnus, Cheilinus,* and *Oxycheilinus* Wrasses Among Indo-Pacific Coral Reefs

4.1 Abstract

Patterns of reproductive ontogeny in four species of coral reef wrasses (F: Labridae) *Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus,* and *Oxycheilinus digramma* were investigated. Populations of each species were sampled from two unfished island groups of the central Great Barrier Reef (GBR), Australia and from heavily fished coral reefs in the central Philippines. These three sampling locations span 30° of latitude. The GBR and Philippine reefs have distinct differences in water temperature, geography, and human activity. Gonad histology and demographic information were obtained across the entire size and age range of *H. melapterus, C. fasciatus,* and *O. digramma* from the GBR and the Philippine reefs. Analysis identified three methods of male recruitment into wrasse populations; functional gonochorism and both forms of protogynous hermaphroditism, monandry and diandry. The expression of these different sexual ontogenies was locality dependent. Populations of the four species (the three indicated above, plus *H. fasciatus*) on the GBR showed consistently simple patterns of sexual ontogeny, with all species being exclusively monandric, as all males were recruited by transition from mature females. The three species investigated in the Philippines displayed complex sexual ontogenies, with all species displaying histological evidence of both diandry and functional gonochorism. Reproductive investment in gonadal tissue, and population sexual structure, also differed between GBR and Philippine coral reefs. Philippine populations had substantially lower gonadosomatic indices than populations on the GBR. However, Philippine populations matured more rapidly and displayed a protracted timing of sex change over a large size and age range. Thus, mature females appeared earlier and persisted later into ontogeny in the Philippines than on GBR reefs. Protracted timing of sex change on Philippine reefs is likely linked to the presence of primary males in the population, which likely reduced the strength of selection for mature females to undergo sex change and become male. Hypotheses based on social structure of fish populations, environmental factors, and evolutionary history were developed to account for the frequent appearances of functional gonochorism in the focal wrasses in the Philippines.

4.2 Introduction

A diversity of sexual patterns exists in teleost fishes, which in turn points to equally complex patterns of reproductive biology and ecology. These include gonochorism, where individuals function as a female or male, and hermaphroditism, where individuals function as both sexes, either simultaneously or sequentially (Avise and Mank, 2009). Additionally, protogynous hermaphrodites can be either monandric, where all males derive from functionally mature females (i.e., secondary males); or diandric, where males are both born directly into the population (i.e., primary males) and are also derived from functional females (i.e., secondary males; Sadovy De Mitcheson and Lui, 2008). The challenge is to develop the description of sexual patterns into explanatory analyses of the underlying processes that drive functional biology development (Sadovy De Mitcheson and Liu, 2008; Erisman *et al.*, 2009; Kazancıoğlu and Alonzo, 2010).

Anatomical classification based on microscopic and macroscopic analysis of gonad structure has been the method of choice for evaluating the behavioural and ecological features associated with the diverse sexual patterns in teleost fish. Chief among these has been the use of male testicular morphology to distinguish patterns of male recruitment into populations, manifested as monandry and diandry (Atz, 1964; Devlin and Nagahama, 2002). Yet, difficulties arise because although gonad structure can suggest phylogenetic relationships, it does not always reflect reproductive function (e.g., Roede, 1975). Specifically, the distinction between functional hermaphroditism, in which an individual acts as both sexes during its life (e.g., protogyny), and non-functional hermaphroditism, where the sexual pattern is gonochoristic despite the animal possessing both testicular and ovarian tissues, has generated considerable difficulty and controversy among scientists (reviewed in Sadovy De Mitcheson and Liu, 2008). For example, in protogynous Epinephelidae and Labridae some testes are secondary in anatomical configuration but occur in individuals that have not passed through a functional female phase (Warner and Robertson, 1978; Fennessy and Sadovy, 2002; Adams, 2003). In other species, males develop prior to maturation, with their gonads appearing bisexual in configuration, which means that they are not functionally protogynous, but rather are functional gonochores (Hamilton *et al.*, 2008). Yet, whether sex ‘change’ has occurred in individuals that have not yet differentiated sexually (i.e., differentiated pre-maturationally) according to histological criteria, remains unclear (Liu and Sadovy, 2004a; Sadovy De Mitcheson and Liu, 2008).

The use of gonad anatomy as a guide to functional biology has been most effective through detailed histological examination. This is exemplified by analyses that have examined the lack of concordance between the testicular morphology and functional male development (Sadovy De Mitcheson and Liu, 2008). The use of histological examination to distinguish the sexual developmental pathways leading to different male identities is a case in point. This is particularly important for determining the significance of sexual ontogeny in the life history of a species (i.e., do males function exclusively as males, or as females first and then males?) (Avise and Mank, 2009; Hodge *et al.*, 2020). Indeed, phylogenetic analyses of diverse groups of teleosts with complex sexual ontogenies, specifically the Epinephelinae (Erisman *et al.*, 2009) and the Labridae (Kazancıoğlu and Alonzo, 2010), have been developed based on gonad anatomy.

A substantial literature has demonstrated that patterns of sexual development in reef fishes are highly flexible and can be influenced by local social conditions (Robertson and Choat, 1974; Warner *et al.*, 1975; Warner, 1984). An added complication is that modes of sexual ontogeny may also be sensitive to variation in environmental factors (Munday *et al.*, 2006b), particularly when juveniles enter an unpredictable, heterogeneous environment where certain sexes are favoured in particular habitats (Charnov and Bull, 1977). Yet, a better understanding of which environmental conditions, social factors, and mating systems may influence the functional sexual patterns of teleost fish is required (Warner 1991; Munday *et al.*, 2006b; Hodge *et al.*, 2020). Importantly, the mode of sexual development will impact upon almost all biological rates, including maturation, population turnover, lifetime reproductive output, and thus resilience to environmental perturbations and fishing (Stearns, 1992; Petersen and Warner, 2002; Alonzo *et al.*, 2008). As such, it is important to understand the species-specific mode of sexual development, and whether it varies spatially prior to comparing demographic rates (Petersen and Warner, 2002; Munday *et al.*, 2006a, 2006b).

Reef-fishes from the family Labridae (wrasses, parrotfishes, and odacines) are a species-rich group that display considerable demographic flexibility. Labrids have often been used as a model in studies of reef fish life history evolution (Robertson and Choat, 1974; Choat and Robertson, 1975; Dipper and Pullin, 1979; Jones, 1980; Charnov, 1982; Warner, 1984). Labrids can be gonochoristic, or express both types of protogyny, monandry and diandry, depending upon the magnitude of social control that large males have over females, or on the availability of resources on which females depend (Robertson and Choat, 1974; Warner *et al.*, 1975; Warner and Robertson, 1978). Sexual ontogenies are thought to initiate in very young reef fish, either genetically or prior to sexual maturity, thus it is important to examine gonads of pre-maturational individuals when possible (Charnov and Bull, 1977; Jones, 1980). Yet, to date, the sexual developmental pathways of juvenile labrids is poorly understood, impeding our ability to distinguish sexual patterns. Once comprehensive descriptions of sexual ontogenies, and their variation in space and time, have been made, the adaptive significance of functional sexual patterns and their utility as a phylogenetic character can be discussed (Munday *et al.*, 2006b; Sadovy De Mitcheson and Liu, 2008; Hodge *et al.*, 2020).

Here, I compare detailed reproductive information for four large-bodied labrids, *Hemigymnus melapterus*, *Hemigymnus fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma*, on a regional scale, between two inshore island groups of the Great Barrier Reef, Australia (GBR) separated by 2° of latitude (350km), and on a biogeographic scale, spanning 30° of latitude, between unfished GBR and fished Philippine populations. Such reproductive data have not previously been determined in detail for these species. Specifically, this study will address the following questions:

1. Is the early gonadal development and mode of sexual ontogeny of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* consistent across species and/or locations?
2. Does species-specific investment in reproductive tissue differ spatially between GBR coral reefs, or between high latitude GBR and low-latitude Philippine coral reefs?
3. Are there differences in the population structure of *H. melapterus, H. fasciatus*, *C. fasciatus* and *O. digramma*, between GBR coral reefs, or between GBR and Philippine coral reefs?

Philippine and GBR coral reefs located at each end of this latitudinal gradient have very different histories, present day configurations, and are subject to different anthropogenic impacts (e.g., fishing pressure) (Carpenter and Springer, 2005; Hopley *et al.*, 2007). Moreover, the focal wrasse populations on GBR reefs, separated by only 2° of latitude, have been subject to different environmental disturbance histories and thus population dynamics (Lowe *et al.*, 2019; 2020). Historical fishing effort and environmental differences between GBR reefs, and GBR and Philippine reefs, may influence demographic and reproductive characteristics of these species.

For this reason, I investigate whether inter- and intra-specific variation in reproductive biology is evident across multiple spatial scales.

4.3 Materials and Methods

4.3.1 Study Species and Location of Sampling Sites

Hemigymnus melapterus, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* are widespread, common components of tropical coral reef labrid assemblages that are increasingly subject to exploitation by artisanal fisheries in developing regions of the Indo-Pacific. Conversely in developed nations, such as Australia, these wrasses are rarely targeted by commercial or recreational fishers. Despite their historical importance in reef fisheries of the Indo-Pacific, no published age-based demographic assessments exist for these species of wrasses. Multiple studies suggest negligible impacts of fishing pressure, but strong effects of habitat variation, on the abundance of these species of wrasse (Russ *et al.*, 2017). Yet, the relative extent to which biological factors and fishing influence the reproductive traits of these species is unknown. *Hemigymnus melapterus* and *H. fasciatus* grow to 60cm and 50cm TL, respectively, and are two of the largest species in the crown Julidine clade of wrasses (Kuiter, 2002; Westneat and Alvaro, 2005). *Cheilinus fasciatus* and *O. digramma* grow to 36cm and 30cm TL, respectively, and form a clade with the parrotfishes (scarines), a group also characterised by large body size (Kuiter, 2002; Clements *et al.*, 2004; Westneat and Alvaro, 2005).

Hemigymnus melapterus, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* were collected from fringing coral reefs surrounding the Palm and Whitsunday Island groups in the central GBR and purchased from fish markets in the southern Philippines (Fig. 4.1). The Palm and Whitsunday Island groups are inshore island groups in the central GBR (18°34′ S, 146°29′ E; 20°08′ S, 148°56′ E). Exposed sides of these islands are structurally complex and dominated by branching corals, while westward, sheltered sides of each island are characterised by a gradual reef slope with little bottom relief. Major habitats of juvenile and adult *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* were sampled at collection sites at each island group between 2016 and 2019 (Fig. 4.1). Philippine samples were purchased primarily from fish markets in Dumaguete, Negros Oriental, Philippines (Fig. 4.1).

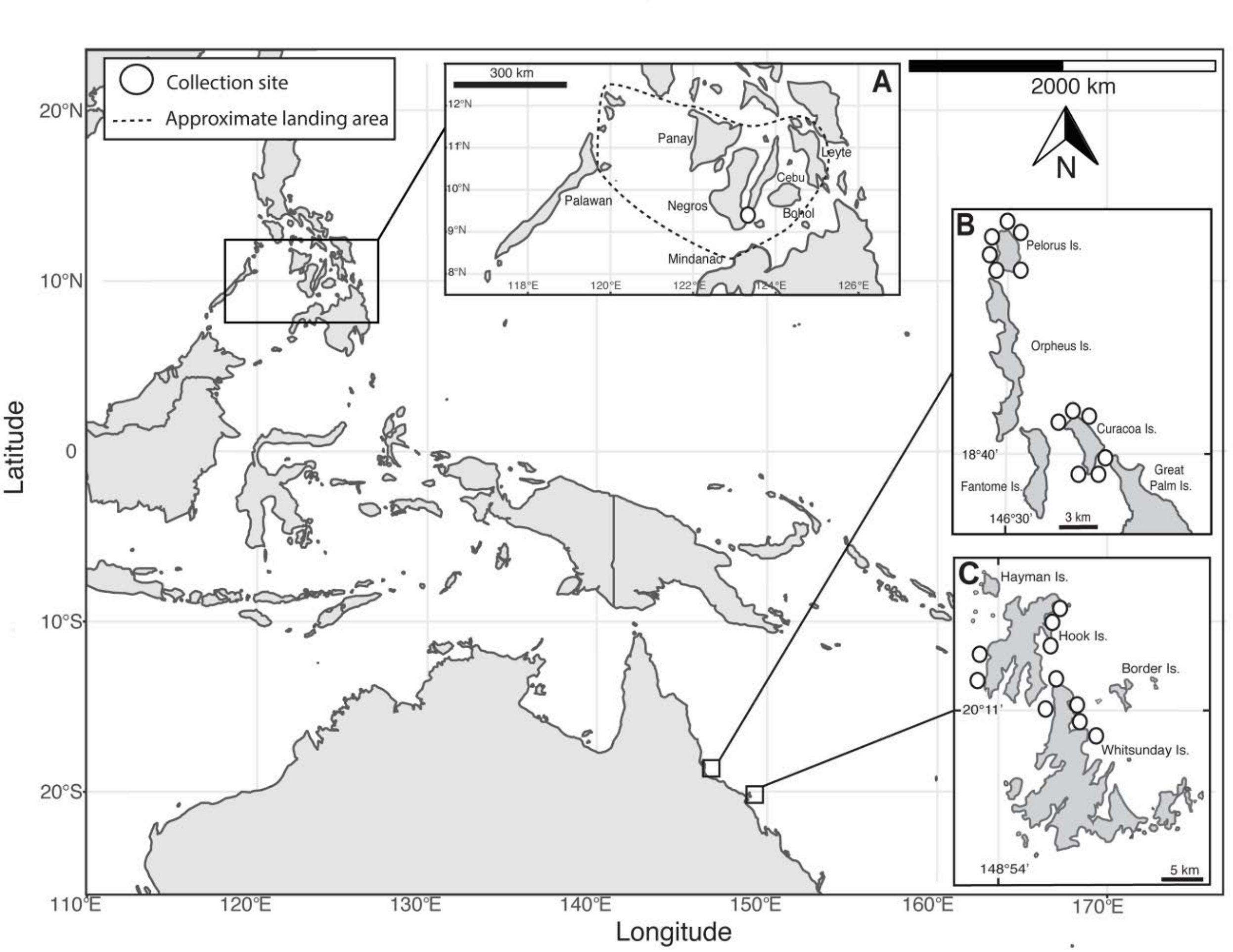


Figure 4. 1: Map of primary collection sites indicating the likely landing area of fishery-dependent samples collected from fish markets in the Philippines (A) and of fishery-independent sampling at the Palm (B) and Whitsunday (C) Island Groups, GBR, Australia.

4.3.2 Sample Collection

Fishery-independent sampling of *H. melapterus*, *H. fasciatus*, *C. fasciatus* and *O. digramma* was undertaken using spears on SCUBA at depths of 1-12m on fringing coral reefs of the Palm and Whitsunday Island groups, GBR, Australia. Philippine samples were purchased primarily from fish markets in south-eastern Negros Island (Fig. 4.1A). In the Philippines it was not possible to track the source reef of each purchased wrasse specimen, but conversations with fish vendors indicated supply chains that were quite short (reefs in the vicinity of Negros) as well as those that originated from reefs as far as 300 – 500 km away (e.g., Palawan) (Fig. 4.1A). Adult wrasse samples from the Philippines were often caught with spearguns or fish traps, while juveniles were commonly caught in gill nets.

In total, 309 *H. melapterus*, 225 *C. fasciatus,* and 216 *O. digramma* were collected from the Great Barrier Reef, Australia and from fish markets in the Philippines (see Table 5.1 for location-specific sample sizes). *Hemigymnus fasciatus* were rare in Philippine fish markets surveyed from October to December 2019 and consequently reproductive data for *H. fasciatus* were obtained only from 115 fish collected across reefs of the Palm and Whitsunday island groups, GBR. Once fish were purchased or collected, they were placed on ice and processed immediately on return to the closest research station or processing area. The body size of both *Hemigymnus* spp. and *O. digramma* was recorded as total length (TL; nearest mm) due to their rounded tail. Conversely fork length (FL; nearest mm) was used for *C. fasciatus* due to its emarginate tail with pronounced dorsal and ventral lobes (in adults) which were commonly damaged at the tips prior to, or during sampling. Total weight (W; nearest 0.1 g) was also recorded for each specimen. Age was estimated for each individual through interpretation of putative annual increments in the microstructure of sectioned sagittal otoliths (see Chapter 5).

4.3.3 Histological Processing

At the time of processing, gonads were dissected from each specimen and weighed whole (gonad weight in g; GW). Gonads were subsequently placed in formaldehyde acetic-acid calcium-carbonate fixative (FAACC) for 2-4 weeks, before being sectioned into proximal, medial, and distal sections, and placed into histology cassettes immersed in 70% ethanol. An analysis of a 20-individual sub-sample per species indicated that histological sections showed no variation in reproductive stage between left and right gonad lobes sectioned, but proximal, medial, and distal sectioning of *Hemigymnus*, *Cheilinus* and *Oxycheilinus* gonads was deemed necessary due to the inconsistency of gonad development longitudinally (Appendix 4.1). Consequently, transverse sectioning of the proximal, medial, and distal regions of one randomly chosen gonad lobe accurately represented reproductive developmental stage and sexual identity of each individual.

Histology cassettes containing the proximal, medial, and distal gonad sections of each individual were placed into 70% ethanol for 24 – 48 hours. , Then, sections were dehydrated via an Automatic Tissue Processor, embedded in paraffin wax, sectioned at 5µm, mounted onto glass microscope slides, and stained with Mayers Haematoxylin and Young’s eosin–erythrosine (H&E). Histological sections of each species were later examined blind with respect to collection location, age, and size under a high-power microscope with transmitted light. Samples were interpreted for sexual identity and stage of sexual development based on the most mature germinal cells present in the proximal, medial, and distal sections of each individual gonad.

4.3.4 Histological Interpretation

4.3.4.1 Stages of Maturation and Reproductive Function

Reproductive stages were based upon the histological examination of gonad morphology from West (1990) and Ackerman (2004).

Ovary F1: immature female with chromatin nuclear (stage 1) and peri-nuclear (stage 2) oocytes. Gonad is lamellar in structure, with thin gonad wall, and no indication of previous spawning (no post-ovulatory follicles, brown bodies, atretic oocytes, or intra-lamellar bundles).

F2: ripe females with stage 1, 2, and cortical alveoli (stage 3) oocytes present. Previous spawning indicated by post-ovulatory follicles, brown bodies, thick gonad wall, and/or intra-lamellar bundles. Oocytes may be atretic. Developing females may be sexually immature and lack signs of spawning.

F3: running ripe female. Oocytes of stages 1, 2, 3, and vitellogenic, hydrating oocytes (stage 4) present. Degenerating stage 3 and stage 2 oocytes also present.

F4: spent female. Oocytes of stages 1, 2, 3, 4, and hydrated (stage 5) oocytes present; recent spawning indicated by post-ovulatory follicles (POFs), atresia of vitellogenic oocytes, and generally disrupted appearance of gonad. The ovarian wall may be thick in recently post-spawned females. The ovarian wall contracts post-spawning.

Transitional: Degenerating atretic oocytes with proliferating spermatogenic tissue. Gonad has lamellar structure and post-ovulatory follicles indicating previous female function. Interlamellar bundles and stage 1 and 2 oocytes are common. Proliferating spermatogenic tissue is evident throughout gonad and does not only appear in islets positioned towards the gonad periphery, as in bisexuals (see below).

Testis: immature or mature males (M) with evidence of spermatogenesis. If mature, spermatozoa tails within individual cysts are evident and sperm sinus containing sperm are present. In post-spawning males, seminiferous lobules are collapsed and partially empty, and stages of early spermatogenesis, and gonia are apparent. Lamellar structure indicates previous-female function (i.e., secondary male), while non-lamellar structure or the presence of efferent ductules (which connect the rete testis to the head of the epididymis) in the proximal section indicates direct male development (i.e., primary male). In some secondary males, occasional occurrence of previtellogenic oocytes scattered within mature testicular tissue was evident, but these isolated cells are assumed to be of little functional significance and thus these individuals were not characterised as bisexuals (Fennessy and Sadovy, 2002).

4.3.4.2 Bisexual Stages of Gonad Development

Individuals with gonads containing both ovarian and testicular tissues at different stages of development (both immature and mature), or gonads containing both ovarian and presumptive testicular tissue, were defined as bisexuals based on anatomical structure. The term bisexual refers to gonad morphology only and not gonad function. Following Sadovy and Domeier (2005), the functional sex of each bisexual was determined based on the most advanced stage(s) of germ cell development.

Undifferentiated juvenile: Gonad is immature, disorganised in structure (i.e., gonad is not lamellar or convoluted), and contains stage 1 and 2 oocytes intermixed with inactive spermatogenic tissue. Germ cells are evident and are yet to differentiate into lamellae or sperm sinuses/ducts. Functional sex has not been determined.

BF: functionally female bisexual gonad with lamellar structure, oocytes, and cysts of spermatogenesis in testicular islets which are commonly positioned toward the gonad periphery. Immature female bisexuals have stage 1 and 2 oocytes in the absence of POFs. Mature bisexual females have oocytes of stage 1, 2, 3, and 4 that may be degenerating following spawning. POFs may be evident in mature bisexual females following spawning. The reproductive function of this stage is female.

BM: immature or mature male bisexual with stage 1, 2 and/or stage 3 oocytes that may or may not be degenerating which appear in cysts. Male tissue is in late stages of spermatogenesis with medial sperm sinuses evident. The reproductive function of this stage is male.

4.3.5 Length and Age of Maturity and Sex Change

The length and age of maturity of fish was estimated by fitting a logistic curve to the proportional frequency of immature to mature females in 2cm size class bins and 1-year age class bins. Fish aged <1 were split into half year age class bins to increase resolution of maturity estimates in the Philippines. Separate logistic curves and respective 95% confidence limits were fitted for each species at each location. Normal distributions closely approximate the error in logistic regression (Antle *et al.*, 1970), and thus 95% confidence intervals were estimated assuming a normal error distribution. The same protocol was used to estimate the length and age of sex change, by using the proportional frequency of female to male samples per length or age bin.

Previous studies have reported that gonad weight relative to total body weight and length (i.e., Gonadosomatic index: GSI) provides insights into sexual mating systems in labrids and can indicate the timing of maturity (Roede, 1972; Robertson and Choat, 1974; Choat and Robertson, 1975). As such, gonad weight as a proportion of total body weight of each individual was estimated and plotted against body-length to determine differences between sexual development stages.

4.4 Results

4.4.1 Reproductive Development

In total 883 wrasse gonads were examined histologically for information on sexual identity and reproductive development. Hydrated oocytes and post-ovulatory follicles, indicating recent spawning, were evident in gonads of *H. melapterus, H. fasciatus, C. fasciatus,* and *O. digramma* collected throughout most of the year (southern summer, winter, autumn). Fifty-seven transitional individuals showed evidence of proliferating male testis and degenerating oocytes, indicating female to male sex change, and all four species exhibited male dominated sex ratios in the higher age classes, which is typical of protogynous development (Fig. 4.2, 4.3). Primary males were evident in Philippine populations of *H. melapterus, C. fasciatus* and *O. digramma*, the smallest being a 10.5 cm *C. fasciatus* that had no evidence of ex-ovarian function (Fig. 4.2). In addition, a small proportion of juvenile gonads of Philippine wrasses anatomically presented as bisexual and contained spermatogenic material and maturing oocytes (Fig. 4.4, 4.5). Conversely, no primary males or bisexuals were identified in GBR populations of *H. melapterus*, *C. fasciatus*, or *O. digramma* (Fig. 4.2, 4.3). The presence of primary males, bisexuals, and females in Philippine populations suggested two alternate sexual pathways to becoming male in each species on Philippine reefs; diandric protogyny and functional gonochorism (Table 4.1; Fig. 4.2, 4.3, 4.4, 4.5). In contrast, primary males were not evident in unfished, low-latitude GBR populations of *H. melapterus*, *C. fasciatus* and *O. digramma* and these species were monandric on the GBR (Table 4.1; Fig 4.2, 4.3, 4.5). *Hemigymnus fasciatus* was not common in fish markets sampled in the Philippines and showed evidence of monandry on GBR reefs, that is, had no primary males in the population, with all males secondarily arising from females (Table 4.1; Fig. 4.2, 4.3).

Table 4. 1: Proposed sexual development pathways of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* sampled from the Palm and Whitsunday Island groups, GBR and from Philippine fish markets.

Species	**Palm Island group**	**Whitsunday Island group**	**Philippines**
H. melapterus	Monandric protogynous hermaphrodite	Monandric protogynous hermaphrodite	Diandric protogynous hermaphrodite / functional gonochore
H. fasciatus	Monandric protogynous hermaphrodite	Monandric protogynous hermaphrodite	
C. fasciatus	Monandric protogynous hermaphrodite	Monandric protogynous hermaphrodite	Diandric protogynous hermaphrodite /functional gonochore
O. digramma	Monandric protogynous hermaphrodite	Monandric protogynous hermaphrodite	Diandric protogynous hermaphrodite / functional gonochore

Insufficient samples of *H. fasciatus* were obtained in the Philippines to determine the sexual development pathway of this species in this location (see methods).

The difference in age of maturity between GBR reefs, and GBR and Philippine reefs (Fig. 4.2, 4.3) for all species will be discussed in detail in Chapter 5. In addition, sex ratios and GSIs differed among GBR and Philippine reefs. On GBR reefs, GSIs were greater for a given size or age when compared to the same species in the Philippines (Fig 4.4; Appendix 4.2). Furthermore, mature female wrasses on Philippine reefs persisted later into ontogeny (length, age) than those on GBR reefs (Fig. 4.2, 4.3, 4.4). Consistent with this, the timing of sex change was protracted on Philippine reefs and occurred over a large size and age range (Fig 4.2, 4.3; Appendix 4.2). Few bisexual gonads were identified in the Philippines (n=29 across species), however when weighed, bisexual GSIs were comparable to that of mature females. Primary male gonads in Philippine populations weighed slightly more than that of secondary males. Secondary male GSIs were similar across Palm, Whitsunday, and Philippine reefs.

Across all three populations there was a disproportionate increase in GSIs at the approximate length and age of maturity, and a disproportionate decline at sex change (Fig. 4.2, 4.3, 4.4; Appendix 4.2).

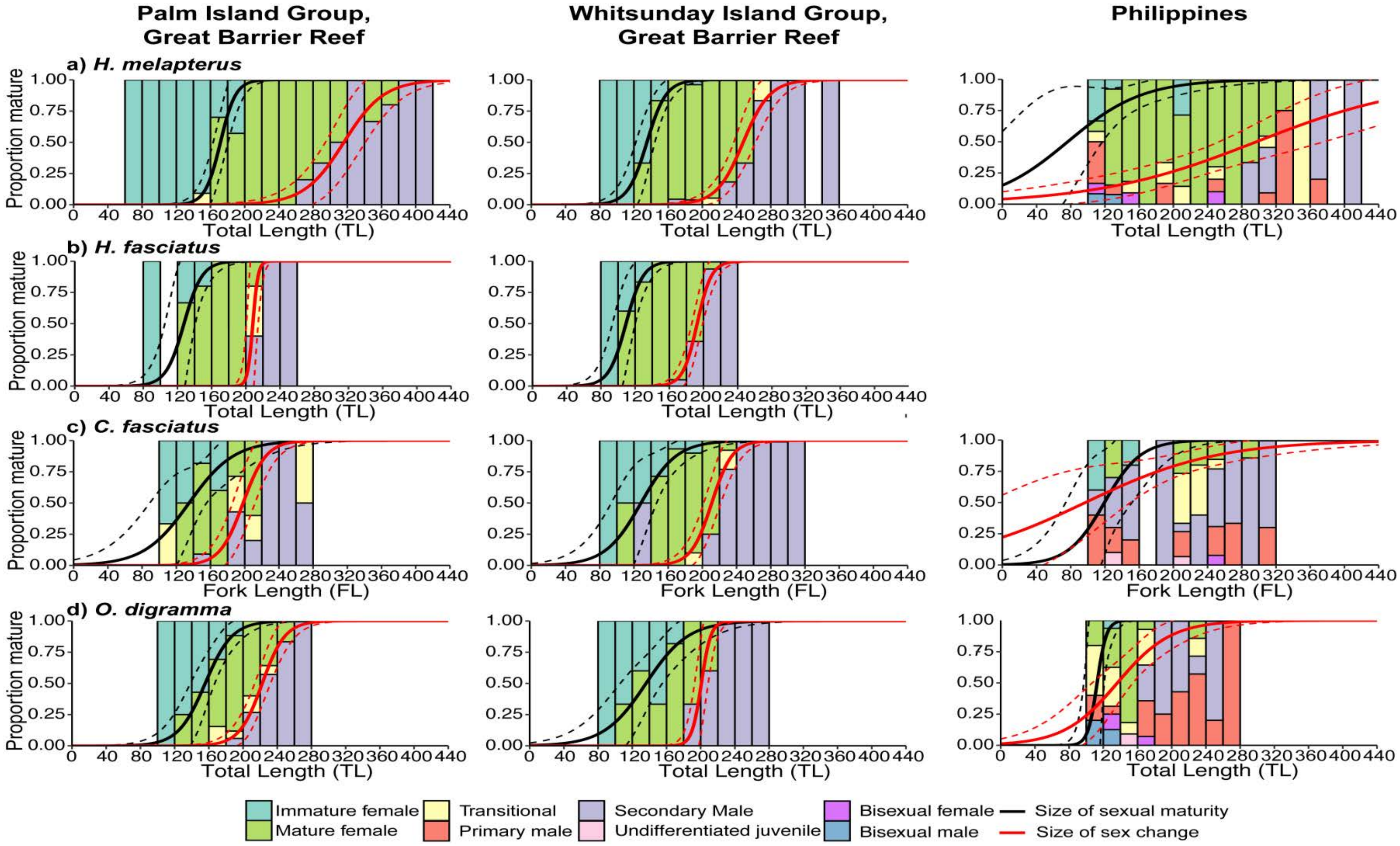


Figure 4. 2: Proportional frequency distributions of the sex-specific size structure for (a) *H. melapterus,* (b) *H. fasciatus,* (c) *C. fasciatus,* and (d) *O. digramma* sampled from the Palm and Whitsunday Island groups, GBR and from Philippine fish markets. Logistic curves of estimated maturity and sex change schedules are shown by black and red lines, respectively. Associated 95% confidence limits are shown as dotted lines.

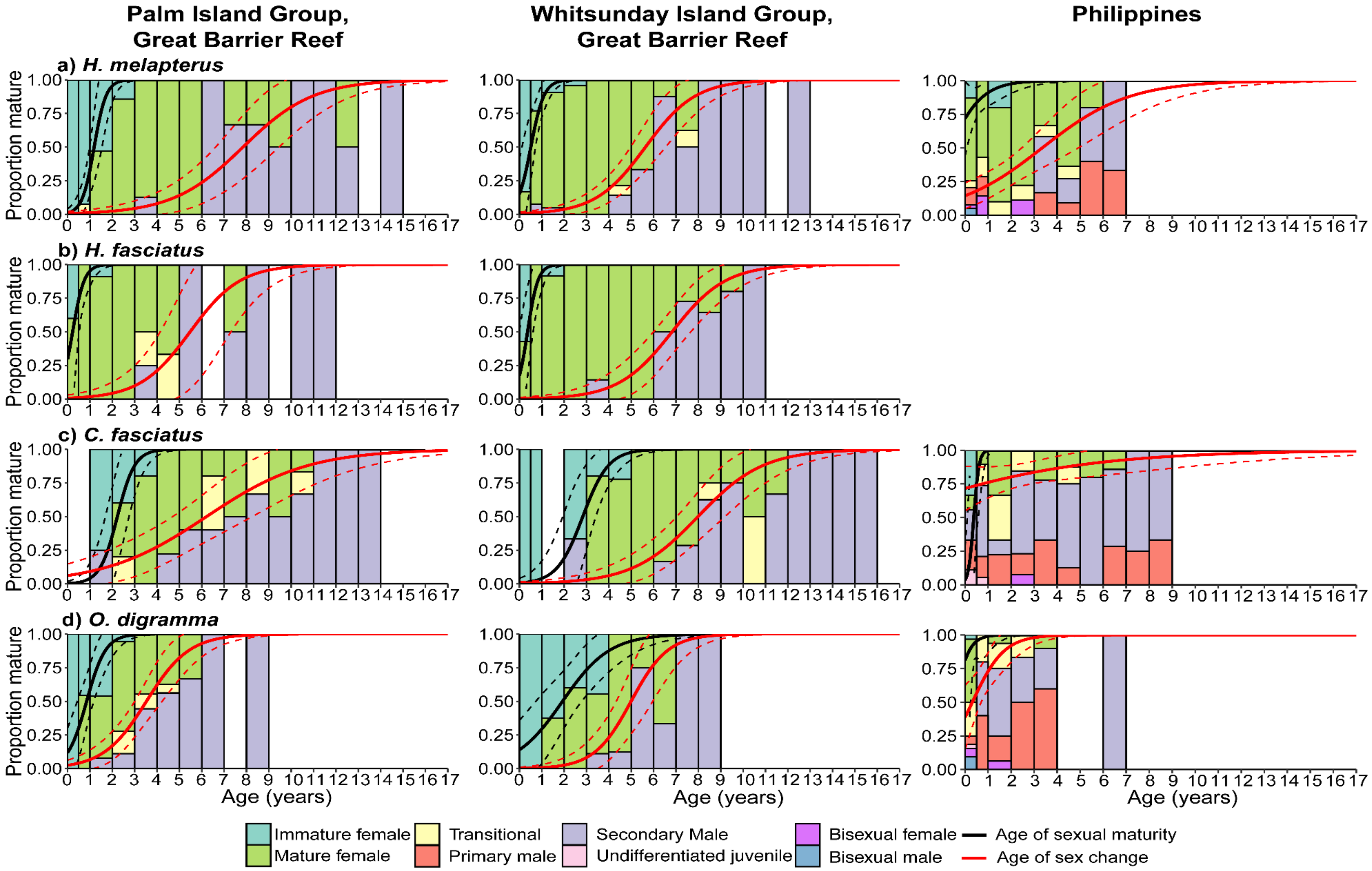


Figure 4. 3: Proportional frequency distributions of the sex-specific age structure of (a) *H. melapterus,* (b) *H. fasciatus,* (c) *C. fasciatus,* and (d) *O. digramma* sampled from the Palm and Whitsunday Island groups, GBR and from Philippine fish markets. Logistic curves of estimated maturity and sex change schedules are shown by black and red lines, respectively. Associated 95% confidence limits are shown as dotted lines.

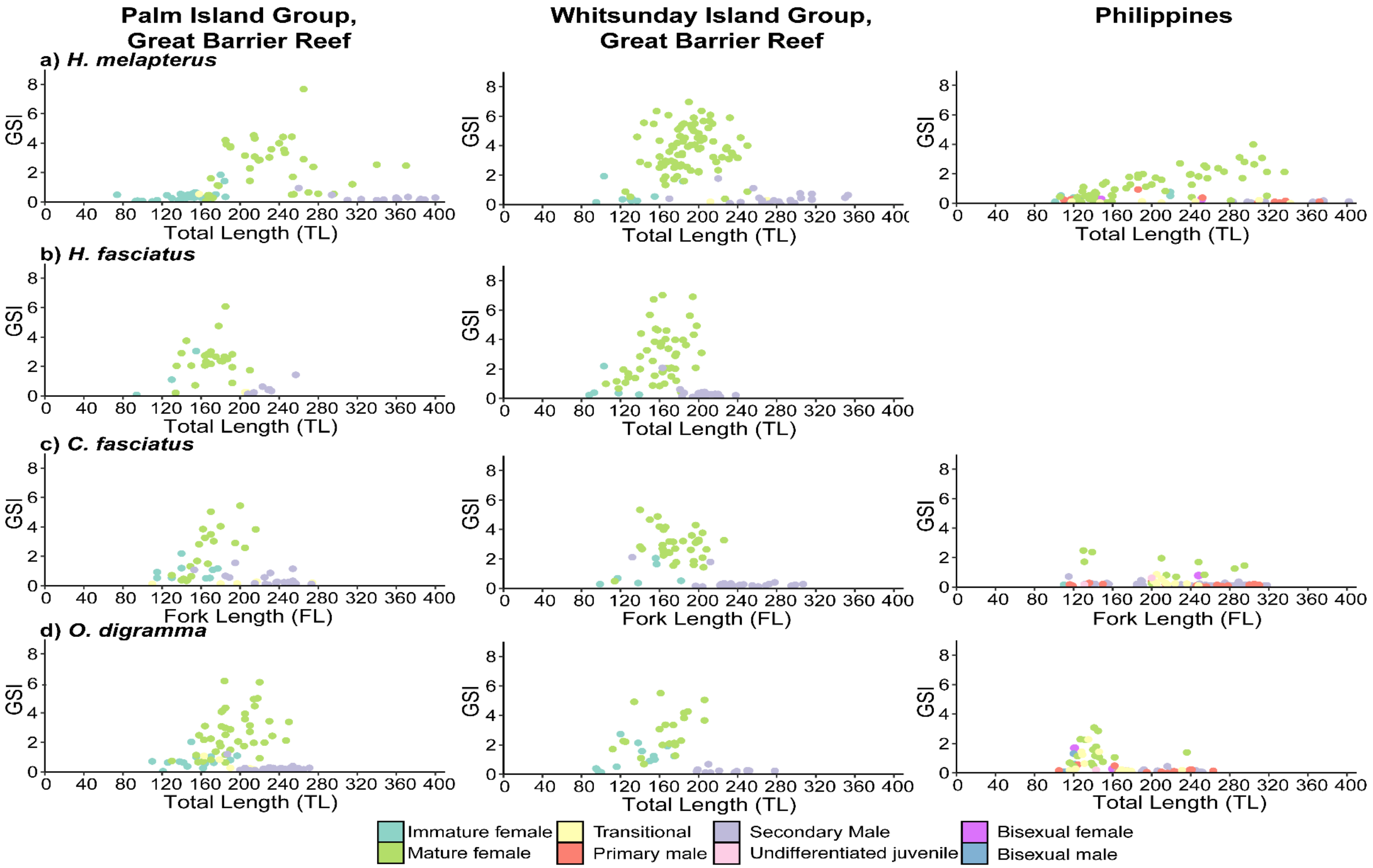


Figure 4. 4: Gonadosomatic indices vs. length of (a) *H. melapterus,* (b) *H. fasciatus,* (c) *C. fasciatus,* and (d) *O. digramma* sampled from the Palm and Whitsunday Island groups, GBR and from Philippine fish markets.

4.4.2 Hypothesised Sequence of Sexual Ontogeny on GBR and Philippine Reefs

On GBR reefs, histological evidence of gonad morphology in association with body-size suggested that all juveniles were immature females (Fig. 4.5a). Undifferentiated juvenile gonads, containing disorganised spermatogenic material, primary stage oocytes, and germ cells were evident in very young wrasses (<0.5 yr) examined from Philippine reefs (Fig. 4.5 b, c). However, few individuals of comparative age to Philippine fish were collected from GBR reefs and future studies are required to determine whether individuals develop from undifferentiated juveniles on the GBR or not. No evidence of primary males or bisexual individuals was evident in GBR populations and thus all species were classified as monandric protogynous hermaphrodites, whereby all males were derived from a functional female phase (i.e., secondary males; Fig. 4.2, 4.3, 4.7e; Table 4.1). Conversely, on Philippine reefs, anatomical evidence based on germ cell development suggested undifferentiated juvenile gonads of *H. melapterus*, *C. fasciatus*, and *O. digramma* matured into either immature females (identical to 4.5a), primary males (Fig. 4.5f), or bisexual juveniles containing spermatogenic material and oocytes simultaneously with either lamellae (Fig. 4.5d) or sperm sinuses evident (Fig. 4.5e). In primary males and females derived through diandry, tissues of the non-functional sex from the undifferentiated juvenile phase diminished rapidly with increasing body size (e.g., Fig. 4.5 c, f). Bisexual gonads were defined as bisexual males (BM) if sperm sinuses (e.g., Fig. 4.6d) or efferent ductules were evident in histological sections. If lamellae were evident (e.g., 5d), bisexual gonads were defined as bisexual females (BF). Immature bisexual males and females had gonads that contained primary stage oocytes (stage 1, 2, and sometimes 3) and spermatogenic tissue in testicular islets that were commonly positioned towards the periphery of the gonad. Mature BM and BF gonads contained simultaneous mature oocytes with yolk globules (sometimes hydrating) and spermatozoa, prior to- and following- histological evidence of spawning (Fig. 4.6). On two occasions distal gonad sections of mature bisexual males showed completely mature male tissue, while the medial and proximal sections contained degenerating oocytes and anatomically appeared bisexual in appearance (disorganised, oviform structure with testicular islets and mature oocytes; e.g., Fig. 4.6c, d). Longitudinal testicular gonad development in bisexual males, from the distal to proximal sections, further suggests tissues of the non-functional sex are lost ontogenetically (Fig. 4.6c, d, 4.8). Differing stages of maturation based on longitudinal gonad development also indicates the importance of sampling proximal, medial, and distal portions of the gonad to accurately derive sexual development pathways. Consequently, two sexual pathways were evident for *H. melapterus, C. fasciatus,* and *O.*

digramma in the Philippines; functional gonochorism and diandric protogynous hermaphroditism (Table 4.1; Fig. 4.8).

Gonads of adult diandric primary males could be distinguished by their convoluted testicular structure (e.g., Fig 4.5f), while primary males that developed from a juvenile bisexual phase (i.e., functional gonochores) had an oviform structure and were visually indistinguishable from adult secondary males. As such, the strength of diandry and functional gonochorism sexual pathways is unclear in Philippine populations. Immature females in both the Philippines and GBR matured at different lengths and ages (Fig. 4.2, 4.3), but data suggests that all underwent typical protogynous development and matured, mated, and spawned as a female prior to undergoing sex change to become a secondary male (Fig. 4.7, 4.8). The likely developmental pathway of each species among GBR and Philippines reefs is summarised in Figure 4.8.

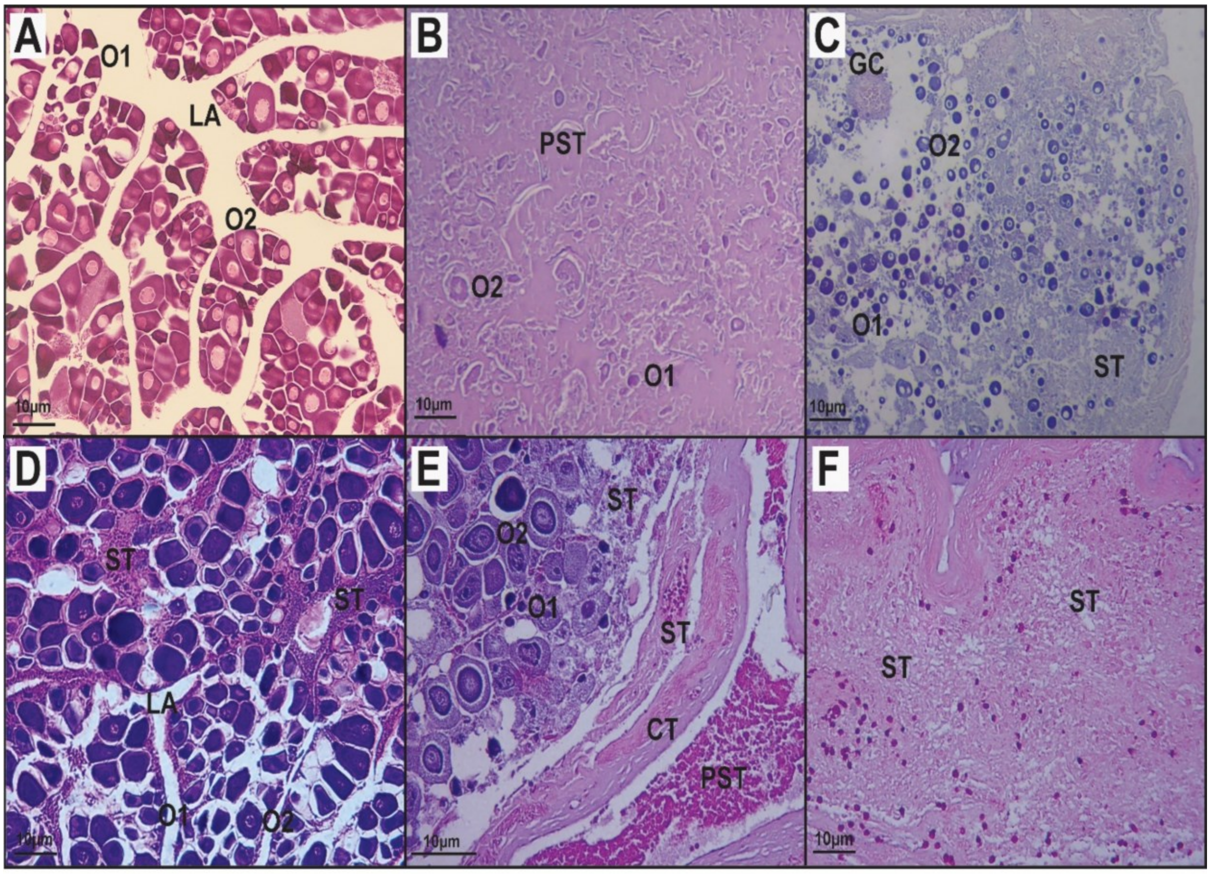


Figure 4. 5: Transverse sections of immature gonads of *H. melapterus, H. fasciatus, C. fasciatus,* and *O. digramma* showing histological features of sexual development. (A) Immature (F1) female *C. fasciatus* from the Palm Island group, GBR, Australia, FL = 115mm, Age = 1 yr; (B) early stage undifferentiated juvenile *O. digramma* from the Philippines, TL = 121mm, age = 0.42 yr; (C) later stage undifferentiated juvenile *C. fasciatus* from the Philippines, FL = 131mm, age = 0.43 yr; (D) Immature bisexual female (BF) *H. melapterus* from the Philippines, TL = 101mm, age = 0.3 yr; (E) Immature bisexual male (BM) *H. melapterus* from the Philippines, TL = 136mm, age = 0.46 yr; (F) Immature primary male *C. fasciatus* from the Philippines, FL = 116mm, age = 0.43 yr. LA, lamellae; O1 and O2, primary stage oocytes; GC, germ cell; ST, spermatogenic tissue; PST, presumptive testicular tissue; CT, connective tissue.

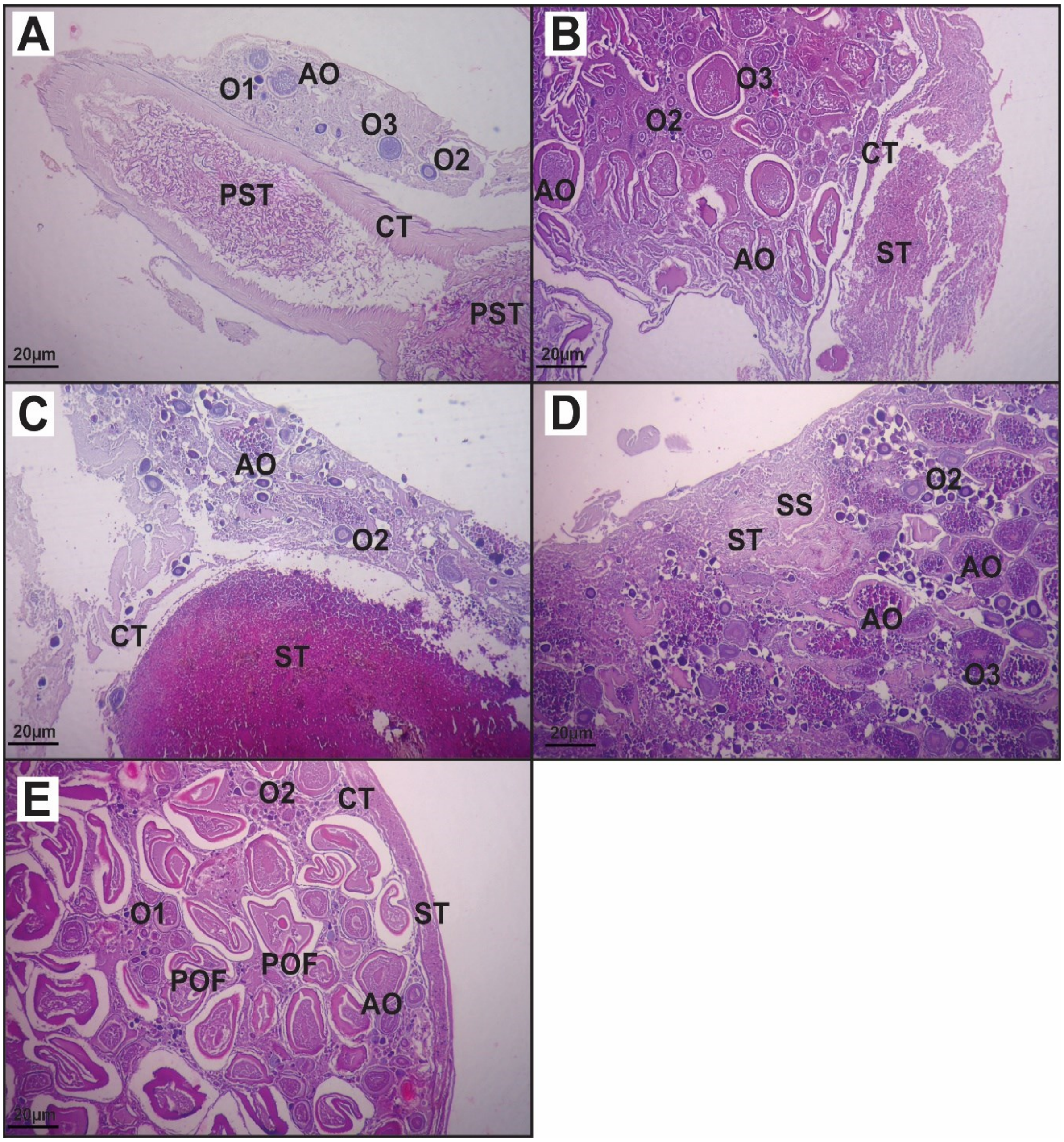


Figure 4. 6: Mature bisexual reproductive stages of *H. melapterus, C. fasciatus,* and *O. digramma* from Philippine reefs indicating functional gonochorism. (A) Bisexual male (BM) *O. digramma* from the Philippines, TL = 110mm, age = 0.43yr; (B) Bisexual female (BF) *O. digramma* from the Philippines, FL = 150mm, age = 0.42yr; (C) Distal section of bisexual male (BM) *O. digramma* from the Philippines, FL = 120mm, age = 0.37yr; (D) Same individual as C, but showing the medial section; (E) Bisexual female *O. digramma* from the Philippines, FL = 120mm, age = 0.38 yr. CT, connective tissue; O1 and O2, primary stage oocytes; O3, cortical alveolar oocytes; AO, atretic oocytes; PST, presumptive testicular tissue; ST, spermatogenic tissue; SS, sperm sinus; POF, post-ovulatory follicle.

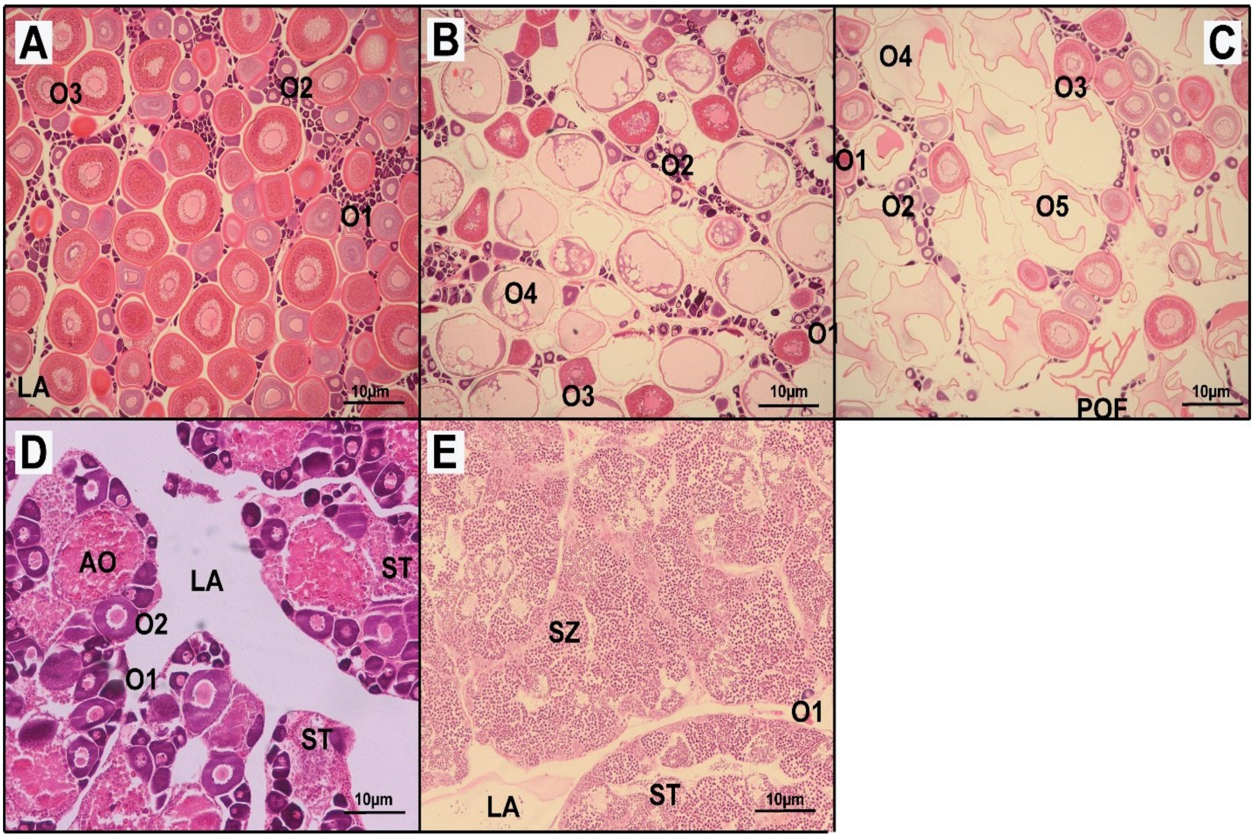


Figure 4. 7: Mature reproductive stages of protogynous *H. melapterus, H. fasciatus, C. fasciatus,* and *O. digramma* on reefs of the GBR, Australia, based on histological features of sexual development. (A) Ripe female *H. melapterus* from the Palm Island group, TL = 210mm, age = 5yr; (B) Running ripe female *C. fasciatus* from the Palm Island group, FL = 150mm, age = 3yr; (C) Spent female *O. digramma* from the Whitsunday Island group, TL = 218mm, age = 5yr; (D) Transitional *H. melapterus* from the Whitsunday Island group, TL = 213mm, age = 2yr; (E) Secondary male *H. melapterus* from the Palm Island group, TL = 362mm, age = 6yr. O1 and O2, primary stage oocytes; O3, cortical alveoli oocytes; O4, vitellogenic oocytes; O5, hydrating oocytes; POF, post-ovulatory follicle; AO, atretic oocytes; SZ, spermatozoa; ST, spermatogenic tissue; LA, lamellae.

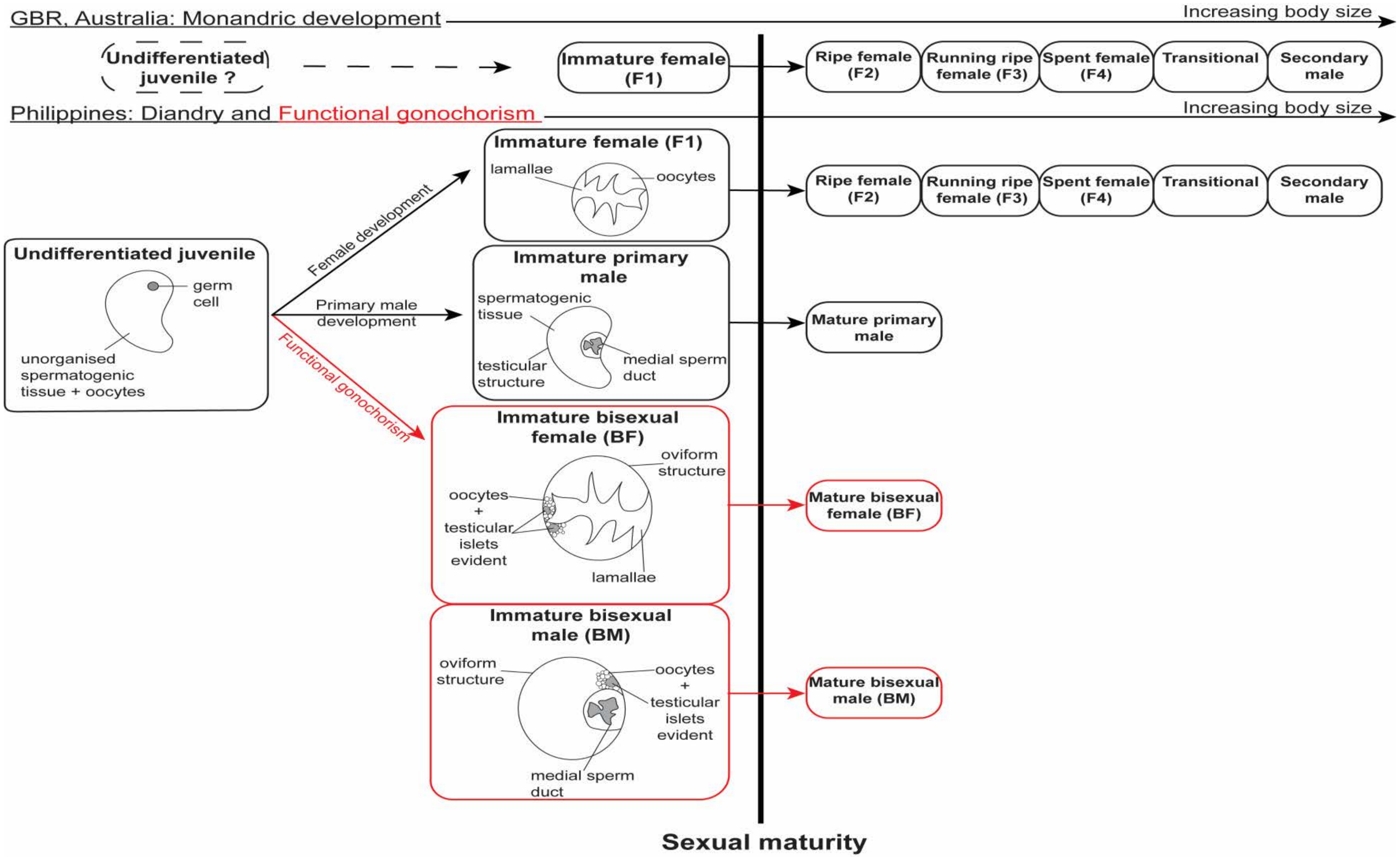


Figure 4. 8: Hypothesised schematic diagram of gonad development in *Hemigymnus melapterus*, *C. fasciatus,* and *O. digramma* on reefs of the Great Barrier Reef, Australia and in the Philippines. Further histological work is needed on sexually immature fish to understand the earliest stages of gonadal development on the GBR (indicated by dotted lines) and to determine the relative strength of each reproductive development pathway in the Philippines.

4.5 Discussion

Protogynous hermaphroditism is the most common reproductive mode among the Labridae and is typically assigned to a species by histological anatomy of the gonads, demographic information, and, most conclusively, by direct observation of female to male adult sex change (Sadovy De Mitcheson and Liu, 2008). Yet, few studies have determined male developmental pathways via histological analysis that included very young, immature individuals, or assessed the spatial variation in these processes. Histological and demographic information of *H. melapterus*, *C. fasciatus*, and *O. digramma* from GBR and Philippine reefs suggests three alternative modes of sexual development in the same species, depending upon the location; functional gonochorism and both forms of protogyny, monandry and diandry. The expression of these different sexual ontogenies was locality dependent. My finding of labile sex allocation strategies in the studied wrasses provides detailed histological support for previous visual observations of spatially labile mating systems in *Hemigymnus*, *Cheilinus*, and *Oxycheilinus* wrasses on Guam reefs (Donaldson *et al.*, 2013). *Hemigymnus fasciatus* was rare in Philippine fish markets and was monandric on GBR reefs, where all individuals were born female.

Given that protogynous hermaphroditism is an ancestral trait of the Labridae (Sadovy De Mitcheson and Liu, 2008; Kazancıoğlu and Alonzo, 2010), the monandric sexual development of the focal labrids on GBR reefs was not surprising. Evidence suggests that sex change will occur when fitness increases with size or age at a greater rate in one sex than the other (i.e., the size-advantage hypothesis; Ghiselin, 1969; Warner *et al.*, 1975; Kazancıoğlu and Alonzo, 2010). Thus, on GBR reefs, the absence of primary males suggests that larger males are more successful in obtaining reproductive opportunities than small males, while female reproductive success is not strongly dependent on size (Robertson and Choat, 1974; Warner *et al.*, 1975). Mating systems play a critical role in determining social conditions which govern size-advantage in reef fishes, particularly in labrids (Munday *et al.*, 2006a; Kazancıoğlu and Alonzo, 2010). Notably, mating systems where large males monopolise breeding opportunities with females via territorial or haremic behaviour, result in low reproductive success for small males, and thus selection favours protogyny (Warner *et al.*, 1975; Leigh *et al.*, 1976). Indeed, haremic mating systems, where a single dominant male breeds with multiple females, have been observed in *C. fasciatus, H. fasciatus,* and species of *Oxycheilinus* (*O. unifasciatus*) on reefs of the Western Pacific

(Donaldson, 1995; Donaldson *et al.*, 2013). Furthermore, lek-like mating systems, where males compete for breeding opportunities with females by establishing temporary mating territories, have been observed in *H. melapterus* (Donaldson et al., 2013). Conversely, in the Philippines, the anatomical appearance of primary males and bisexual individuals at a similar size and age to immature females suggests that functional males of *H. melapterus, C. fasciatus,* and *O. digramma* developed in two ways. Either directly as a primary male (i.e., diandric protogyny) or after passing through a bisexual phase prior to sexual maturity (i.e., functional gonochorism). This developmental pattern clearly differs from the majority of labrids studied so far, but is consistent with the sexual development pathway of several functionally gonochoristic parrotfish (*Bolbometapon muricatium,* Hamilton *et al.*, 2008; *Calatomous spindens* and *Leptoscarus vaigiensis,* Robertson *et al*., 1982; *Sparisoma cretense,* Girolamo *et al*., 1999). Functional gonochorism has also been described in members of the Serranidae (Hastings, 1989; Sadovy and Colin, 1995; Fennessy and Sadovy, 2002), Epinephelinae (Siau, 1994; Adams, 2003; Liu and Sadovy, 2004a), and Pomacanthidae (Kuwamura and Nakashima, 1998). Similar to other functionally gonochoristic species, the histological anatomy of functional males that underwent a juvenile bisexual phase was oviform in structure, indistinguishable from adult secondary males that underwent protogynous development (Liu and Sadovy, 2004a; Hamilton *et al.*, 2008). Consequently, the formation of peripheral sperm sinuses and retention of a lumen cannot be used as characteristics of protogyny in this group. As such, in the Philippines, it is not clear whether adult males develop predominantly from bisexual juveniles or whether a substantial number of males are derived through the sex change of adult females.

Evidence suggests the presence, and relatively high abundance, of primary males in Philippine wrasse populations has a strong social basis (Warner *et al*., 1975; Warner, 1984; Munday *et al*., 2006a). Studies suggest that diandry becomes more prevalent with increased social group size, as the control of large males over females is reduced and primary males can achieve some level of reproductive success (Robertson and Choat, 1974; Warner *et al.*, 1975; Munday *et al.*, 2006a). As mating systems become even more promiscuous (e.g., group spawning) selection trends towards gonochorism (Hodge *et al.*, 2020). For example, the development of primary males in *Thalassoma bifasciatum* is flexible. Where local conditions favour resource defence polygyny, most males are derived by adult sex change (i.e., secondary males) (Warner and Hoffman, 1980a, 1980b; Warner, 1984; Munday *et al.*, 2006a). Conversely, when high local densities of fish make resource defence polygyny uneconomic, *T. bifasciatum* males develop prior to maturation (i.e., primary males) (Warner and Hoffman, 1980a, 1980b; Warner, 1984; Munday *et al.*, 2006a). While the exact area of capture is unknown for Philippine wrasse samples, it is notable that the focal wrasses have lower long-term density on southern Philippine reefs compared to those of the GBR (Russ *et al.*, 2017; Lowe *et al.*, 2019; Chapter 5), yet exhibit primary males and bisexuals consistent with multi-male mating systems, social groups which are often large in size. Two possible explanations are that small males remain close to the territory of a larger male, overwhelm the territory holder during spawning, and spawn with females waiting to breed with larger-bodied males ("sneaking"), or small males may join the dominant male and female at the climax of spawning ("streaking") (Warner *et al.*, 1975; Robertson *et al.*, 1976). However, GSIs of primary males engaging in streaking are characteristically larger than secondary males of similar body-length (Robertson and Choat, 1974; Choat and Robertson, 1975), and therefore in the wrasses studied here sneaking seems more likely. Additionally, in the Philippines the focal wrasses may only hold temporary spawning territories, and the anonymity of monochromatic small males studied here may facilitate their interference with the spawning activities of larger, territorial males (Choat and Robertson, 1975; Warner *et al.*, 1975; Warner and Robertson, 1978). In this system, small males with similar GSIs to adult males should attain a much higher level of breeding success compared to a haremic or group spawning type system. Indeed, the adult focal wrasses differed in coloration from juveniles, but not markedly (i.e., were largely monochromatic), and primary and secondary males had relatively similar GSIs irrespective of size or age. Protracted timing of sex change in the Philippines further supports the likelihood of promiscuous mating by young males. Topography and historical fishing pressure may also play an important role in determining social group size and the number of spawning sites on Philippine reefs (Robertson *et al.*, 1976; Warner and Robertson, 1978; see Chapter 5).

Alternatively, differences in sex allocation may reflect evolutionary trends rather than local environmental conditions. Despite the lability of sex change in labrids, Hodge *et al.*, (2020) found that monandric lineages rarely transitioned directly to diandric protogyny, instead transitioning through functional gonochorism on the pathway from monandry to diandry. Consistent with this, Cheilines (including *C. fasciatus* and *O. digramma*) are a largely monandric lineage (Sadovy de Mitcheson *et al.*, 2010; Hodge *et al.*, 2020), but histological evidence in the present study suggests that the sex allocation of *C. fasciatus* and *O. digramma* was indicative of functional gonochorism and diandric protogyny on Philippine reefs. Sex allocation in Julidine wrasses (including *Hemigymnus*) is variable, with both diandry and monandry evident throughout the clade, but rarely has gonochorism been reported (Hodge *et al.*, 2020). Differences in sex allocation between GBR and Philippine reefs at the same time may also reflect the overarching evolutionary trend toward monandric protogyny and haremic polygyny in labrids (Hodge *et al.*, 2020). Consistent with this, all species in the present study were found to be monandric protogynous hermaphrodites on GBR reefs, and evolutionary biogeography suggests that GBR populations evolved from those on Philippine reefs, from the early Oligocene onwards (Cowman and Bellwood, 2013).

Ultimately, future studies that examine the mating systems of the focal species should determine mechanisms responsible for increased presence of primary males in Philippine wrasse populations. It has been suggested that if sex determination is flexible and the adult environment is unpredictable, individuals should delay choosing which sex to be until they are about to mature (Charnov and Bull, 1977; Jones, 1980). It is unclear whether this strategy results in increased presence of bisexuals on Philippine reefs. Given that bisexuality characterises the juvenile phase, the initial direction and timing of sex differentiation is not apparent and future studies should collect very young individuals (<0.4 yr) to determine whether functional males are primarily derived from bisexual juveniles or via protogyny.

Unlike most species of parrotfish that exhibit accurate sexual dimorphism in colour phases, allowing for rapid non-invasive sex determination (Robertson and Choat, 1974; Taylor *et al.*, 2018), wrasses studied here were largely monochromatic, limiting the ability to sample sexual identity of individuals from visual census alone. Moreover, GSIs did not distinguish between male sexual identities (primary, secondary). However, I show that sampling GSIs across size classes can indicate the age and size of female sexual maturity in the focal wrasses, irrespective of local mating systems. This offers significant advantages for the sampling of these species across Indo-Pacific reefs, as gonad and body weights are easy to sample compared to histological analysis. The latter is often laborious, expensive, and logistically difficult to perform in developing nations. However, prior to comparing demographic rates between species or populations, I stress that it is critical to characterise the local sexual development pathway via a histological subsample of the population, or through observation of local mating systems (which often reflect sexual ontogenies in labrids; Munday *et al*., 2006a; Hodge *et al*., 2020).

Across the literature, it is clear that the improper use of descriptive terminology used to describe histological gonad morphology has confounded our perception of the diverse sexual developmental pathways in reef fishes. For example, the term ‘pre-maturational sex change’ infers that individuals destined to become one sex have changed to the other prior to sexual maturation. But whether sex ‘change’ has occurred in an individual that has not differentiated sexually is unclear (Liu and Sadovy, 2004a). It is equally possible that early gonad development involves the natural production of a lumen and the appearance of this feature has nothing to do with sex change. The lack of consistency between descriptive terminology, phylogenetic position, and gonad function within the literature likely stem from under-sampling young individuals, and from a lack of intra-specific spatial comparisons of sexual ontogenies. Other studies which report diverse male developmental pathways in very young reef fish have also stressed these points (Liu and Sadovy, 2004a; Sadovy and Domeier, 2005; Hamilton *et al.*, 2008). Therefore, to properly determine the diversity of sexual patterns in the Labridae, and their respective variation across space and time, it appears imperative to apply suitably neutral descriptive terminology across a large sample of fish that include very young individuals, ideally taken throughout the year, via histological examination along the length of the gonads. Only then can we begin to partition environmental and phylogenetic drivers of the sexual ontogeny of reef fishes, and determine the correlative impacts on demographic rates.

Now that spatial variation in the sexual ontogenies of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* among Philippine and GBR reefs has been resolved, the associated consequences of environmental variation and fishing pressure on life histories can be better understood (Chapter 5).

Chapter 5: Spatial Variation in the Demography of Fished and Unfished *Hemigymnus*, *Cheilinus,* and *Oxycheilinus* Wrasse Populations Among Indo-Pacific Coral Reefs

5.1 Abstract

Age-based demographic parameters of large-bodied wrasses (*Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus*, and *Oxycheilinus digramma*) were estimated from fished populations in the Philippines and from two unfished populations on the Great Barrier Reef (GBR), Australia to investigate drivers of demography across varying spatial scales. Histological analysis and age-based demographic assessments indicated distinct differences in growth patterns, sexual ontogenies, and estimates of longevity, mortality, size and age of maturity and sex change, body condition, and maximum size across both small (2°) and large (30°) latitudinal distances. Wrasses sampled from Philippine reef fisheries (9 – 11° N) exhibited significantly faster growth rates, rapid maturation, shorter lifespans, and greater mortality rates than conspecifics on unfished GBR reefs (19 – 20° S). Despite this, Philippine wrasses attained a similar asymptotic and maximum length, and had better relative body condition than GBR populations. Significant differences in demography were also evident at regional spatial scales between inshore GBR reefs separated by 2° of latitude. *Oxycheilinus digramma* and *C. fasciatus* grew slower, matured later, and lived longer on higher-latitude reefs (Whitsunday Islands: 20.05 – 20.21° S) than on reefs to the north (Palm Islands, GBR: 18.53 – 18.70° S and the Philippines). Conversely, *H. melapterus* and *H. fasciatus* populations on Whitsunday reefs had lower asymptotic sizes and longevity than on Palm reefs, and *H. melapterus* matured earlier on Whitsunday reefs than on Palm reefs to the north. Across locations, demographic variation was species-specific, and was largely inconsistent with predictions of the Temperature-Size Rule for ectotherms, the metabolic theory of ecology, and the expected effects of fishing on size structures. These unexpected relationships suggest that localised sources of demographic variation are impact life histories of the focal wrasses across various spatial scales.

5.2 Introduction

Life histories reflect trade-offs in energy allocation between growth and reproduction, and such trade-offs result in traits which have important implications for ecology, evolutionary biology, and ecosystem management (Adams, 1980; Perez and Munch, 2010). Age and body-size at maturity are two of the most important covarying life history traits, as they affect nearly all biological rates (Kingsolver *et al.*, 2001; Perez and Munch, 2010) and are important determinants of individual fitness. These traits are thus critical elements in life history theory and are an important part of the explanation of demographic trade-offs that result from the response of individuals and their offspring to environmental variation (Stearns, 1977; 1992). Ectothermic organisms are highly responsive to changes in temperature, resources, and factors that directly modify mortality rates of populations.

The life history traits of individuals within ectothermic populations are largely mediated by the surrounding environment (Bradshaw, 1965; Pfennig *et al.*, 2010). For example, temperature differences across gradients of latitude affect metabolism and thus growth and longevity of many taxa (Atkinson, 1994; Clarke, 2006; Munch and Salinas, 2009). Concomitantly, many life history theories suggest that age of maturity should be positively correlated with the organism’s lifespan (Stearns, 1977). Empirical studies support this (Stearns, 1976; Stearns and Crandall, 1981; Charnov, 1989). However, correlative changes in life history traits across latitudinal gradients of temperature do not necessarily demonstrate an understanding of natural population responses to different environments (Huey and Kingsolver, 2019; White *et al.*, 2020). This is because, across various spatial scales, temperature has complex interactive effects with food availability and food consumption, predator-prey interactions, behaviour, and metabolic regulation, mechanisms responsible for species-specific variability in life history responses (Jeppesen *et al.*, 2010; Taylor *et al.*, 2014b; White *et al.*, 2020). As marine ectotherms frequently display wide geographic distributions, they make excellent research subjects for determining the relationship between environmental variation and life history features. For this reason, many fish species in both temperate and tropical environments have been the subject of life history studies, with particular emphasis on salmonid, atherinopsid, and gadid taxa in temperate regions (Brett, 1971; Dunn and Matarese, 1987; Conover and Present, 1990), and labrid fish in tropical reef systems (Warner *et al.*, 1975; Taylor *et al.*, 2014a).

Species of teleosts that are subject to both commercial and subsistence fisheries often show rapid changes in life history traits (Rochet, 1998; Audzijonyte et al., 2016). This may reflect evolutionary responses to increased mortality rates and size-selectivity from fishing, and natural environmental variation in widely distributed species (Jørgensen *et al.*, 2007; Audzijonyte *et al.*, 2016; Taylor *et al.*, 2018). Additionally, many tropical lineages subject to fishery exploitation, such as the Labridae and Epinephelidae, display complex sexual ontogenies, including protogynous hermaphroditism (Erisman *et al.*, 2009; Kazancıoğlu and Alonzo, 2010). This adds additional challenges to the demographic analysis of coral reef fishes (Munday *et al.*, 2006b; Sadovy De Mitcheson and Liu, 2008). Moreover, unlike laboratory experiments, which often focus on a single factor, wild populations are subject to the simultaneous influence of numerous factors, resulting in complex patterns of phenotypic change (Stearns, 1992; Roff, 1993; Flatt and Heyland, 2011). For this reason, the demographic changes seen in natural populations distributed across environmental gradients may not align with predictions based on laboratory experiments and life history theory (Morrongiello *et al.*, 2019).

Significant variability in life histories can have detrimental effects on the success of management of reef fishes if variation occurs on a local scale that is not accounted for in management plans (Audzijonyte *et al.*, 2016). Therefore, a management priority is determining the spatial scale at which various sources of demographic variation play important roles in driving life histories of natural populations (Sale, 1998; Jones *et al.*, 2007; Taylor *et al.*, 2014b). Furthermore, as most management decisions concerning harvested fish populations seek to incorporate rate processes (e.g., growth, recruitment, mortality etc.), an important element is the collection of age-based demographic information via the interpretation of annual signals in skeletal features of fish (Hilborn and Walters, 1992; Jennings *et al.*, 1998; Choat and Robertson, 2002). In contrast, length-based assessments usually assess rate processes via indirect methods, and often provide less accurate estimates of vital rates (Hoenig *et al.*, 1987; Francis, 1988b; Choat *et al.*, 2003). Moreover, fish size-structures are highly sensitive to local features of the environment, and body-size is often somewhat decoupled from age, which in turn obscures accurate estimates of the underlying rates (Choat *et al.*, 2003; Trip *et al.*, 2008; Munch and Salinas, 2009). As such, there is great interest in collecting spatially-explicit age-based demographic information for fishery-targeted reef fish species, particularly in multi-species

Indo-Pacific reef fisheries that are under increasing levels of exploitation (Choat and Robertson, 2002; Newton *et al.*, 2007; Taylor *et al.*, 2018)

Fishery exploitation has led to localised declines in the abundance of several large-bodied labrids (Sadovy *et al.*, 2003b; Donaldson and Dulvy, 2004; Ferreira *et al.*, 2005; Nañola *et al.*, 2011; Comeros-Raynal *et al.*, 2012; Muallil *et al.*, 2014; Lavides *et al.*, 2016). High exploitation rates of the Labridae have been partly attributed to their relative ease of capture, and a shift in target species from overexploited top predators (e.g., groupers, snappers) to lower trophic level yet large-bodied reef fishes (Dalzell *et al.*, 1996; Friedlander and DeMartini, 2002; Sadovy *et al.*, 2003b; Stockwell *et al.*, 2009). In particular, labrids on coral reefs of the Indo-Pacific contribute a considerable proportion of the reef fishery harvest (Dalzell *et al.*, 1996; Houk *et al.*, 2012; Lavides *et al.*, 2016). Short-lived, early maturing labrids are often considered relatively resilient to the impacts of fishing and environmental perturbations, while slow-growing, late maturing labrids often suffer disproportionately for a given level of mortality (Adams, 1980; Alonzo and Mangel, 2004 ; Taylor *et al.*, 2014a). However, this is not always the case (Chapter 4; Choat *et al.*, 2006; Hamilton *et al.*, 2008; Caselle *et al.*, 2011). Rather, populations generally harbour considerable genetic variation in life-history traits, and evidence suggests that some species can respond quickly to altered mortality regimes via plasticity in the timing and/or mode of reproductive development (Rochet, 1998; Hamilton *et al.*, 2007; Audzijonyte *et al.*, 2016; Chapter 4). The primary research goals are therefore to determine how age-based life history features in reef fishes vary over environmental gradients and through time, and the extent to which these life history features may be modified by fishing activity (Taylor *et al.*, 2014b).

Hemigymnus melapterus, *H. fasciatus*, *Cheilinus fasciatus*, and *Oxycheilinus digramma* are examples of widely distributed, fishery-exploited labrids. Ecologically, the four focal species of wrasse are large-bodied (maximum length 30–60 cm) and abundant, mobile predators of benthic invertebrates on coral reefs in the Indo-Pacific (Kuiter, 2002; Kramer *et al.*, 2015). In developing regions, such as the Philippines, these wrasses are commonly captured by spear, trap, hook and line, and gill nets in small-scale fisheries (Dalzell *et al.*, 1996; Russ and Alcala, 1998; Sadovy *et al.*, 2003a; Abesamis *et al.*, 2014). In Australia, the four study species are not targeted by recreational or commercial fisheries. Demographic consequences of environmental change and fishery exploitation on the focal wrasses have yet to be quantified. However, it is notable that the sexual ontogenies of the focal wrasses differ among Philippine and Australian reefs, with *H. melapterus, C. fasciatus*, and *O. digramma* exhibiting evidence of functional gonochorism and both forms of protogyny, monandry and diandry, depending upon the location (Chapter 4). Different pathways of sexual development and the correlative impacts of such varied development on other demographic traits may be mediated by differences in local habitat, benthic productivity, and dietary resource levels between Australian and Philippine coral reefs. These factors often play a prominent role in driving population dynamics of the focal and related labrid species (Ackerman, 2004; Taylor *et al.*, 2018; Lowe *et al.*, 2019). Conversely, the fishing pressure exerted on these wrasses in the Philippines may be a more prominent driver of demography, as is the case for the moderate to long-lived wrasses *Cheilinus undulatus* (Choat *et al.*, 2006), *Bolbometopon muricatum* (Hamilton *et al.*, 2008), and *Semicossyphus pulcher* (Hamilton *et al.*, 2007).

Here, I utilised fishery-dependent and fishery-independent sampling to determine life history traits (growth rates, mortality rates, body condition, long-term density, mean and maximum size and age, age and size at maturity and sex change) in the four focal wrasse species. Wrasses were collected from fish markets in the southern Philippines, and from populations at two unfished locations on the Great Barrier Reef (GBR), Australia. By comparing life history traits between the Philippines and GBR, and between the two locations within the GBR, I aim to determine the extent of demographic variation across both small (2°) and large (30°) latitudinal distances. I expect that:

1) Based on studies of other labrids, and the metabolic costs of living at low latitudes, wrasse growth rates will increase with temperature, while longevity and the age and length of maturation will decline on low latitude reefs (Atkinson, 1994; Munch and Salinas, 2009; Trip *et al.*, 2014). Conversely, if demographic differences are more strongly driven by resource differences than by ambient water temperature, I expect that low latitude locations will have fast growth and early maturation at a larger size than those at high latitudes (Berrigan and Charnov, 1994).
2) The maximum size and age achieved would be greatest at higher-latitude GBR reefs where lower water temperatures are experienced during development and populations are under negligible fishing pressure. In addition to the negative effects of increasing

temperature on ectotherm body-size and age (Atkinson, 1994; Munch and Salinas, 2009), wrasses from low-latitude Philippine reefs are expected to experience additional mortality and lower maximum size and age due to fishing, consistent with the effects of fishing on labrids and other target species of reef fish (Stearns, 1992; Hamilton *et al.*, 2007).

I was unable to sample fished and unfished wrasse populations at each locality, thus some confounding of fishing and local environmental effects between regions was inevitable from the outset. By documenting demographic variation in the four species of wrasse at multiple spatial scales, the patterns observed here will enable a more comprehensive analysis of the response of wrasses to environmental effects and fishing pressure.

5.3 Methods

5.3.1 Sampling Locations

Hemigymnus melapterus, H. fasciatus, Cheilinus fasciatus, and *Oxycheilinus digramma* were collected from fringing coral reefs surrounding the Palm and Whitsunday Island groups in the central GBR region and purchased from fish markets in the Philippines (Fig. 5.1). Collections were designed to obtain an adequate and representative sample of each species examined to determine life-history parameters. On the GBR, samples were collected using spearguns while SCUBA diving and individual fish were collected without preference for body size. Collection sites were positioned on fringing reefs surrounding Pelorus and Curacoa in the Palm Island group and Hook and Whitsunday in the Whitsunday Island group (Fig. 5.1B, C). Reef flats, crests, and slopes were sampled for adult and juvenile wrasses at each collection site. Philippine samples were primarily purchased from fish markets in south-eastern Negros Island (Fig. 5.1A). It was not possible to track the source reef of each purchased wrasse specimen, but conversations with fish vendors indicated supply chains that were quite short (reefs in the vicinity of Negros) as well as those that originated from reefs as far as 300 – 500 km away (e.g., Palawan) (Fig. 5.1A). Adult wrasse samples from the Philippines were often caught using spearguns or in fish traps, while juveniles were commonly caught using gill nets.

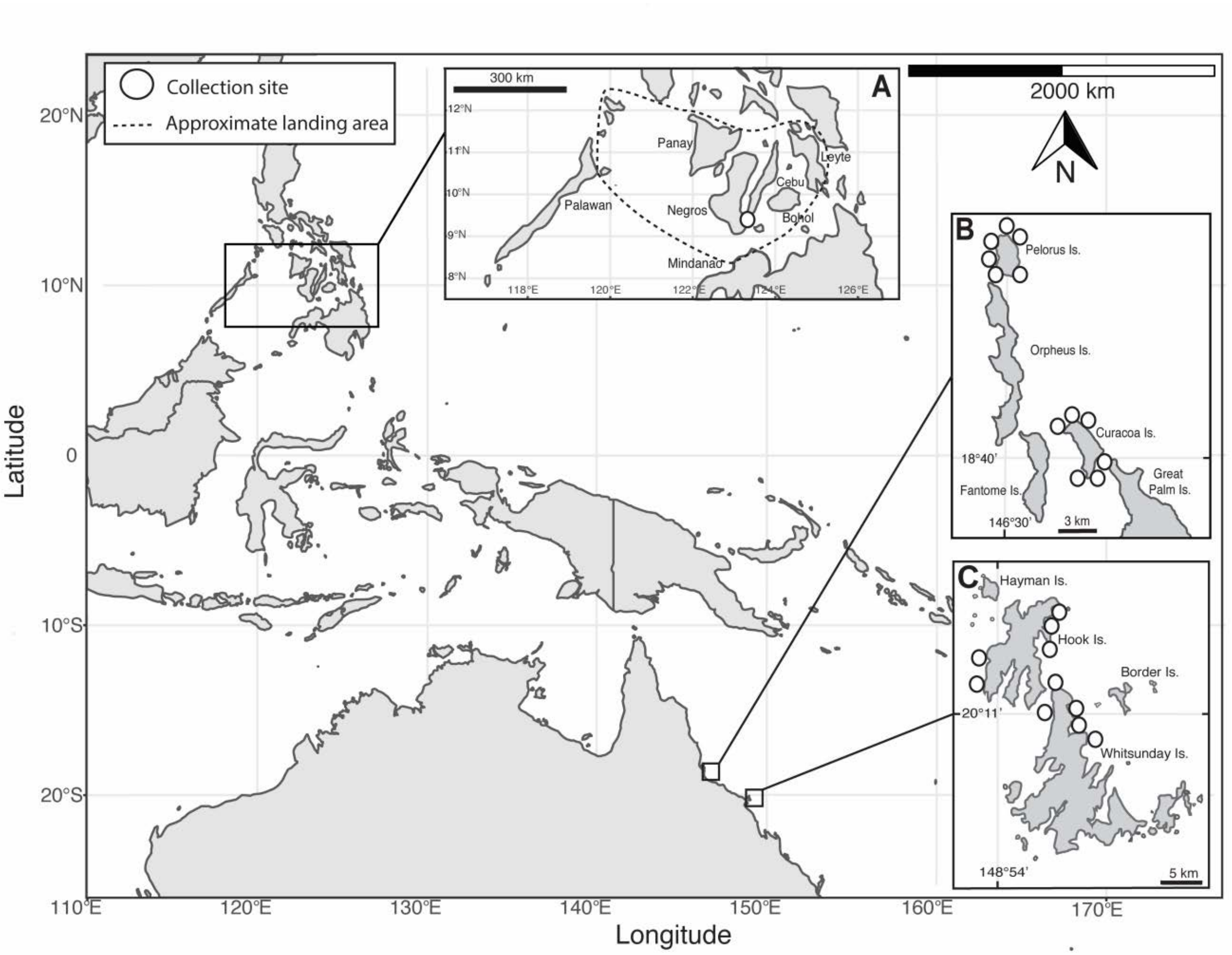


Figure 5. 1: Maps indicating primary collection sites and likely landing area of fishery-dependent samples collected in the Philippines (A), and areas of fishery-independent sampling at the Palm (B) and Whitsunday (C) Island groups, GBR, Australia.

5.3.2 Age Determination

In total, 309 *H. melapterus*, 227 *C. fasciatus*, and 216 *O. digramma* were collected from the Great Barrier Reef, Australia and from fish markets in the Philippines (See Table 5.1 for location-specific sample sizes). *Hemigymnus fasciatus* was rare in Philippine fish markets and an insufficient number of samples were collected for the estimation of life history parameters for this species in the Philippines. Consequently, all life history parameters for *H. fasciatus* were estimated from 115 samples collected on GBR reefs. Once samples were collected, fish were placed on ice and processed immediately on return to the processing area. The body-size of both *Hemigymnus* spp. and *O. digramma* were recorded as total length (TL; nearest mm) due to their rounded tail, conversely fork length (FL; nearest mm) was used for *C. fasciatus* due to its emarginate tail with pronounced dorsal and ventral lobes (in adults) which were commonly damaged at the tips prior to, or during sampling. Total weight (W; nearest 0.01g in Australia, 1g in Philippines) was also recorded for each specimen. Age was estimated for each individual through interpretation of putative annual increments in the microstructure of sectioned sagittal otoliths. Otoliths were removed from each specimen, cleaned, and stored dry at the time of processing. Subsequently, one otolith from each sagittal pair was weighed to the nearest 0.0001g on the GBR and 0.001g in the Philippines for analysis of otolith weight and age (Appendix 5.1). Each otolith was then fixed to a glass slide using thermoplastic glue (Crystalbond 509), with the primordium located just inside the edge of the slide and the sulcul ridge perpendicular to the slide edge. Using a grinding wheel, each otolith was then ground to the slide edge using an 800 – 1200 grit diamond lapping disc along the longitudinal axis. Otoliths were then re-affixed to a clean slide and ground to produce a thin transverse section ≈200 µm thick that was covered in thermoplastic glue to improve clarity of microstructures. Sectioned otoliths were examined twice by a single observer (JRL) and age in years was estimated by counting annuli using transmitted light on a stereo microscope. When the two age estimates differed, a third blind read was conducted. Age in years was assigned when two age assignments agreed, which occurred for ≈97% of specimens. Daily otolith sections (individuals <1yr in age) were further polished using 9, 5, 3, and 0.3µm lapping film, sequentially. Daily age was assigned to individuals by counting the number of daily bands from the otolith core along the longest axis of the otolith section on three separate occasions and was taken as the mean of these three counts assuming all were within 10% of the median.

5.3.3 Statistical Analysis

To estimate biologically important life history parameters from size-at-age data, separate von Bertalanffy growth functions (VBGFs) were fit for each species at each location using the FSA package in R (von Bertalanffy, 1938; Ogle *et al.*, 2019). The original parameterisation of the VBGF, $\mathrm{Lt} = \mathrm{L}\infty - (\mathrm{L}\infty - L_0)e^{-Kt}$, was used to determine estimates of K and L∞ at a common length at settlement (L_0). Where Lt is the length (TL or FL) of a fish at age t (years), L∞ is the mean asymptotic body length, K describes the curvature of growth towards L∞, and L_0 is the length at which $t = 0$. Settlement length (L_0) was fixed at 10mm to improve parameter estimates, and was based on the approximate larval duration of the focal wrasses across locations multiplied by an average pre-settlement growth rate determined for Indo-Pacific wrasses (Victor, 1986; 1987; Kritzer *et al.*, 2001). While equivalent to the original VBGF from von Bertalanffy (1938), the most commonly used parameterisation of the VBGF in the literature is from Beverton and Holt (1957): $\mathrm{Lt} = \mathrm{L\infty}\left[1 - e^{-K(t-t0)}\right]$. The Beverton and Holt parameterisation differs from the original von Bertalanffy parameterisation in that it includes the parameter t0 as the theoretical age at which Lt = 0, rather than L_0 as in the original parameterisation. Consequently, to allow for comparisons between studies, I also extrapolated estimates of t_0 using non-linear least squares regression from the original VBGF fit with a fixed L_0. Length-at-age data were subject to random re-sampling with replacement and were analysed to produce 1000 bootstrap samples of parameter estimates for each species, at each location.

To quantify differences in growth rate and mean size-at-age between Palm, Whitsunday, and Philippine wrasse populations the Francis VBGF parameterisation (rVBGF) was also fit to size-at-age data (Francis, 1988a; Ogle *et al.*, 2019). The rVBGF differs from the VBGF in that biologically important ages (τ, ω, and μ) and their corresponding mean lengths (Lτ, Lω, and Lμ) can be specified within the model, which offers many benefits over the VBGF (Roff, 1980; Francis, 1988a). The rVBGF is represented by $\mathrm{Lt} = \mathrm{L}_{\tau} + (\mathrm{L\mu} - \mathrm{L\tau})\,\frac{1-\mathrm{r}^{2\frac{(\mathrm{t}-\tau)}{(\mu-\tau)}}}{1-\mathrm{r}^{2}}$, where $\mathrm{r} = \frac{\mathrm{L\mu}-\mathrm{L\omega}}{\mathrm{L\omega}-\mathrm{L\tau}}$. For *H. melapterus*, *H. fasciatus*, and *C. fasciatus*, ages τ, ω, and μ were set at 1, 3, and 5 years, respectively, to estimate initial, mid-life, and approximate asymptotic growth of these species across locations. A similar rationale was used for *O. digramma,* with τ, ω, and μ set at 1, 2, and 3 years, respectively, as the growth of Palm populations were largely asymptotic by the age of 3 and only one individual was recorded >3yrs in the Philippines. 1000 bootstrap estimates of Lτ, Lω, and Lμ parameters for each species and location, along with estimates of total mortality (Z year^{-1}), mean maximum age (Tmax), and mean maximum length (Lmax) of the oldest and largest 15% of the sample at each location were used to determine whether growth profiles differed between GBR and Philippine populations.

Mean annual sea surface temperature (SST, °C) was used to describe latitudinal gradients between Whitsunday, Palm, and Philippine reefs. Average SST at each location was calculated from 2001 to 2016 (January to December), incorporating a 15-year timespan, the maximum lifespan of the focal wrasse species (Rayner *et al.*, 2003). To visualise regional (within GBR) and biogeographic (Australia vs. Philippines) trends in life history traits across a gradient of SST, linear models were fit to life history variables of interest.

Species-specific otolith-weight to age relationships at each location were modelled using linear regressions (Appendix 5.1).

Estimates of instantaneous mortality rates (Z year^{-1}) were calculated as the absolute value of the slope from a curve fitted to the natural logarithm of age-frequency, fitted with the *FSA* package in R (Beverton and Holt, 1957; Ogle, 2019). Each population was considered fully recruited to the sampling regime at the modal age of samples obtained in each location and age classes without samples were excluded from the analysis. Instantaneous mortality estimates were subsequently converted to estimates of annual mortality (A), with $A= 1 – e^{-Z}$. Age-based catch curves used to estimate mortality were compared between locations via analysis of covariance (ANCOVA) and subsequent Tukey Honestly Significant Difference (HSD) tests, results of which are located in Appendix 5.2.

The timing of female maturity was estimated by fitting a logistic curve to the proportional frequency of immature to mature females in 2cm size class bins and 1-year age class bins (Chapter 4). Fish aged <1 were split into half year age class bins to increase resolution of maturity estimates. Separate logistic curves and respective 95% confidence limits were fit for each species at each location. The same protocol was used to estimate the age and size of sex change by using the proportional frequency of females to males per size or age bin. Reproductive life history traits estimated via this method were the length of 50% and 90% female maturity (Lm50, Lm90), age of 50% and 90% female maturity (Tm50, Tm90), length of 50% and 90% sex change (Ls50, Ls90) and the age of 50% and 90% sex change (Ts50, Ts90).

The length and age of female maturation and sex change were examined relative to maximum length and age of each species at each location, by dividing Lm50, Tm50, Ls50 and Ts50 estimates by the respective mean maximum length (Lmax) and age (Tmax). The relative timing of maturity and sex change were compared for intra-specific variation, by considering the amount of inter-specific variation in the timing of sex change among populations. Traditional ANOVA’s were not conducted, as the relative timing of maturity and sex change is based on population specific Lmax and thus the assumption of independence is violated. Rather, visual comparisons of 95% confidence intervals surrounding the relative size and age of maturity and sex change allow for the biological variance surrounding the proportional timing of maturity and sex change to be compared.

Separate length-weight and otolith-weight relationships were estimated for *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* at the Palm and Whitsunday Island groups, GBR, Australia and in the Philippines. Length-weight relationships were routinely estimated in the form $W = \alpha L^b$ via a logarithmic transformation of each individual's length (L) and weight (i.e., with α and *b* estimated by ordinary least squares regression). Length-weight relationships were compared for significant differences across locations using ANCOVA's and Tukey HSD tests, results of which are located in Appendix 5.3. To determine relative differences in fish condition with size between locations, a generalised logarithmic length-weight model was fit to all populations. Residuals for each individual were then extracted, plotted with body-size, and fit with linear models (i.e., relative condition = body weight/ predicted mean weight for the same observed length across locations). Male and female sexes are not differentiated here, although I am aware that males and females may have different length-weight relationships.

Long-term wrasse density in the Philippines was calculated across 32-years, from 1983 – 2014, at Apo and Sumilon Island fished areas, which are located in the immediate catchment area of markets sampled in south-eastern Negros. Long-term wrasse densities in Australia, were calculated over 12-years, from 2007 – 2018, adjacent to collection sites at the Palm and Whitsunday Island groups. Wrasse densities in both locations were obtained via underwater visual census across multiple sites; Details of collections can be found in Russ *et al.*, (2017) and Lowe *et al.*, (2019).

Finally, I compared the relative variance in age- and length-based life history traits across regional and biogeographic scales. Relative variance at biogeographic scales was determined by calculating the coefficient of variation (CV) between Philippine life history traits and a mean estimate of Palm and Whitsunday Island life history traits for each species. Regional CVs for each species were calculated by comparing Palm and Whitsunday life history traits of interest.

5.4 Results

Discernible, regularly spaced growth increments were evident in *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* otoliths across GBR and Philippine populations (Fig. 5.2). Optical clarity and interpretability increased from low to high latitudes, and across all locations and only ≈3% of samples were deemed unreadable and discarded from analysis. Otolith weight to fish age relationships indicated that all four species accrete calcium carbonate in the otoliths throughout the lifetime of the fish, and that Philippine populations of *H. melapterus*, *C. fasciatus*, and *O. digramma* often had heavier otoliths per age class compared to samples obtained from GBR reefs (Appendix 5.1). While the periodicity of increment deposition in otolith microstructure of the focal species was not validated in this study, I deemed otoliths of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* suitable for ageing based on the strong support for annual periodicity of increments in the otoliths of many other labrids (Choat and Robertson, 2002; Choat *et al.*, 2009), the presence of regularly spaced growth increments in the otolith microstructure (Fig. 5.2), and due to the positive otolith weight-to-age relationship for each species (Appendix 5.1). Otolith increment counts of readable samples were in relatively good agreement with ≈71% of the first two counts being identical, ≈24% of reads differed by 1 year and ≈4% differed by 2 – 4 years.

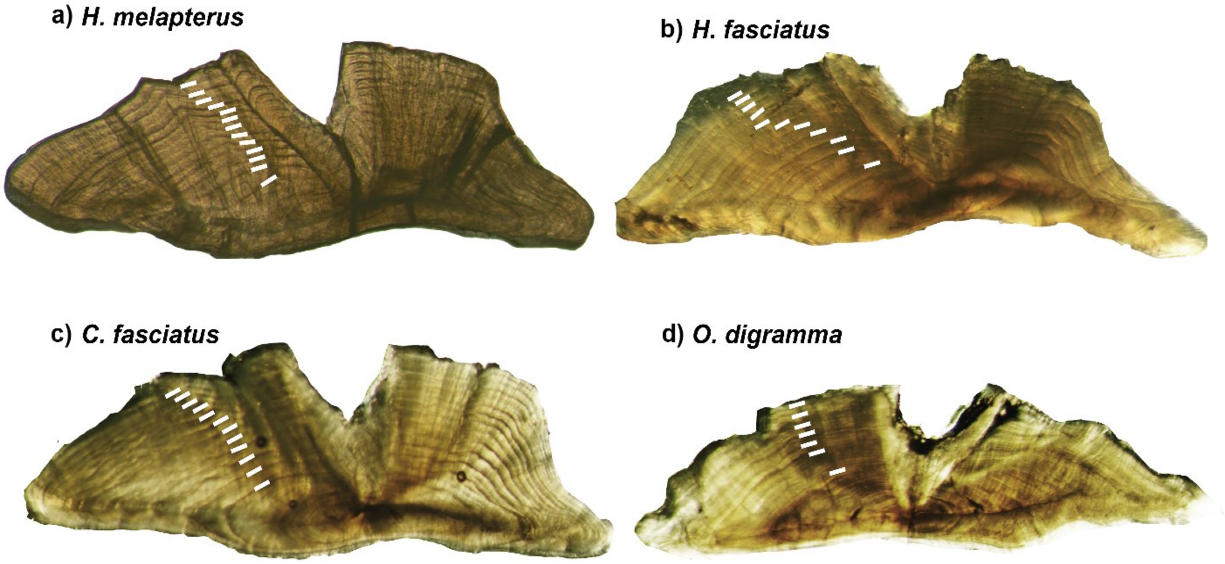


Figure 5. 2: Transverse sections of sagittal otoliths displaying putative annual increments: (a) *Hemigymnus melapterus*, (b) *H. fasciatus*, (c) *Cheilinus fasciatus*, (d) *Oxycheilinus digramma*. White lines indicate annual bands. Otolith sections are from GBR populations, images are not to one scale.

5.4.1 Geographic Variation in Growth, Maturity, and Sex Change

Table 5.1 summarises the sample size, mortality rate, length range, growth, and longevity estimates for each species at each location. Variation in life histories were evident at both regional (between inshore GBR locations) and biogeographic scales (between GBR and Philippine populations). Three trends were clear across species: 1) longevity was positively correlated with latitude between Philippine and GBR reefs (Table 5.1; Fig. 5.3, 5.5, 5.7); 2) Philippine populations grew faster, matured earlier, and experienced a higher mortality rate than those on unfished GBR reefs (Table 5.1, 5.2; Fig. 5.3, 5.4, 5.6, 5.7); 3) Despite this, Philippine wrasses were heavier for a given size (i.e., had greater relative body condition) and achieved a similar asymptotic and maximum length to populations on the GBR (Table 5.1; Fig. 5.3, 5.6, 5.8).

Among GBR reefs demographic variation was species-specific. *Hemigymnus melapterus* and *H. fasciatus* populations on high-latitude Whitsunday reefs grew slower, had reduced longevities, and attained a smaller maximum size than on the Palm reefs (Table 5.1; Fig. 5.3). While *C. fasciatus* and *O. digramma* from Whitsunday reefs also grew slower than those on Palm reefs, these species reached a larger asymptotic size and matured later on high-latitude Whitsunday reefs (Table 5.1; Fig. 5.3). On Palm reefs, unfished *H. melapterus* and *H. fasciatus* populations achieved a maximum longevity of 14 and 11 years, respectively (Table 5.1; Fig. 5.3). *Cheilinus fasciatus* lived to 15 years on Whitsunday reefs and *O. digramma* was found to live to 8 years on both Palm and Whitsunday reefs (Table 5.1; Fig. 5.3). In comparison, *O. digramma* were only collected to 6 years old on fished Philippine reefs and longevity estimates of *H. melapterus* and *C. fasciatus* were substantially lower on Philippine reefs at 6 and 8 years, respectively (Table 5.1; Fig. 5.3).

Table 5. 1: Wrasse life history parameters (+/- 95% confidence intervals) on GBR and Philippine reefs.

Species	Region	n	Z	Lmax (mm)	Size range (mm)	Tmax (yr)	Max. Age (yr)	L∞ (mm)	K	t0	L_τ (mm)	L_ω (mm)	L_μ (mm)
H. melapterus	Whitsunday Island Group, GBR, Australia	125	0.26 (0.07) $R^2 = 0.87$	297.67 (11.93)	95-353	7.56 (0.73)	12	236.35 (10.33)	1.17 (0.21)	-0.14 (0.12)	162.23 (6.99)	204.24 (6.62)	240.45 (7.66)
	Palm Island Group, GBR, Australia	86	0.19 (0.04) $R^2 = 0.92$	364.08 (12.09)	74-400	10.15 (0.96)	14	304.82 (17.24)	0.70 (0.12)	-0.17 (0.11)	157.98 (8.78)	231.69 (11.48)	279.72 (11.88)
	Philippines	98	0.34 (0.18) $R^2 = 0.73$	348.93 (14.32)	101-402	4.79 (0.42)	6	314.03 (9.49)	1.21 (0.11)	-0.11 (0.16)	201.80 (9.30)	301.90 (7.75)	329.39 (11.73)
H. fasciatus	Whitsunday Island Group, GBR, Australia	78	0.09 (0.14) $R^2= 0.16$	215.73 (5.54)	88-238	8.64 (0.40)	10	186.19 (6.08)	1.82 (0.35)	-0.13 (0.10)	135.82 (5.31)	151.97 (5.08)	164.94 (5.64)
	Palm Island Group, GBR, Australia	37	0.13 (0.15) $R^2 = 0.47$	234.20 (11.55)	94-257	9.20 (1.44)	11	204.58 (9.17)	2.05 (0.18)	-0.07 (0.08)	162.52 (6.29)	186.06 (8.51)	200.49 (8.64)
C. fasciatus	Whitsunday Island Group, GBR, Australia	70	0.12 (0.06) $R^2 = 0.65$	272.70 (13.61)	99-307	13.60 (0.78)	15	267.51 (19.50)	0.22 (0.04)	-0.65 (0.35)	122.71 (13.56)	163.64 (5.45)	200.18 (5.52)
	Palm Island Group, GBR, Australia	57	0.14 (0.14) $R^2 = 0.38$	257.38 (7.31)	110-274	11.00 (0.83)	13	217.39 (17.09)	0.59 (0.10)	0.57 (0.43)	167.70 (6.39)	196.60 (6.39)	215.90 (4.94)
	Philippines	100	0.22 (0.08) $R^2 = 0.80$	304.67 (4.52)	100-318	6.73 (0.40)	8	277.64 (6.52)	1.31 (0.12)	-0.03 (0.02)	201.62 (8.34)	271.64 (5.62)	278.73 (6.96)
O. digramma	Whitsunday Island Group, GBR, Australia	46	0.32 (0.12) $R^2 = 0.91$	255.67 (10.98)	90-278	6.50 (0.67)	8	226.70 (22.04)	0.52 (0.16)	-0.31 (0.24)	120.36 (12.70)	143.18 (8.31)	164.92 (8.08)
	Palm Island Group, GBR, Australia	92	0.34 (0.23) $R^2 = 0.81$	252.62 (4.49)	110-271	5.31 (0.64)	8	220.83 (7.03)	1.56 (0.24)	-0.07 (0.09)	168.59 (7.16)	196.72 (6.73)	214.61 (6.00)
	Philippines	78	0.49 (0.45) $R^2 = 0.70$	243.36 (5.30)	105-263	3.27 (0.53)	6	225.78 (7.94)	1.99 (0.20)	-0.04 (0.03)	187.08 (6.68)	221.43 (6.27)	231.56 (8.73)

n = sample size; Z = instantaneous mortality rate; L_{∞}, K, and t_0 are bootstrapped coefficients of the VBGF (described in methods); L_{τ} ,L_{ω}, and L_{μ} are bootstrapped coefficients of the rVBGF (described in methods); T_{max} = mean age of oldest 15% of sample; L_{max} = mean length of the largest 15% of sample. Where appropriate 95% confidence intervals for each parameter estimate are shown in brackets.

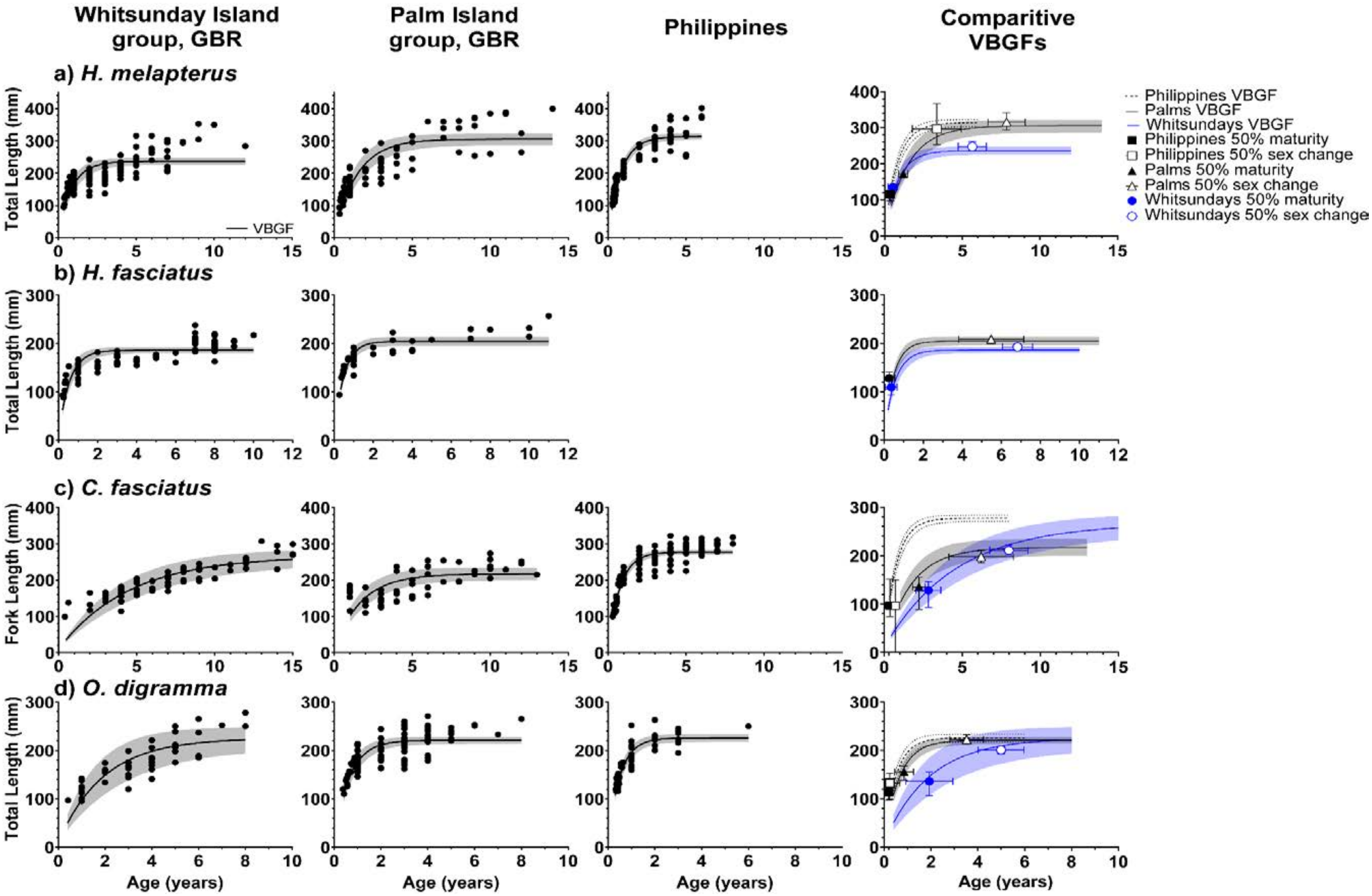


Figure 5. 3: Size-at-age data for (a) *H. melapterus*, (b) *H. fasciatus*, (c) *C. fasciatus*, and (d) *O. digramma* at the Whitsunday and Palm Island groups, GBR, and from fishery-dependent sampling of Philippine fish markets. Data are fit with von-Bertalanffy growth

functions (VBGF). Parameter estimates are in Table 5.1. Comparative VBGF curves with age and size of maturity (black symbols) and sex change (white symbols) for each location are shown in the fourth column for a simplified comparison of regional differences in growth trajectories. Long-term mean annual SST were 25.92°C, 26.39°C, and 28.85°C for the Whitsundays (20.05-20.21°S), Palms (18.53-18.70°S), and Philippines (9.0-11.0°N), respectively.

Sizes at maturity and sex change for each species at each location are presented in Table 5.2. Female maturation schedules varied considerably among populations, with estimates of 50% maturity ranging from <1 year for many populations, to 2.83 years for Whitsunday Island group *C. fasciatus* (Table 5.1; Fig. 5.4). All populations achieved 50% female maturity by approximately 17cm, the smallest being an estimated ≈7.5cm size of 50% female maturity for *O. digramma* from the Philippines (Table 5.2). On GBR reefs, female *C. fasciatus* and *O. digramma* reached maturity over a broad size range, whilst *H. melapterus* and *H. fasciatus* showed little difference in the size of 50% and 90% maturity (Table 5.2). Overlapping 95% confidence intervals suggest comparable estimates of Lm50 and Tm50 for Palm and Whitsunday populations of *H. fasciatus*, *O. digramma,* and *C. fasciatus* despite separation of approximately 350km (Table 5.2; Fig. 5.3, 5.4). Yet, despite a lack of significant difference in the age of maturity in both locations, the mean age of maturity was later in the Whitsundays for all three species, consistent with slower growth and extended longevities in the Whitsundays. Conversely, *H. melapterus* matured 8-10cm longer in the Palm Island group compared to the Whitsunday Island group, consistent with a substantially larger maximum size in the Palm Island group and marginally lower juvenile growth rate evident from overlapping VBGF curves (Fig. 5.3, 5.4) Maturity was attained particularly rapidly in Philippine populations. Despite sampling fish that were just 6cm in length, very few immature juveniles were sampled from the Philippine fish markets. It was clear that all species matured before the age of 1 year, and data suggests that sexual maturity occurs within 6 months of settlement, at <12cm in length, irrespective of the species (Table 5.2). In the Philippines, *C. fasciatus*, *H. melapterus,* and *O. digramma* populations matured at comparable sizes to GBR populations but reached 50% maturity more rapidly, consistent with rapid growth and significantly reduced longevity in this location (Fig. 5.3, 5.4). The size of maturity in all populations was supported by the disproportionate increase in gonadosomatic index of individuals at this size (Appendix 5.1).

Despite having the most rapid attainment of maturity of all 11 populations, Philippine *H. melapterus* exhibited the largest size of sex change (Fig. 5.3a). Similarly, Philippine populations of *C. fasciatus* and *O. digramma* changed sex over a broader size range compared to GBR populations, despite 50% sex change occurring at a significantly earlier age than in GBR populations (Table 5.2). Consistent with reduced longevities on Philippine reefs, sex change occurred at an earlier age in Philippine populations of *H. melapterus*, *C. fasciatus*, and *O. digramma*. On the GBR, 95% confidence intervals surrounding estimates of the 50% timing of sex change overlapped for all species, but, the mean age of sex change always occurred later on high-latitude Whitsunday reefs consistent with slower lifetime growth in this location (Table 5.2; Fig. 5.3, 5.4).

Table 5. 2: Reproductive life history traits of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* populations from the Whitsunday and Palm Island groups, GBR and from Philippine fish markets.

Species	**Location**	***Lm*50 (mm)**	***Lm*90 (mm)**	***Tm*50 (yrs)**	***Tm*90 (yrs)**	***Ls*50 (mm)**	***Ls*90 (mm)**	***Ts*50 (yrs)**	***Ts*90 (yrs)**
H. melapterus	Whitsundays	135.2 (122.3 – 144.6)	159.9 (145.3 – 170.5)	0.51 (0.2 – 0.8)	1.15 (0.9 – 1.6)	247.8 (236.78 – 262.34)	282 (259.3 – 299.27)	5.64 (4.98 – 6.55)	8.1 (6.65 – 9.27)
	Palms	171.69 (163.3 – 180.7)	191.32 (177.7 – 202.7)	1.19 (1.1 – 1.6)	1.77 (1.4 – 2.3)	316.01 (294.41 – 341.12)	367.5 (328.83 – 396.16)	7.85 (6.63 – 9.47)	11.3 (8.84 – 13.18)
	Philippines	76.4 (0.1 – 117.2)	174 (55.2 – 222.7)	<0.91*	0.91 (0.05 —2)	297.1 (253.36 – 376.21)	503.8 (377.3 – 440.01)	3.35 (2.47 – 4.93)	7.49 (4.98 –9.81)
H. fasciatus	Whitsundays	109.4 (93.6 – 120.3)	131.4 (111.3 – 143.9)	0.36 (0.1 – 0.7)	0.87 (0.6 – 1.3)	192.6 (186.3 – 199.11)	210.9 (200.37 – 219.6)	6.83 (6 – 7.6)	9.46 (8.08 – 10.71)
	Palms	127.7 (105.4 – 141)	151 (118.5 – 165.8)	0.23 (0.1 – 0.6)	0.80 (0.1 – 1.3)	208.2 (200.67 – 214.45)	215 (204.34 – 221.83)	5.48 (4.15 – 7.31)	7.94 (5.41 – 9.79)
C. fasciatus	Whitsundays	128.2 (93.6 –146.6)	174.3 (143.3 – 197.1)	2.83 (2 – 3.5)	4.10 (3.2 – 4.9)	211 (201.72 – 221.62)	237.4 (220.64 – 251.1)	7.98 (7.04 – 9.2)	11.2 (9.27 – 12.83)
	Palms	135 (89.1 – 155.5)	193 (159.9 – 234.3)	2.23 (1.8 – 2.8)	3.08 (2.4 – 3.8)	198 (185.79 – 212.12)	228 (206.48 – 244.45)	6.21 (4.71 – 8.27)	11.2 (8.05 – 14.08)
	Philippines	97.1 (74.2 – 151.7)	266.9 (114.3 – 208.1)	0.38 (0.02 – 0.7)	0.62 (0.30 – 1)	97.1 (0.01– 149.83)	266.9 (209.97 – 338.17)	0.72^ (0.55 – 0.88)	5.41 (2.43 –11.10)
O. digramma	Whitsundays	136.1 (106 – 155.2)	190.4 (159.5 – 222.6)	1.93 (0.8 – 2.9)	4.25 (3 – 5.7)	200.8 (192.78 – 208.72)	213 (201.14 – 221.87)	4.99 (4.34 – 5.97)	6.81 (5.44 – 7.99)
	Palms	155.8 (138.5 – 167)	190.6 (173.4 – 207)	0.85 (0.5 – 1.3)	1.78 (1.4 – 2.4)	222.5 (213.67 – 232.15)	252 (236 – 265.48)	3.52 (3.01 – 4.24)	5.63 (4.46 – 6.68)
	Philippines	112.8 (97.2 – 121.3)	124.7 (102.2 – 135)	<0.16*	0.16 (0.01 – 1.3)	132.7 (98.91 – 152.26)	208.1 (174.77 – 244.88)	0.24 (0.01 – 0.67)	1.91 (1.14 –2.91)

n = number of samples, Lm50 = length at 50 % maturity, Lm90 = length at 90% maturity, Tm50 = age of 50% maturity, Tm90 = age of 90% maturity, Ls50 = length at 50% sex change, Ls90 = length at 90% sex change, Ts50 = age at 50% sex change, Ts90 = age at 90% sex change. Associated 95% confidence limits of each parameter estimate are shown in brackets. Tm50 estimates marked with * indicate less than 50% of age <1 were immature females and thus each estimate is based on its corresponding 90% size of maturity. In reality Tm50 is likely smaller than these (*) values. Ts50 estimates marked with ^ are based on the y-intercept (+/- 95% CI) of the logistic model estimating the timing of sex change, because less than 50% of samples were female for any given age class.

When differences in the mean maximum length (Lmax) and mean maximum age (Tmax) of populations were accounted for, the relative length and age of maturity was not significantly different among GBR reefs for 3 of 4 species (Fig. 5.4). However, 95% confidence intervals surrounding estimates of the relative age of maturity and sex change were considerable, and relationships among taxa and populations were far from invariant, even among GBR reefs separated by only 350 kms (Fig. 5.4). Variation in the relative age of maturity and sex change was particularly clear when comparing Philippine and Australian reefs. *Cheilinus fasciatus* changed sex at a smaller proportion of Tmax and Lmax and matured earlier in the Philippines compared to the GBR, despite maturity occurring at a similar relative size in all locations (Fig. 5.4). *Oxycheilinus digramma* also changed sex at a significantly lower relative size and age to those on GBR reefs and *H. melapterus* had a lower relative size of maturity on Philippine reefs, despite undergoing sex change at a similar relative size and age in all locations (Fig. 5.4).

These data indicate that, depending on the location, most of these wrasse populations reach 50% sexual maturity at 45% – 62% of their respective mean maximum length, with *H. melapterus* and *C. fasciatus* in the Philippines laying well outside this at 21% and 32% of Lmax, respectively (Fig. 5.4a). Sex change was achieved between 77% – 89% of all population's respective mean maximum length, with Philippine *C. fasciatus* and *O. digramma* changing sex at 32% and 53% of population-specific Lmax, respectively (Fig. 5.4c). The relative age of sexual maturity and sex change was considerably more variable than relative size of sexual maturity and sex change (Fig. 5.4c, d).

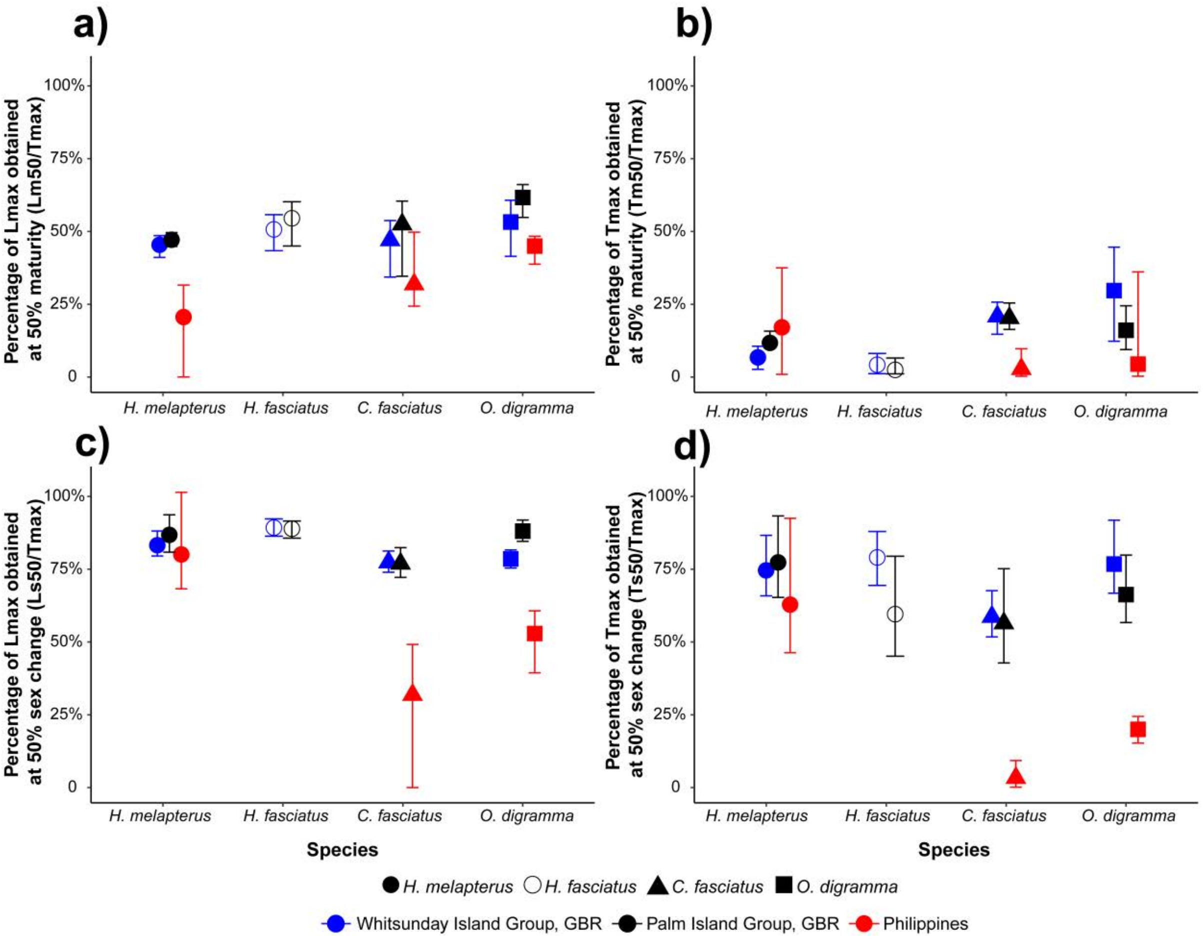


Figure 5. 4: Relative timing of maturity (a, b) and sex change (c, d) of *H. melapterus*, *H. fasciatus*, *C. fasciatus,* and *O. digramma* at the Whitsunday and Palm Island groups, GBR, and from fishery-dependent sampling of Philippine fish markets. Blue = Whitsunday Island group; 25.92° C, black = Palm Island group; 26.39° C, red = Philippines; 28.85° C. ● = *H. melapterus*, ○ = *H. fasciatus*, ▲= *C. fasciatus*, and ■ = *O. digramma.*

Species-specific longevity, maximum and asymptotic size varied considerably among locations (Table 5.1; Fig. 5.5). Philippine populations had substantially lower Tmax estimates and maximum age for all species investigated (Table 5.1; Fig 5.5a, c). Conversely, L∞ and Lmax estimates were positively related to mean annual SST and were equivalent (*H. melapterus* and *O. digramma*) or significantly larger (*C. fasciatus*) on low latitude, fished Philippine reefs compared to high-latitude unfished GBR populations (Table 5.1; Fig. 5.5b, d).

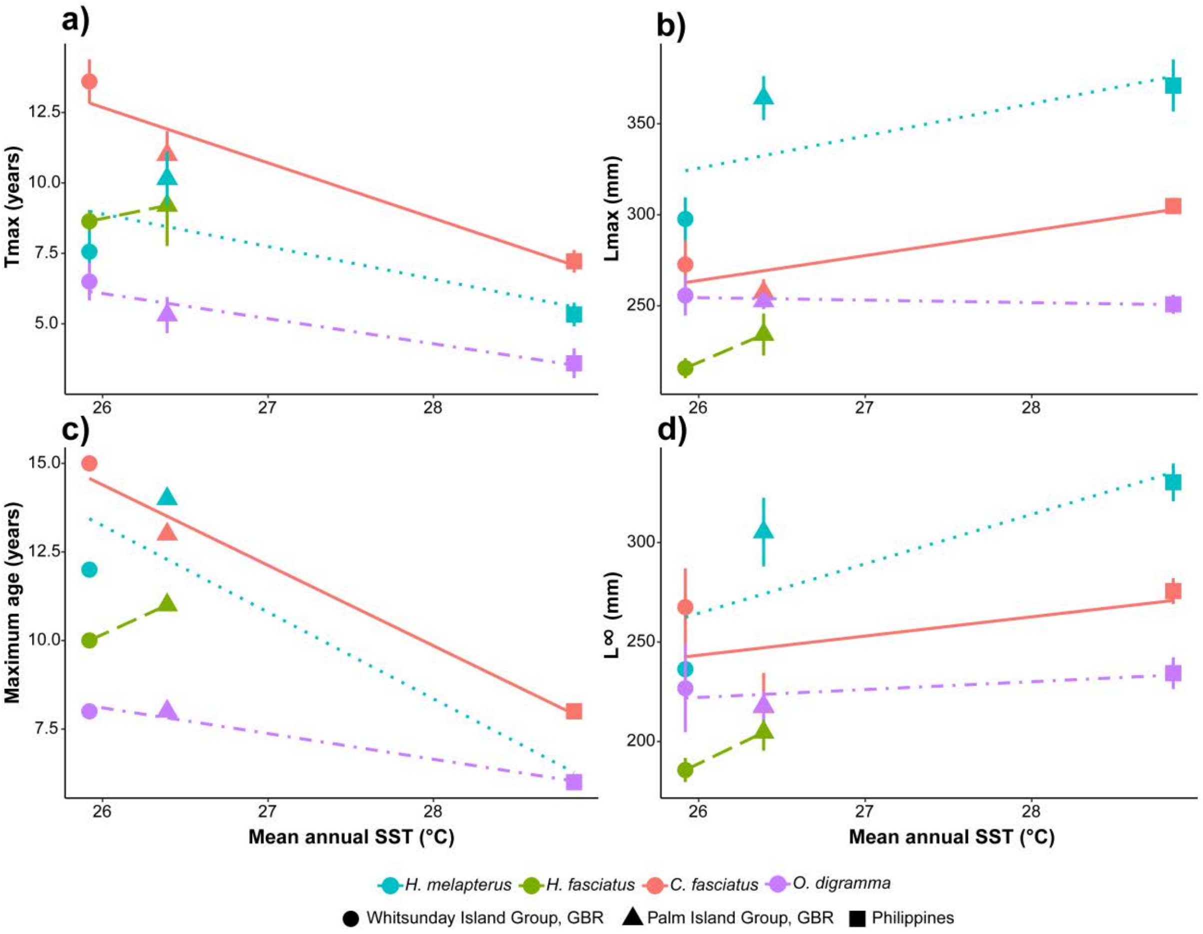


Figure 5. 5: Linear regressions of (a) Tmax, (b) Lmax, (c) Maximum age, and (d) L∞ with mean SST at each sampling location from 2001 to 2016 (January to December). ● Whitsunday Island group = 25.92°C, ▲ Palm Island group = 26.39°C, ■ Philippines = 28.85°C. Blue = *H. melapterus*, green = *H. fasciatus*, red = *C. fasciatus*, and purple = *O. digramma.*

Similarly, estimates of Lτ, Lω, and Lμ for each species showed that species-specific mean size-at-age, and thus growth rate, increased with increasing SST (Table 5.1; Fig. 5.6). Differences in mean-size-at-age were significant between Philippine and GBR wrasse populations for all species, and for *O. digramma* and *H. fasciatus* a significant positive relationship between mean-size-at-age 1, asymptotic size and SST was also evident between the Whitsunday and Palm Island groups.

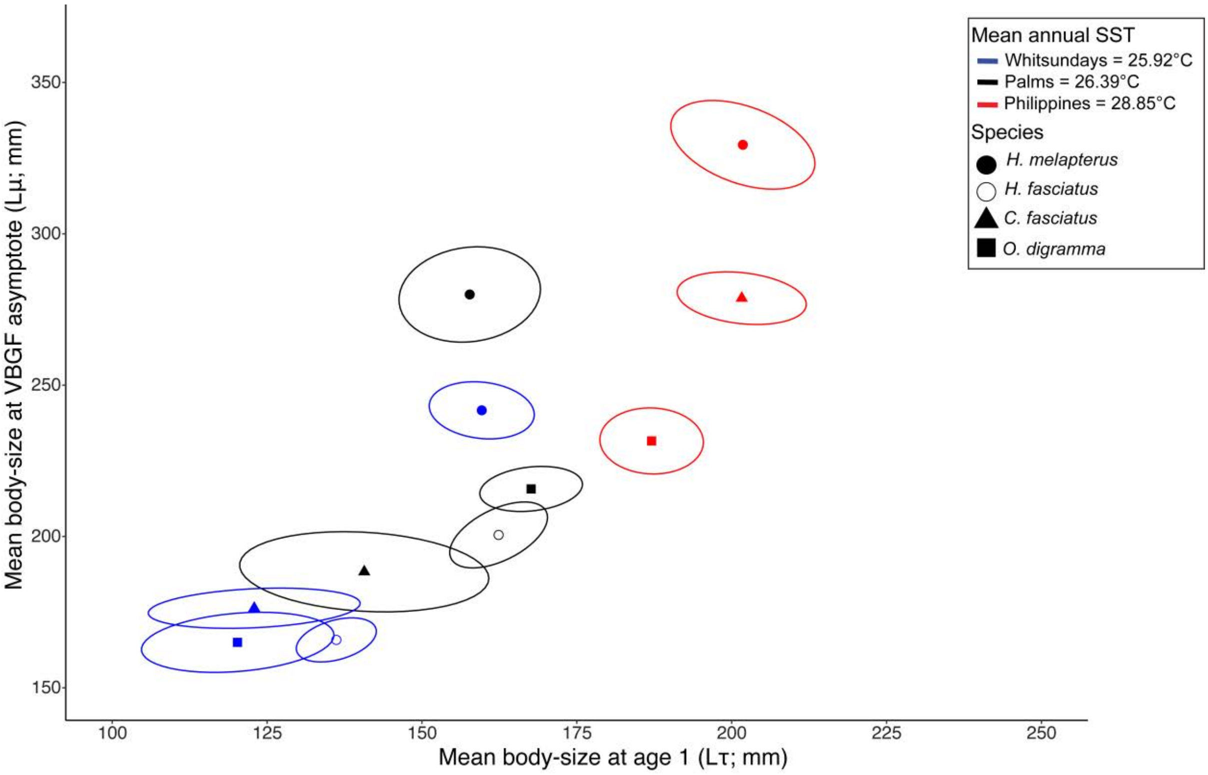


Figure 5. 6: Bootstrapped 95% confidence ellipses surrounding rVBGF estimates of Lτ and Lμ, describing growth from year 1 until approximate asymptotic size for each species at each location. Mean SST estimated from 2001 to 2016 (January to December). Whitsunday Island group = 25.92° C, Palm Island group = 26.39° C, Philippines = 28.85° C. Filled circles = *H. melapterus*, open circles = *H. fasciatus*, triangles = *C. fasciatus*, and squares = *O. digramma.*

5.4.2 Mortality

Species-specific mortality rates on GBR reefs were similar for all species investigated (ANCOVA; p=>0.05), and fished Philippine wrasse populations had higher mortality rates than unfished GBR populations (Table 5.1; Fig. 5.7). Differences between Whitsunday and Philippine mortality rates were significant for *C. fasciatus* (ANCOVA; p=0.015, Tukey HSD; p=0.002), whereas Palm and Philippine mortality rates were not significantly different for this species (Tukey HSD; p=0.06). *Hemigymnus melapterus* and *O. digramma* had higher mortality rates in the Philippines (Fig. 5.7), but differences between mortality slopes were not statistically significant (ANCOVA; p= 0.076 and 0.21, respectively). Depending on the species and location, mortality rates from unfished GBR wrasse populations ranged from 0.009 to 0.34 (Table 5.1). Comparatively, mortality rates of low latitude, fished Philippine wrasse populations ranged from 0.22 to 0.49 (Table 5.1). On both regional (within GBR) and biogeographic (GBR vs. Philippines) scales, mortality rates of all species exhibited a positive relationship with mean annual SST. Anomalously, high age class frequencies of age 7 and 8 *H. fasciatus* were sampled from the Whitsunday Island group (Fig. 5.7b). However, a modal age of 1 was used in mortality estimates, rather than age 8, as fitting a regression from ages 8+ onwards would result in an unrealistic mortality rate for an unfished population of *H. fasciatus*, particularly considering mortality rate estimates for the same species at the Palm Island group and the relative difference between Palm and Whitsunday mortality rates for other species studied here (Fig. 5.7).

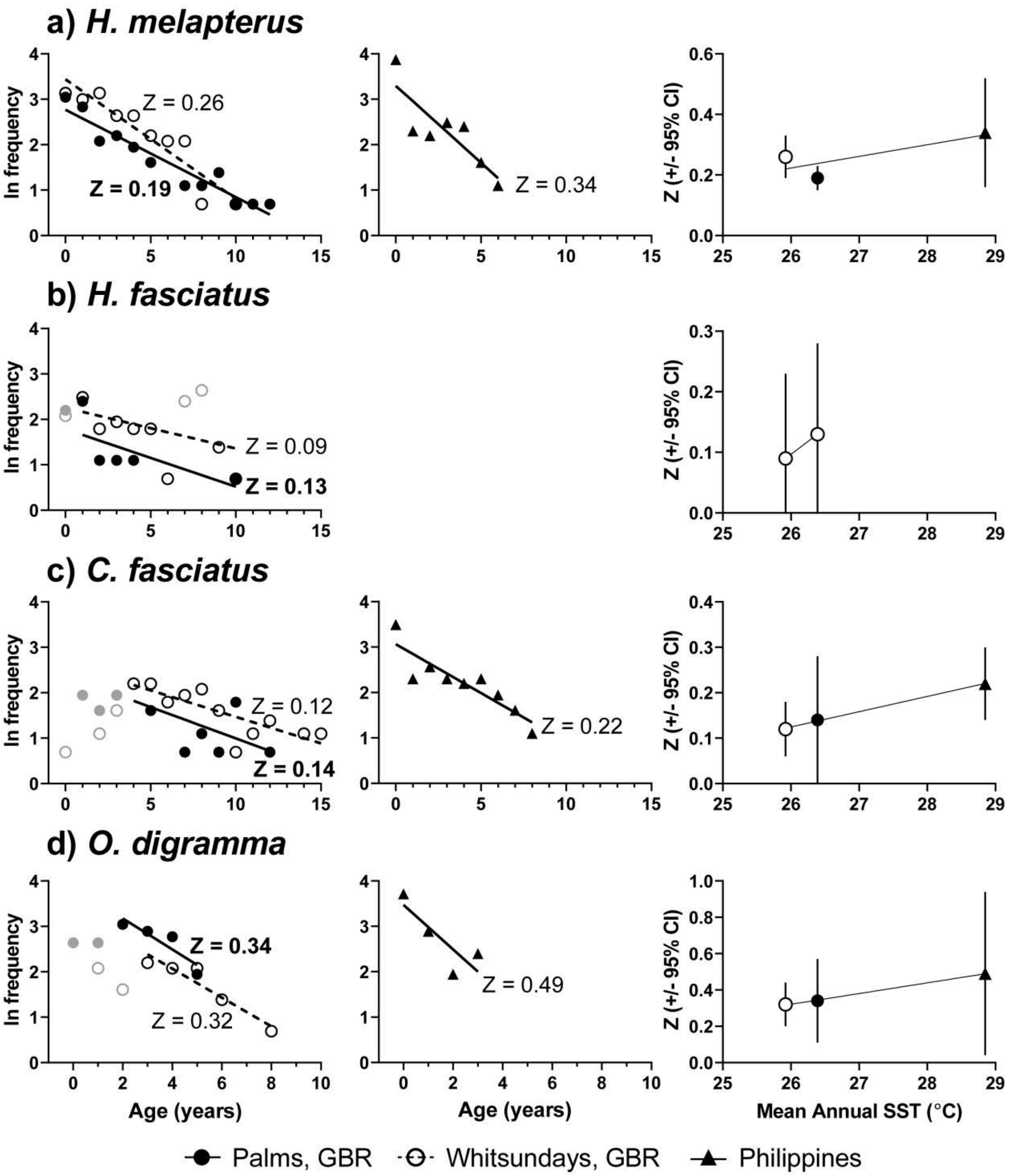
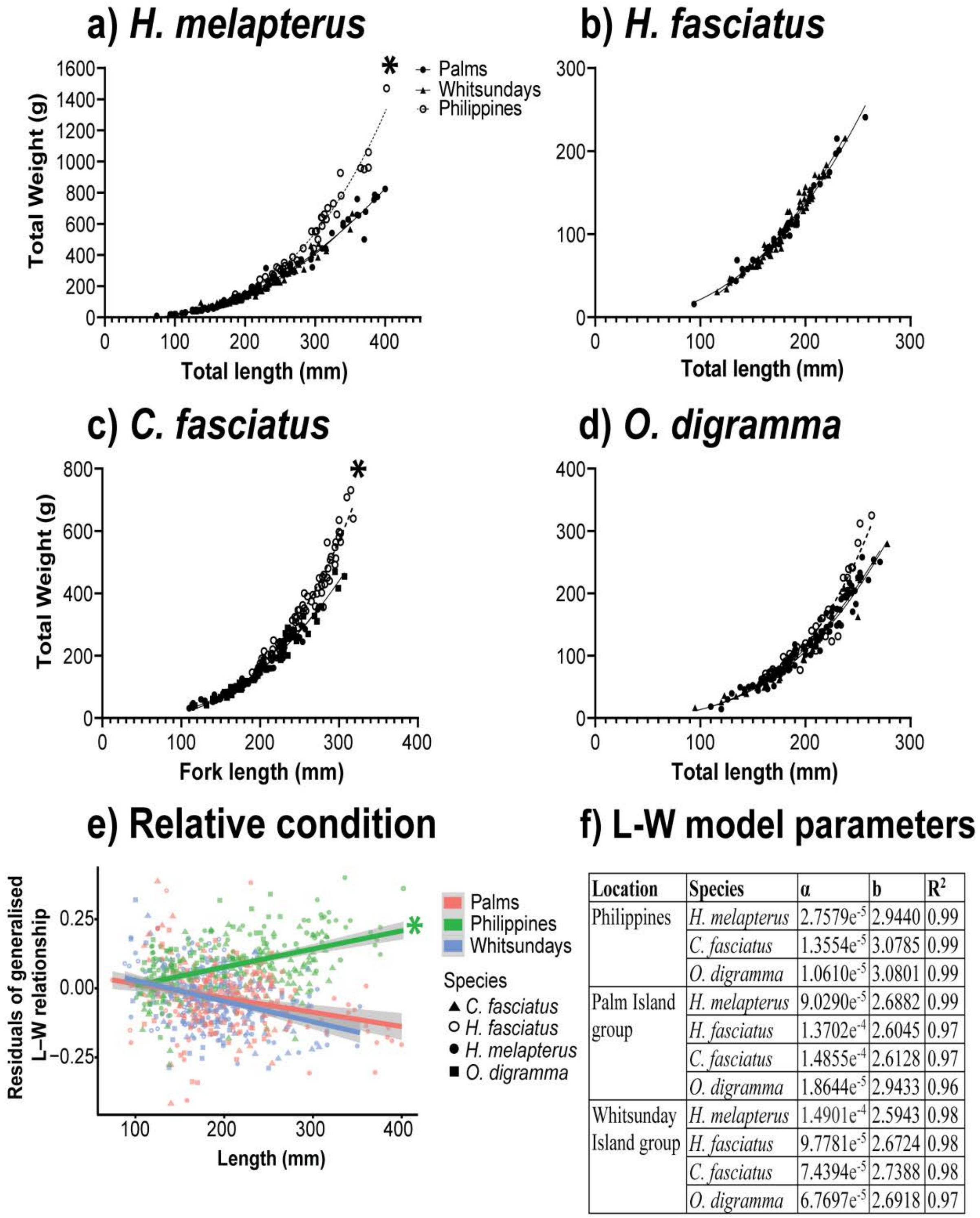


Figure 5. 7: Age-based catch curves for (a) *H. melapterus*, (b) *H. fasciatus*, (c) *C. fasciatus*, and (d) *O. digramma* populations on Palm and Whitsunday reefs (left column), Philippine reefs (center column), and the relationship between mortality (Z) and mean annual SST (+/- 95% CIs) at each location (right column). A modal age of 1 was used for mortality

calculations of Whitsunday *H. fasciatus* populations, despite anomalously high age class frequencies of ages 7 and 8 (explained in methods). Grey points were excluded from analysis and represent age-classes not fully recruited to the sampling regime (see Methods).

5.4.3 Length-Weight and Body-Condition relationships

Length-weight relationships of all four species indicated allometric growth ($b \neq 3$) in all locations (Fig 5.8a, b, c, d, f). Philippine *H. melapterus* and *C. fasciatus* individuals were significantly heavier for a given length to those on Palm and Whitsunday reefs, GBR (Fig. 5.8a, b, c, d, ANCOVA’s; $p<0.05$, Tukey HSD; $p < 1*e^{-4}$, and $<1*e^{-5}$, respectively). This was particularly clear for large-bodied fish (Fig. 5.8a, b, c, d). Philippine *O. digramma* were significantly heavier for a given length to those on Whitsunday reefs, GBR (ANCOVA; $p<0.05$, Tukey HSD; $p < 1*e^{-4}$) but were not significantly different to those on Palm reefs (Tukey HSD; $p = 0.093$). *Hemigymnus melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* did not exhibit a significant difference in length-weight relationships between Palm and Whitsunday reefs, GBR (Fig. 5.8a, b, c, d, Tukey HSD; $p > 0.05$). Linear models fit to relative estimates of body condition (described in methods) indicated that significant differences in body condition began to occur at approximately 15cm length across species on Philippine and Australian reefs (Tukey HSD; $p=<1e^{-5}$, Fig. 5.8e).



Location	Species	α	b	R^2
Philippines	*H. melapterus*	$2.7579e^{-5}$	2.9440	0.99
	C. fasciatus	$1.3554e^{-5}$	3.0785	0.99
	O. digramma	$1.0610e^{-5}$	3.0801	0.99
Palm Island group	*H. melapterus*	$9.0290e^{-5}$	2.6882	0.99
	H. fasciatus	$1.3702e^{-4}$	2.6045	0.97
	C. fasciatus	$1.4855e^{-4}$	2.6128	0.97
	O. digramma	$1.8644e^{-5}$	2.9433	0.96
Whitsunday Island group	*H. melapterus*	$1.4901e^{-4}$	2.5943	0.98
	H. fasciatus	$9.7781e^{-5}$	2.6724	0.98
	C. fasciatus	$7.4394e^{-5}$	2.7388	0.98
	O. digramma	$6.7697e^{-5}$	2.6918	0.97

Figure 5. 8: Length-Weight relationships of Palm and Whitsunday Island group, GBR and Philippine (a) *H. melapterus*, (b) *H. fasciatus*, (c) *C. fasciatus*, (d) *O. digramma*, (e) linear models comparing relative condition at body-length across locations and species (explained in methods), (f) Length-Weight model parameters estimated based on $W = \alpha L^b$ relationship for each species at each location. * indicates significant difference in body condition between GBR and Philippine reefs.

5.4.4 Long-term Density

Long-term densities of *C. fasciatus* on GBR reefs were significantly greater than those recorded on Philippine reefs, at approximately 4.03 and 0.34 fish per 1000m^2, respectively (Fig. 5.9). *Hemigymnus melapterus* were also more abundant on Australian reefs compared to those of the Philippines, but not significantly (Fig. 5.9). *Hemigymnus fasciatus* occurs at approximately comparable densities in both locations and *O. digramma* was more abundant in the Philippines than on the GBR (Fig. 5.9).

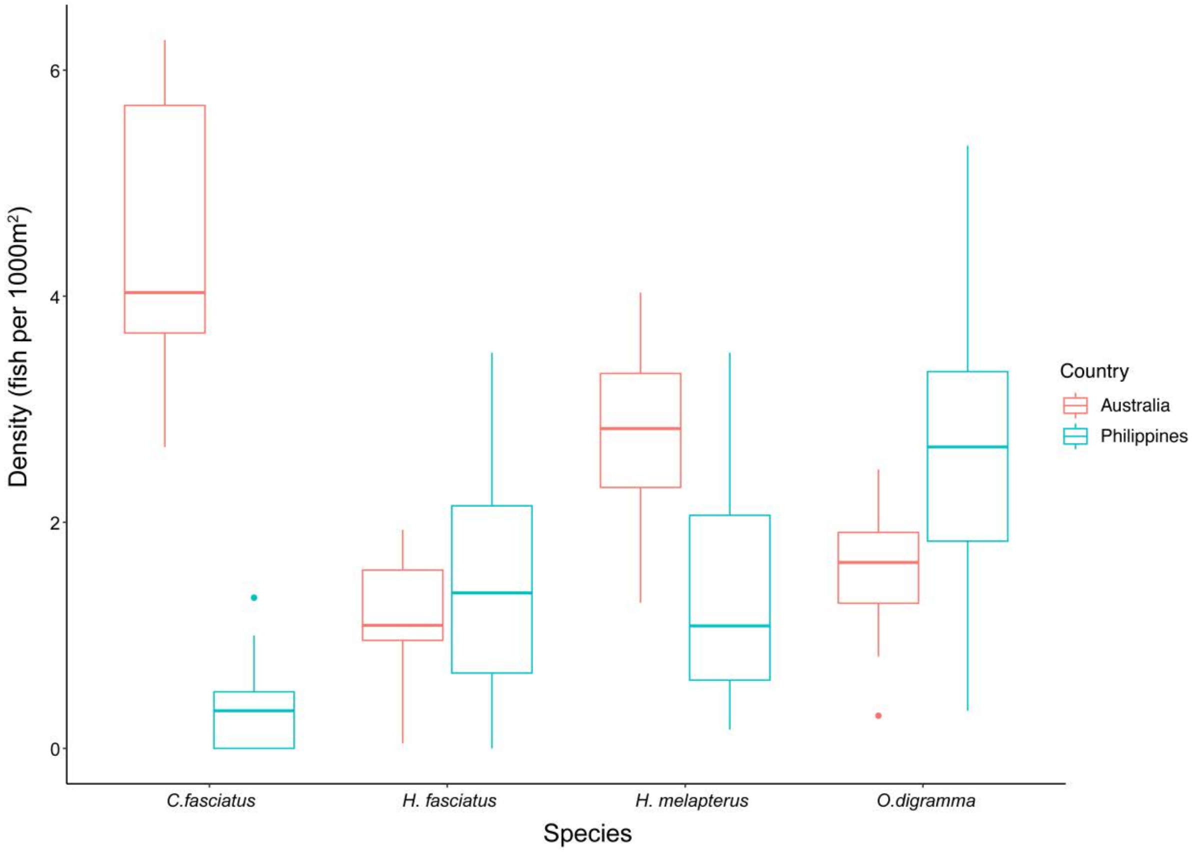
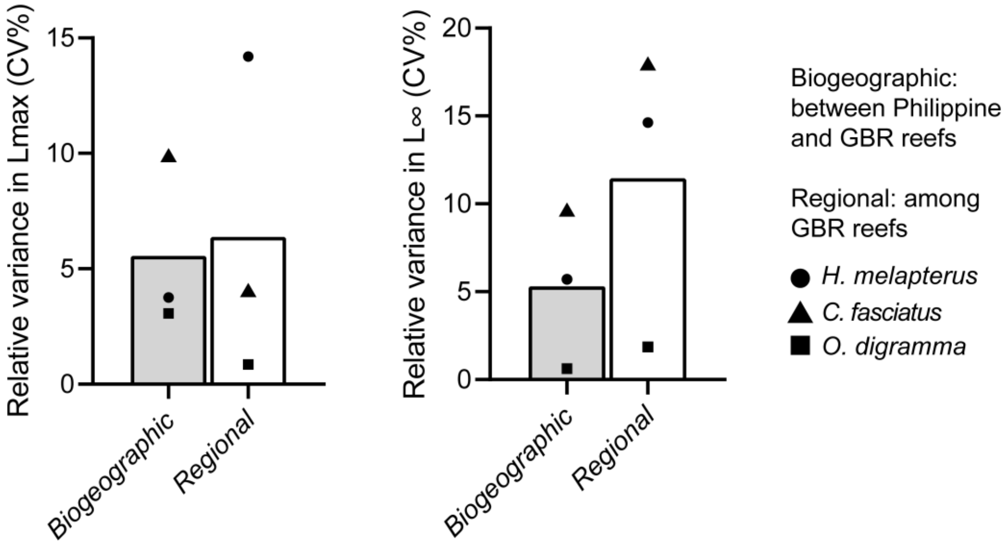


Figure 5. 9: Long-term densities for *C. fasciatus, H. fasciatus, H. melapterus,* and *O. digramma* calculated over 31-years from Apo and Sumilon Island fished areas, Philippines (blue) and over 12-years at the Palm and Whitsunday Island Groups, Australia (red). Boxplots extend from the 25 to 95% percentiles with outliers shown as individual points. Horizontal lines indicate the long-term median density of each species in each location.

5.4.5 Relative Variance in Age- and Length-based Traits

The relative variance in age- and length-based life history traits were compared to determine their relative utility for determining variation in life histories at regional to biogeographic scales (Fig. 5.10). Similar or greater variation in length-based traits, mean maximum and asymptotic size, were evident at regional scales compared to biogeographic scales (Fig 5.10a). This suggests that variation in length occurred at the local population level and thus length-based traits are not suitable for determining differences in life histories across biogeographic scales in the focal species. Age-based traits, mean maximum age and mortality, varied considerably more at biogeographic scales than regional (among GBR) scales (Fig. 5.10b) suggesting that age-based traits are more suitable for determining differences in life histories between populations at both regional and biogeographic scales.

a) Length-based traits



b) Age-based traits

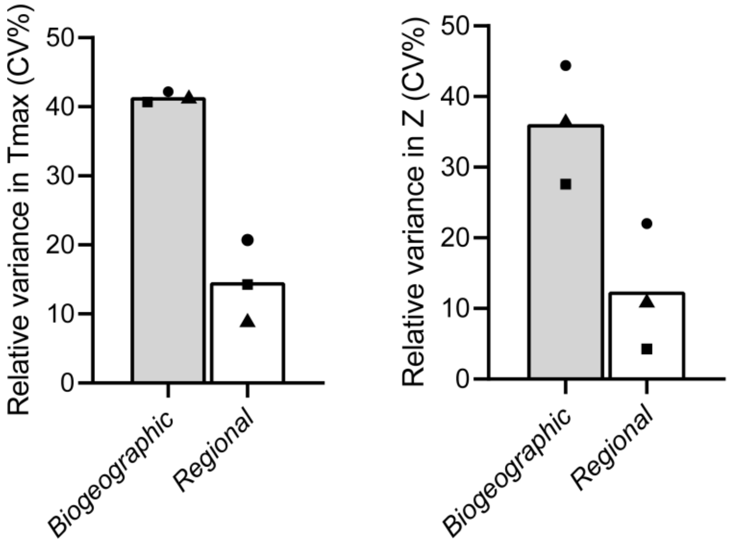


Figure 5. 10: Percentage of relative variance (CV %) in (a) length-based traits: mean maximum (Lmax) and asymptotic length (Linf), and (b) age-based traits: mean maximum longevity (Tmax) and mortality (Z) at two spatial scales: between GBR reefs (regional) and between GBR and Philippine locations (biogeographic).

5.5 Discussion

Because the metabolism of ectotherms slows at low temperatures, generally the largest and oldest ectotherms can be found in high latitude locations (Bergmann, 1847; Roff, 1993). This relationship is consistent with the metabolic theory of ecology (Munch and Salinas, 2009) and the Temperature-Size Rule (TSR), which predicts that ectotherms in warm environments (lower latitudes) will have reduced maximum size, reduced size of maturity, and faster initial growth than individuals living in colder environments (higher latitudes) (Atkinson, 1994; Arendt, 2011). Fishing is also expected to result in increased mortality, more rapid maturity, and reductions in mean size and age of exploited stocks (Stearns, 1992; Hamilton *et al.*, 2007). Indeed, wrasses studied here had higher mortality rates, lower longevity, rapid growth, and early maturation on low-latitude, fished Philippine reefs compared to GBR reefs, likely due to the combined effects of fishing and the metabolic costs of living at low latitudes (Adams, 1980; Munch and Salinas, 2009). However, Philippine wrasses studied here also attained a similar or larger maximum size and had higher relative body condition than unfished populations at high-latitudes, results not consistent with the metabolic theory of ecology, the TSR, and the expected effects of fishing on body-size. On regional scales, variation in life histories were species-dependent and did not reflect an overarching effect of temperature, evident via the presence of both crossed and nested growth profiles between Palm and Whitsunday Island groups (Atkinson, 1994; Berrigan and Charnov, 1994). These unexpected relationships suggest that localised sources of demographic variation are affecting life histories of the focal wrasses across various spatial scales (Huey and Kingsolver, 2019).

In many fish species, larger body-size results in fitness advantages due to higher fecundity, increased survival, and superior mate and territory acquisition (Kingsolver *et al.*, 2001; Perez and Munch, 2010). Assuming resources are constant, partitioning energy towards reproduction early in life usually results in demographic trade-offs with longevity and maximum body size. However, when resources and temperature change simultaneously, either directly as a result of environmental variation, or indirectly as a result of behavioural restrictions on activity, trade-offs between growth and reproduction will depend upon the optimum operating temperature of the organism and its respective demographic flexibility across space and time (Huey and Kingsolver, 2019). In the Philippines, the observed large body-size, rapid growth, greater relative body condition, and early maturation suggests that benthic invertebrates on which the focal species prey are not limiting the growth of the focal wrasses. But how do the focal species obtain a large body size and greater relative body condition when increased food consumption should require increased activity and foraging time or larger space use? Both adjustments should effectively reduce food consumption and reproduction, even if environmental food levels are unchanged. Notably, the focal wrasses have lower GSIs for a given size or age compared to those on the GBR (Chapter 4). Moreover, Philippine populations have different sexual ontogenies and protracted timing of sex change, which results in a higher proportion of mature females that persist later into ontogeny than on GBR reefs (Chapter 4). Lower investment in reproductive tissues and weak selection for sex change will allow more energy to be invested into somatic growth early in ontogeny, assuming that the costs of oxygen supply do not change considerably, or are offset via other demographic trade-offs in the focal wrasses between GBR and Philippine reefs. Oxygen limitation has been proposed as a key mechanism determining smaller ectotherm body size at higher temperatures (Pauly, 1980, 1981; Atkinson *et al.*, 2006). Yet, the present study is not the first to show an increase in organism size with increasing temperature (Angilletta and Dunham, 2003; Conover *et al.*, 2009). This suggests that it is unlikely that oxygen supply could be perceived as a universal mechanism determining optimal body sizes of ectotherms under differing mortality regimes (reviewed in Lefevre *et al.*, 2017; Audzijonyte *et al.*, 2019).

In numerous taxa, abundant or higher quality food supply results in larger adult body size at low latitudes (Conover, 1990; Arnett and Gotelli, 2003). As such, future studies should endeavour to quantify the food supply for these wrasses (benthic invertebrate density) on Philippine and Australian coral reefs to allow for a better understanding of the role that dietary resources may play in determining the abundance and growth rates of the focal wrasse species. Interestingly, ecological assessments of the focal wrasse species on GBR and Philippine reefs indicates a lack of fishing effects on local densities, but strong impacts of benthic habitat variation on local density, biomass, and size structure of wrasse assemblages over time (Russ *et al.*, 2017; Lowe *et al.*, 2019). Similarly, assessments of demographic variation in other labrids report scale-dependent drivers of demography, whereby anthropogenic pressure only influences assemblage structure at a within-island scale, and natural environmental variation better predicts biogeographic trends (Taylor *et al.*, 2014b). As such, strong wrasse-habitat relationships on Philippine reefs may have confounded evaluations of fishing effects in the present study. Ultimately, without sampling more locations across a gradient of fishing pressure, identifying the most prominent cause of demographic variation between GBR and Philippine wrasse populations remains difficult. To partly resolve this, I recommend sampling wrasse populations in the same habitat, inside and outside well protected and old no-take marine reserves in the same geographic location. Such sampling of no-take marine reserve fish populations in Australia and the Philippines is sometimes not permitted. However, considering that the focal species are relatively short-lived, mature rapidly, and are fast growing, I argue that removing 50-100 individuals per species of wrasse would pose little threat to local populations.

Fishing that selectively targets large body size is predicted to induce rapid evolution toward smaller body sizes and earlier maturation (Trippel, 1995; Law, 2000; Audzijonyte *et al.*, 2016). Thus, mean length and mean maximum length have both been widely adopted as reliable indicators of high levels of fishing on exploited fishes through time (Shin *et al.*, 2005), across space (Hawkins and Roberts, 2004; Taylor *et al.*, 2014b; Valles and Oxenford, 2014), and in fishery models (Ault *et al.*, 2005). In contrast, here I report no effect of fishing on mean maximum size of *H. melapterus, C. fasciatus,* or *O. digramma* on Philippine reefs. While the effects of commercial fisheries on the life histories of exploited species are generally well understood (reviewed in Law, 2000), small-scale coastal fisheries which dominate Indo-Pacific nations are historically data poor (Johannes, 1998; Prince *et al.*, 2015). Given the regular and intensive use of gillnets and traps which target all or most size and age classes of reef fishes, it is possible that fishing pressure on large size classes is similar to that of small size classes in these regions. The harvesting of small and medium-bodied fishes could, in turn, result in directional selection toward attaining a large body size (Carlson *et al.*, 2007; Edeline *et al.*, 2009). The evolution of body-size and, hence, adaptability to anthropogenic perturbations has rarely been investigated in wild reef-fish populations. Philippine *H. melapterus*, *C. fasciatus,* and *O. digramma* offer an opportunity to investigate the effects of coastal Indo-Pacific fisheries harvest on directional selection of body-size. A critical component will entail accurately accounting for the simultaneous influence of a number of dynamic factors which act on correlated life-history traits in wild populations, such as body size and maturity.

The presence of mature females that persist late into ontogeny, large numbers of primary males, greater body condition for a given size, and larger body sizes for a given age of the focal wrasses on Philippine reefs compared to those of the GBR indicate that the life history traits of *H. melapterus, H. fasciatus,* and *O. digramma* in the Philippines are flexible and somewhat resilient to the current impacts of fishing pressure and high temperature. While the relative importance of environmental and anthropogenic mechanisms driving demographic traits of these species remains unclear, high demographic plasticity between GBR and Philippine conspecific populations may suggest that these species are relatively resilient to potential increases in ocean temperature and fishing pressure predicted elsewhere.

Demographic variation of *H. melapterus*, *H. fasciatus*, *C. fasciatus*, and *O. digramma* growth patterns, mortality rates, age of maturity, mean and maximum length and age were also detected at regional scales, between GBR reefs separated by approximately 350km. *Cheilinus fasciatus* and *O. digramma* populations on the high-latitude Whitsunday reefs grew slower, matured later, reached a larger asymptotic size, and reached an equal or larger maximum age than conspecifics on Palm reefs. While the size of maturation was comparable between GBR populations, the age of maturation was later on high-latitude Whitsunday reefs for *C. fasciatus* and *O. digramma.* This resulted in characteristic crossed growth profiles, consistent with the TSR, indicating that demographic variation between GBR reefs for *C. fasciatus* and *O. digramma* is likely due to differences in sea-surface temperature. Consistent with this, mean annual SST of Whitsunday reefs are approximately 0.5º C cooler than Palm reefs, which have mean SST of 26.39º C and 25.92º C, respectively. Conversely, *H. melapterus* and *H. fasciatus* populations on Whitsunday reefs reached lower asymptotic sizes than those on Palm reefs, exhibited reduced longevities, and *H. melapterus* matured earlier on Whitsunday reefs, observations inconsistent with predictions of the TSR. This may indicate that differences in habitat and/or food availability between Palm and Whitsunday reefs may outweigh the influence of the TSR model for *Hemigymnus*, as has been previously documented for many other species, including labrids, at this spatial scale (Yamahira and Conover, 2002; Floeter *et al.*, 2005; Robertson *et al.*, 2005; Trip *et al.*, 2014).

To date, little age-based demographic information has been published for the focal large-bodied tropical wrasses. Hubble (2003) made estimates of the life history characteristics of *H. melapterus* and *C. fasciatus* on Palm reefs based on a restricted length-range of individuals. Despite this, Hubble (2003) provided similar estimates of longevity of *C. fasciatus* to the present study. The largest and oldest *H. melapterus* collected by Hubble (2003) was approximately 225 mm standard length and 7 years old. Comparatively, this study reports *H. melapterus* to 14 years old and approximately 400 mm on Palm reefs, and thus life history estimates reported here are likely closer to true population values. Similarly, mortality and longevity estimates of *H. melapterus* presented here contrast with those of Eckert (1987), who used length-based techniques to establish longevity estimates for this species at One

Tree Island, Great Barrier Reef, Australia. The significantly lower estimate of longevity provided by Eckert (1987) for *H. melapterus* than in the present study, and for *Thalassoma lunare* (Ackerman, 2004), highlights potential limitations of length-based estimates of life-history parameters for reef fishes that live longer than 3 years (approximate timescale of PhD project) and grow rapidly, then asymptotically for the rest of their life. Age-based demographic studies of parrotfish have also stressed the inaccuracy of length-based estimation of life history traits (Choat *et al.*, 2003). To the best of my knowledge, no published estimates of growth, longevity, or mortality exist for *O. digramma* and *H. fasciatus*.

The observed maximum age in this study was 15 years (*C. fasciatus*; Palm Island group), which represents a relatively low comparative longevity within the family Labridae (Choat *et al.*, 2006; Coulson *et al.*, 2009; Cossington *et al.*, 2010). Size-at-age plots showed that *Hemigymnus spp.*, *C. fasciatus,* and *O. digramma* spent a relatively small proportion of their respective lifespans as juveniles, with all four species displaying rapid somatic growth, rapid maturation, and short life spans, similar to other labrid species (Choat *et al.*, 1996; Gordoa *et al.*, 2000; Gust *et al.*, 2002; Ackerman, 2004). Growth rates showed consistent positive relationships with mean annual SST, and rapid growth was particularly evident in Philippine wrasse populations, where the mean size-at-age for *C. fasciatus* and *H. melapterus* was in excess of 20cm within the first year of growth (Table 5.1).

Consistent with the TSR, ectotherm body size should decline with increases in temperature. In contrast, results from the present study report traits related to body size (Lmax, Linf, and thus K) were highly variable among GBR reefs and did not show any discernible trends across 30° of latitude between GBR and Philippine reefs. Similarly, other multiscale demographic analyses show greater variation of parrotfish (F. Labridae) and surgeonfish (F. Acanthuridae) growth rates, body size, and size of maturity among locations within regions, than across latitudinal and longitudinal clines spanning ocean basins (Clifton, 1995; Gust *et al.*, 2002; Choat *et al.*, 2003; Gust, 2004; Robertson *et al.*, 2005; Trip *et al.*, 2008; Paddack *et al.*, 2009). Instead, among GBR reefs, and between GBR and Philippine reefs, I found age structures were the most consistent signal of life history variation. Other multiscale demographic analyses have reached similar conclusions and, together with the present study, indicate that local variation in size-structures and growth rates may be common in reef fishes (Robertson *et al.*, 2005; Trip *et al.*, 2008; Paddack *et al.*, 2009). Consequently, using local-scale (regional) length-based traits to predict biogeographic traits appears questionable and vice-versa. My results stress that while body size is an important characteristic for differentiating species, variation in life history traits between species and geographic locations complicates use of body size as a life-history proxy.

Another assumption from life history studies has been that the relative timing of maturity and sex change are largely invariant across taxa and therefore natural selection must be fundamentally similar across animals (e.g., Allsop and West, 2003; Gardner *et al.*, 2005). Critically, these studies often use log–log regressions to compare population-specific relative timing of maturity and sex change estimates which often lead to misleadingly high regression fits that obscure much of the interesting biological variance in the timing of maturity and sex change among species (Buston *et al.*, 2004; Nee *et al.*, 2005; Munday *et al.*, 2006b). In contrast to these studies, here I show that the relative age or size of maturity and sex change (+/- 95% CIs) are highly variable, both within and between taxa. As expected, when GBR populations were compared to conspecific Philippine populations that have different sexual ontogenies (Chapter 4) the variation in the relative timing of maturity and sex change was particularly large. As such, results presented here reiterate a lack of broad evolutionary constraints on reef fish life histories (Munday *et al.*, 2006b) and suggest that species-specific demographic flexibility occurs at the individual to population level.

Tropical wrasses have historically been important components of coral-reef fisheries. Wrasses are increasingly more common in fish markets of the Eastern and Central Indo-Pacific, and Indo-Pacific coral reefs are subject to overfishing of high-value target species at an unprecedented rate (Newton *et al.*, 2007; Comeros-Raynal *et al.*, 2012). Here I provide important age-based demographic information that will allow for a better understanding of the impacts of fishing pressure and environmental change on the demography of wrasses at regional and biogeographic scales. To resolve this, future studies must: 1) provide more species-specific demographic and abundance estimates to allow for mixed-effect modelling of demographic responses of tropical wrasses to variations in fishing pressure and environment; (2) establish standardised estimates of the dietary resource levels (e.g., benthic invertebrate density) available to wrasses on Indo-Pacific reefs; (3) develop a better understanding of resource use, dietary flexibility, and correlative effects on growth/development; (4) determine the best suite of age-based demographic variables that relate directly to organism fitness, so that demographic variation can be factored into evolutionarily important parameters.

Chapter 6: General Discussion

In this thesis, I applied a multi-factorial and multi-scale approach to assess the relative impacts of environmental variation and fishing on the demography and ecology of tropical wrasses. This thesis details the strong responses of populations of coral reef wrasses to changes in benthic habitat, and responses of life history traits to environmental change and fishing pressure among Indo-Pacific coral reefs. Understanding the drivers of populations and life histories is critical for two reasons. Firstly, coral reef fishes have a wide geographical distribution. Thus, understanding the drivers that determine life histories, population dynamics, and their respective spatial and temporal variability is important for understanding coral reef ecology and life history evolution. Secondly, life history information and details of the spatial scale at which demographic differences occur in fishery targeted coral reef fishes are important for management and conservation.

6.1 Vulnerability to Habitat Degradation

Degradation of the quality of natural habitats has significant effects on ecological assemblages and is considered one of the greatest contributors to biodiversity loss globally (Brooks *et al.*, 2002; Wilson *et al.*, 2008; Krauss *et al.*, 2010). Causes of habitat degradation on coral reefs vary geographically, but cumulative pressures usually manifest as declines in the cover of live corals and reef habitat complexity (Wilson *et al.*, 2006; Pratchett *et al.*, 2011). Generally, degraded coral reefs support lower abundance, biomass, and diversity of coral reef fishes (Jones *et al.*, 2004; Wilson *et al.*, 2006; Pratchett *et al.*, 2008, 2011; Emslie *et al.*, 2014, but see Cheal *et al.*, 2008), which can have direct effects on fisheries catch composition (Graham *et al.*, 2007, 2017; Robinson *et al.*, 2019). Vulnerability of species to habitat loss will be largely dictated by their individual resource requirements (Emslie and Pratchett, 2018). Most labrids do not directly depend on live hard coral cover *per se* and many studies report either no change or increases in labrid abundance shortly following habitat degradation (Russ and Alcala, 1989; Wilson *et al.*, 2006; Russ *et al.*, 2015c, 2017; Lowe *et al.*, 2019). However, refuges within the reef matrix can mediate competition and predation, enabling recruitment for some labrid species. Thus, when disturbance events cause declines in structural complexity, labrid density and diversity generally declines (Halford *et al.*, 2004; Graham *et al.*, 2006; Wilson *et al.*, 2006; Emslie *et al.*, 2014; Cheal *et al.*, 2017). Results from Chapter 2 of this thesis demonstrate these trends spatially and temporally, across 11 wrasse taxa, and showed that changes in benthic habitat was a stronger influence on wrasse populations than predator density inside and outside of NTMRs. On inshore GBR reefs, reductions in live hard coral cover and/or habitat complexity resulted in density declines for *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, *Labroides* spp., *Oxycheilinus digramma*, and *Thalassoma* spp. Conversely, *Halichoeres* spp. densities correlated positively with increased relative cover of sand and rubble.

The habitat associations of labrids likely arise early in ontogeny, during the period when fish settle to the benthos and thus recruit to benthic populations (Williams, 1980; Tolimieri, 1998; Harborne *et al.*, 2012). Indeed, Chapter 3 confirmed the importance of live hard coral for the juveniles of *Hemigymnus*, *Cheilinus*, and *Oxycheilinus* wrasses. Yet, whether density correlates with live coral cover because complex habitats have higher surface area, and thus more benthic resources for wrasses to prey upon, or whether the structural complexity of live corals are more important in mediating competition and predation by providing shelter, remains an open question (discussed in Chapter 3). A deeper understanding of these factors will be necessary to determine how spatial heterogeneity in coral cover and structural complexity within and across reefs affect wrasse abundances and diversity. Studies on other reef types are also required, as differing coral communities, abiotic inputs (e.g., nutrients, currents, wave energy), and predator assemblages may lead to differing patterns of larval settlement.

6.2 Effects of Marine Reserve Protection

Wrasses are increasingly more common in fish markets of the Eastern and Central Indo-Pacific, and high-value target species on Indo-Pacific coral reefs are subject to overexploitation at an unprecedented rate (Newton *et al.*, 2007; Comeros-Raynal *et al.*, 2012; Lavides *et al.*, 2016; Graham *et al.*, 2017). In the last 10 – 20 years, fishing has led to localised declines of several of the large bodied labrids including *Cheilinus undulatus, Scarus guacamaia*, *Bolbometopon muricatum*, *Chlorurus bowersi*, and *S. trispinosus* (Sadovy *et al.*, 2003b; Donaldson and Dulvy, 2004; Ferreira *et al.*, 2005; Nañola *et al.*, 2011; Comeros-Raynal *et al.*, 2012; Muallil *et al.*, 2014; Lavides *et al.*, 2016). Data presented in Chapter 5 showed that fished Philippine reefs have lower long-term abundance of *C. fasciatus* and *H. melapterus* compared to inshore GBR reefs. Despite this, studies show that long-term NTMR protection did not significantly increase the local density of large-bodied, targeted wrasses in the Philippines (Russ *et al.*, 2017). Different life-histories among labrids may make certain species more or less vulnerable to fishing (see Taylor *et al.*, 2014a). Indeed, some species of parrotfish have been reported to respond positively to NTMR protection (Mumby, 2006; Mumby *et al.*, 2006; Mumby and Harborne, 2010, but see Questel and Russ, 2018). Yet, cumulatively parrotfishes have less than 5% of their range protected by no-take marine reserves (Comeros-Raynal *et al.*, 2012). Moreover, in places where labrids are not targeted by fishing, long-term studies fail to demonstrate direct positive NTMR effects (Smith *et al.*, 2011; Emslie *et al.*, 2015; Russ *et al.*, 2017; Questel and Russ, 2018; Lowe *et al.*, 2019, 2020). Therefore, NTMR protection alone seems unlikely to greatly benefit many labrids, given the cumulative pressures of an increasing human global population reliant on seafood for nutrition and the predicted long-term negative effects of climate change on the availability of coral reef habitat (Merino *et al.*, 2012; Bozec *et al.*, 2015; Golden *et al.*, 2016; Cheal *et al.*, 2017). This is particularly so when one considers that reproductive strategies of labrids may render them more vulnerable to severe depletion by fishing (e.g., their reproductive developmental modes and presence of specific recruitment sites) are rarely accounted for when designing NTMRs (Hamilton *et al.*, 2019). Notably, some locations have banned the capture, sale, or export of some labrids (Montero, 2009; CFM Council, 2010; GoTa, 2011; BFAR, 2017; Steneck *et al.*, 2019), or imposed size limits on fishers catch (CFM Council, 2010; Hamilton *et al.*, 2019). Yet, whether these nations have the capacity to effectively enforce these regulations, and what results these restrictions will have on local labrid populations, remains to be determined.

In addition to direct NTMR effects on targeted species, there are expectations that NTMRs will also have indirect effects on organisms, usually via trophic interactions (Babcock *et al.*, 2010). For example, the build-up of predators inside NTMRs is hypothesised to cause a decline in the abundance of their prey (McClanahan, 1994; Graham *et al.*, 2003; Babcock *et al.*, 2010). In this thesis, Chapters 2 and 3 found little evidence of predator effects on labrid density, even on small-bodied wrasses inside NTMRs that sometimes have 3 – 4 times higher density of wrasse predators (*Plectropomus* spp.) than fished sites. Although some top-down effects between herbivorous fish and algal benthos have been reported on coral reefs (Mumby *et al.*, 2006; Babcock *et al.*, 2010; Humphries *et al.*, 2014; McClanahan, 1994, 2014), there is a growing literature that questions whether NTMRs on coral reefs strongly alter trophic interactions, habitat, and assemblage structure (Kramer and Heck, 2007; Bruno *et al.*, 2009; Questel and Russ, 2018; Russ *et al.*, 2015b, 2020). Instead, studies often demonstrate that NTMRs have limited ability to alleviate the effects of major environmental disturbances on coral reefs which drive long-term changes in trophic structure (Jones *et al.*, 2004; Graham *et al.*, 2007, 2008; Hughes *et al.*, 2017b; Russ *et al.*, 2015b, 2020). Therefore, a fundamental research question is whether the effectiveness of existing NTMRs will change, given that sea surface temperatures on tropical coral reefs are predicted to surpass historical ranges by mid-century and environmental disturbance events are predicted to increase in frequency (Knutson *et al.*, 2010; Bruno *et al.*, 2018; Graham *et al.*, 2020). Moreover, given this ecosystem context, will new NTMRs be more successful if placed in locations where the threats of frequent disturbance are lowest (van Hooidonk *et al.*, 2016; McClure *et al.*, 2020), where recovery from climatic disturbances is most likely (Graham *et al.*, 2015), or on "bright spot" reefs that outperform the average reefs, given local stressors (Cinner *et al.*, 2016)?

6.3 Reproductive Patterns

Experiments and field observations of reef fishes have shown that individual body-size (Warner and Swearer, 1991; Buston, 2003), the sex ratio of the social group (Robertson, 1972; Munday, 2002), and local density (Lutnesky, 1994) have important implications for the reproductive success of an individual and the timing of sex change. For example, alternative pathways of male development in the reef fish *Thalassoma bifasciatum* can occur on neighbouring reefs, suggesting that individuals can change life-history tactics that involve adult sex change, or not, depending on the mating conditions that they experience in a particular habitat patch (Warner and Swearer, 1991; Munday *et al.*, 2006a). The results reported in Chapter 4 found that sexual ontogenies of *H. melapterus*, *C. fasciatus*, and *O. digramma* were spatially labile, whereby wrasses within the one species were diandric hermaphrodites and functional gonochores on heavily fished Philippine reefs, and monandric hermaphrodites on unfished GBR reefs. This finding for three wrasse species from separate genera, based on detailed histological examination, provides evidence that spatially labile pathways of sexual development may be more widespread in the Labridae than previously recognised (Munday *et al.*, 2006a). Hypotheses based on environmental mechanisms driving labile sexual ontogenies in the studied wrasses are detailed in Chapter 4. Here, I expand on the possible role of environmental sex determination and future research directions that have been raised from findings in this thesis.

Environmental sex determination is predicted to occur when juveniles recruit into a heterogeneous, unpredictable environment, and alternate habitat patches confer different survival probabilities (Charnov and Bull, 1977). In these heterogeneous and unpredictable environments, individuals should delay sex determination until they are about to mature (Charnov and Bull, 1977; Jones, 1980). In the Philippines, fishery exploitation of wrasses is spatially patchy and occurs across all size and age classes, over both non-reef and reefal habitats (Dalzell, 1996; McManus, 1997). Moreover, in the Philippines the configuration and history of the island systems results in a more varied range of reef types across small spatial-scales and the high biodiversity on these reefs is thought to result from an intermediate level (frequency and size) of environmental disturbance (Connell, 1978; Kubota and Chan, 2009). Therefore, Philippine reefs are likely more heterogeneous than inshore GBR reefs, due to the high diversity of reef types, effects of frequent disturbance events, and intense fishing pressure across space and time. In this environment, maturing directly as a primary male or delaying sex determination, in the case of bisexuals, likely offers significant survival and reproductive advantages where the population sex ratio is under constant and unpredictable changes. In the present study, fishery-dependent sampling in the Philippines precluded my ability to perform observations of the social groups that wrasses were sampled from. This remains key to determining drivers of wrasse sexual ontogenies. Future studies should employ spatially explicit sampling of populations paired with detailed observations of the immediate habitat and social environment that wrasses are sampled from, to determine the relative effects of each driver. This will require comparing estimates of immediate and lifetime reproductive output at the individual level across environments which affect both immediate and lifetime reproductive success (Warner and Hoffman, 1980a, 1980b; Munday *et al.*, 2006a, 2006b).

In addition, plasticity in the pattern of sexual ontogeny is predicted to have positive effects on population persistence in complex and variable ecosystems (Charnov and Bull, 1977; Munday *et al.*, 2006a). Once mechanisms driving flexible reproductive development have been resolved, studies should determine how the pattern of male development influences other key life history processes, such as the age of maturity, which has direct implications for population turnover. Like sexual differentiation and sex change, environmental and social conditions can also influence the timing of sexual maturation in some reef fishes (Fricke and Fricke, 1977; Jones and McCormick, 2002). Decisions regarding the timing of maturity, sexual differentiation, and sex change may be influenced by the same local environmental conditions, and therefore these processes should not be considered in isolation (Hobbs *et al.*, 2004).

6.4 Spatial Variation in Life Histories

Life history theories generally predict that ectotherms at high-latitudes will have slower growth rates, greater longevity, and delayed maturation at a longer body-length than conspecifics at low latitudes (i.e., the Temperature-Size Rule; Atkinson, 1994). Yet this thesis found that trade-offs between life histories were much more complex and were flexible across regional to biogeographic scales. The results reported in Chapter 5 showed that in addition to differential sexual ontogenies, Philippine wrasses had more rapid growth rates, reduced age of maturity, and decreased longevity when compared to high latitude unfished GBR populations. However, body-length of wrasses in both locations were similar and relative body condition was higher on Philippine reefs. This large size of individual wrasses on Philippine reefs was an important finding, particularly when other evidence suggests the opposite: that fishing reduces the mean size of individuals in targeted stocks, and that metabolic costs, or oxygen limitation, consistently results in smaller fish in warmer waters (discussed in Chapter 5).

In the Philippines, rapid growth and large maximum size in a warm environment is likely obtained via increased food consumption, and via energy trade-offs with reproduction (Chapter 5). Table 2.1 in this thesis provides information on the most common dietary items ingested by tropical wrasses studied here. Yet, determining differences in the availability of these dietary resources on coral reefs remains difficult, due to the cryptic nature of benthic invertebrates and the diversity of invertebrate prey items the focal wrasses prey upon. Despite this, determining the biomass of mobile invertebrates on coral reefs is important, not only for studies of invertivorous fishes, but also for our understanding of coral reef trophodynamics. This remains a significant knowledge gap in coral reef ecology.

6.5 Broader Implications for Future Research

Demographic flexibility enables individuals to cope with environmental variation and is particularly important in reef fishes were dispersive larvae often leads to the recruitment of juveniles into different environmental conditions, such as habitats (Warner, 1997). The more spatially and temporally variable the ecosystem, the more likely demographic and reproductive variation will occur over small spatial scales. On heavily fished Indo-Pacific coral reefs, labrids are likely exposed to more spatial and temporal variability in population dynamics due to the natural variability of the environment (Connell, 1978; Kubota and Chan, 2009) and spatially patchy fishery exploitation of all size and age classes over both non-reef and reefal habitats. Given this framework, a research priority is determining when short-term flexibility of sexual and demographic patterns trump inter-generational adaptation to variability in temperature, resources, sex ratios, fishing pressure, predator density, competitor density, and habitat. To date, common-garden experiments required to partition these sources of demographic variation have largely focused on pomacentrids. However, advances in aquaculture techniques and genomics now allow for the possibility of demographic trade-offs to be resolved across species of labrids in a manner similar to those done on pomacentrids.

Spatially labile sexual ontogenies reported here add to the growing evidence of flexible male development in reef fishes (von Brandt, 1979; Wood, 1986; Warner and Swearer, 1991; Bruslé-Sicard *et al.*, 1994; Liu and Sadovy, 2004a, 2004b; Munday *et al.*, 2006a). Once documented in wild populations, aquarium studies have proven successful for determining social mechanisms responsible for flexible pathways of male development, whether that be the mating system (Munday *et al.*, 2006a) or settlement environment (Liu and Sadovy, 2004a, 2004b). For example, in *Amphiprion bicinctus* and *Premnas biaculeatus*, isolated juveniles were more likely to develop directly into females (von Brandt, 1979; Wood, 1986). In *Cephalopholis boenak* the opposite is true, isolated juveniles develop as males (Liu and Sadovy, 2004b). In *Amphiprion bicinctus* pairs, the larger individual was female and the smaller one was a male, or remained undifferentiated (von Brandt, 1979). In *Amphiprion frenatus*, the largest individual was female, the second largest individual was male, and the smallest individual remained sexually undifferentiated (Bruslé-Sicard *et al.*, 1994). In all of these studies, and in the present thesis, sampling small juvenile fish was required to diagnose potential sexual development pathways. However, to date, reproductive information for reef fishes important to fisheries has focused on larger fish around the time of maturity, while pathways of male development in juveniles have rarely been assessed. This is partly owing to the fact that large-bodied, fishery targeted reef fishes are difficult to maintain in aquaria. It is possible that spatially labile sexual ontogenies in reef fishes are more widespread than is currently recognised. By sampling very young fish from wild populations, spatially explicit pathways of male development can be confirmed. Determining what factors are involved in juvenile sexual differentiation in reef fishes, and why social factors determining sex differentiation vary between species and social groups (see examples above), remains a key research question. Moreover, the mechanisms responsible for anatomical and behavioural differences between primary and secondary males in sex-changing fishes remains to be determined (discussed in Chapter 4). Finally, the effects that flexible reproductive ontogenies will have on species vulnerability to fishing and climate change remains unknown.

Similarly, the drivers of functional gonochorism, reported here for three species of wrasse from separate genera, remain unknown. As outlined above, environmentally driven sex determination is a likely mechanism. It seems unlikely that the appearance of functional gonochorism is a product of genetics alone, given its seemingly haphazard phylogenetic appearance (Robertson *et al.*, 1982; Hastings, 1989; Siau, 1994; Sadovy and Colin, 1995; Kuwamura and Nakashima, 1998; Girolamo *et al.*, 1999; Fennessy and Sadovy, 2002; Adams, 2003; Liu and Sadovy, 2004a; Hamilton *et al.*, 2008; Chapter 4). Moreover, if sex determination was caused purely by genetics, then the differential abundance of primary males or undifferentiated juveniles on a reef would be due to differential mortality or selective recruitment. Empirical data do not support this (Liu and Sadovy, 2004b; Munday *et al.*, 2006a). Functional gonochorism has now been reported in the Labridae (Robertson *et al.*, 1982; Girolamo *et al.*, 1999; Hamilton *et al.*, 2008; Chapter 4), Serranidae (Hastings, 1989; Sadovy and Colin, 1995; Fennessy and Sadovy, 2002), Epinephelinae (Siau, 1994; Adams, 2003; Liu and Sadovy, 2004a), and Pomacanthidae (Kuwamura and Nakashima, 1998). Studies on species in these families are required to determine whether functional gonochorism is socially induced or driven by another mechanism. Given the growing evidence for complex reproductive patterns of reef fishes, and evidence of spatially labile sexual pathways, a review of how we classify sexual development pathways in reef fishes is also warranted. It is critical that future studies determining the sexual development pathways of reef fishes collect very small individuals in order to accurately determine pathways of male development.

Given that sources of demographic variation will affect individuals differently depending on their genetic inheritance and environment, the strong emphasis on population averages that have dominated life history studies, as opposed to documenting the range of individual demographic variation within populations, may be less enlightening than previously believed (Engen *et al.*, 1998; Kendall *et al.*, 2011; Taylor *et al.*, 2019). Studies of reef fish populations have historically differentiated sexes, size, and age classes. Yet, even within these classes, individuals differ in genetic inheritance, the environment they are exposed to, resource use, maternal effects, competitive ability, predator avoidance ability, and abiotic tolerances. In turn, these factors generate variance in demographic parameters within populations. For example, within a *Naso unicornus* (F. Acanthuridae) population, individual growth and survival rates differ greatly (Taylor *et al.*, 2019). Therefore, by tracking a cohort within this population through time, one might falsely conclude that mortality rates are decreasing with age. However, in reality, fast growing individuals die first, so declines in average mortality across age classes do not imply that the risk of mortality is really decreasing for all individuals (Taylor *et al.*, 2019). Accounting for demographic stochasticity within populations is certainly not a new concept and has been used in models of population ecology for decades (MacArthur and Wilson, 1967; Levins, 1969), and probability theory for well over a century (Watson and Galton, 1875; Lotka, 1931). However, demographic trait variation within populations has rarely been compared across geographic scales in reef fishes for the purposes of assessing demographic resilience. This is an area that warrants further attention. By determining the level of demographic synchrony within populations, models of individual demographic stochasticity may indicate a diversity of population responses, whereby low demographic heterogeneity within a population may indicate a population with low resilience to ecosystem change (Taylor *et al.*, 2019). Understanding and incorporating variation in demographic traits within populations may therefore be important for basic ecology and for making predictions about the impacts of global climate change on affected species.

The demographic comparisons presented here provide important age-based demographic information for fishery targeted wrasses of the Indo-Pacific. Yet, simple comparisons of life histories among locations do not facilitate an understanding of the mechanisms responsible for demographic variance, nor the implications for broader fishery and conservation management. Future assessments of wrasse demography should collect spatially explicit environmental data at wrasse collection sites to allow for more comprehensive mixed-effects modelling of the drivers of demographic rates over several spatial scales. Moreover, in the present thesis I focused primarily on spatial variation in demographic rates. However, temporal variation in life histories will likely be of greater importance to fisheries management. Few temporal comparisons of life history data exist for fish species subject to fishing on coral reefs, primarily because little age-based demographic data have been collected. Simple monitoring programs could correct this data shortage and provide valuable information on fishery- and environment-induced demographic changes through time, particularly where labrids are under increasing levels of exploitation. Clearly, such monitoring programs would require sustained funding.

Finally, predicting the responses of populations and communities using life history traits has often been referred to as the ‘holy grail’ of ecology (Grime, 1979; Lavorel and Garnier, 2002; Adams, 2009). Yet, failure to account for the net effect of spatial and temporal variations in demographic traits on organism fitness has left a significant gap in our understanding of demographic flexibility in reef fishes. Furthermore, we lack understanding of how trait-fitness relationships vary across environments, hindering our ability predict species responses to environmental change. Therefore, I encourage future studies to link demographic traits directly to intrinsic growth rates of populations, which are situated across different environments, to test the generality of traits for predicting species performance.

6.6 Concluding Remarks

Chapters of this thesis contribute to our understanding of the ecological drivers of abundance and life histories of Indo-Pacific wrasses under a variety of environmental and anthropogenic influences. A recurring theme in the coral reef literature is that fishing can have considerable negative effects on marine communities (Jackson *et al.*, 2001; Pinca *et al.*, 2012). However, this thesis demonstrates that fishing pressure should not be the default hypothesis used to explain the population dynamics of tropical wrasses. Rather, chapters 2 – 5 suggest that wrasses respond strongly to changes in their surrounding environment, particularly benthic habitat, social structure, and resource availability. As such, models predicting the effects of fishery exploitation on wrasse populations should incorporate benthic habitat and other relevant environmental conditions (e.g., food availability and quality) into analyses. This thesis offers foundational knowledge of the effects of environmental variation on the studied wrasse life histories and presents many promising hypotheses for future research. Yet clearly, a full understanding of the role these factors play in driving sexual lability and demographic variation between GBR and Philippine reefs in the focal wrasses has yet to be achieved. In order to identify the selective pressures operating on wrasse life histories, further spatially explicit sampling of tropical wrasses and environmental data are required. Only by describing demographic trait variation in multiple labrid taxa across diverse environments and through time, can the underlying mechanisms acting directly on organism fitness be elucidated and the generality of trait-fitness relationships in reef fishes understood.

Chapter 7: References

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Appendix 2.1: Collinearity Assessment of Environmental Predictor Variables

While Boosted Regression Trees (BRTs) are known to be fairly robust to collinearity, removing variables with a Pearson correlation coefficient > │0.7│ remains desirable for techniques involving boosting (Dormann *et al.*, 2012). As such, I assessed Pearson correlation coefficients for all environmental predictor variable combinations at the Palm, Whitsunday and Keppel Island groups, respectively (Fig. S1, S2, S3). No variables were above the suggested cut-off of │0.7│ and thus all variables were subsequently included in BRTs to determine taxa-specific benthic drivers of wrasse density on reefs at each island group.

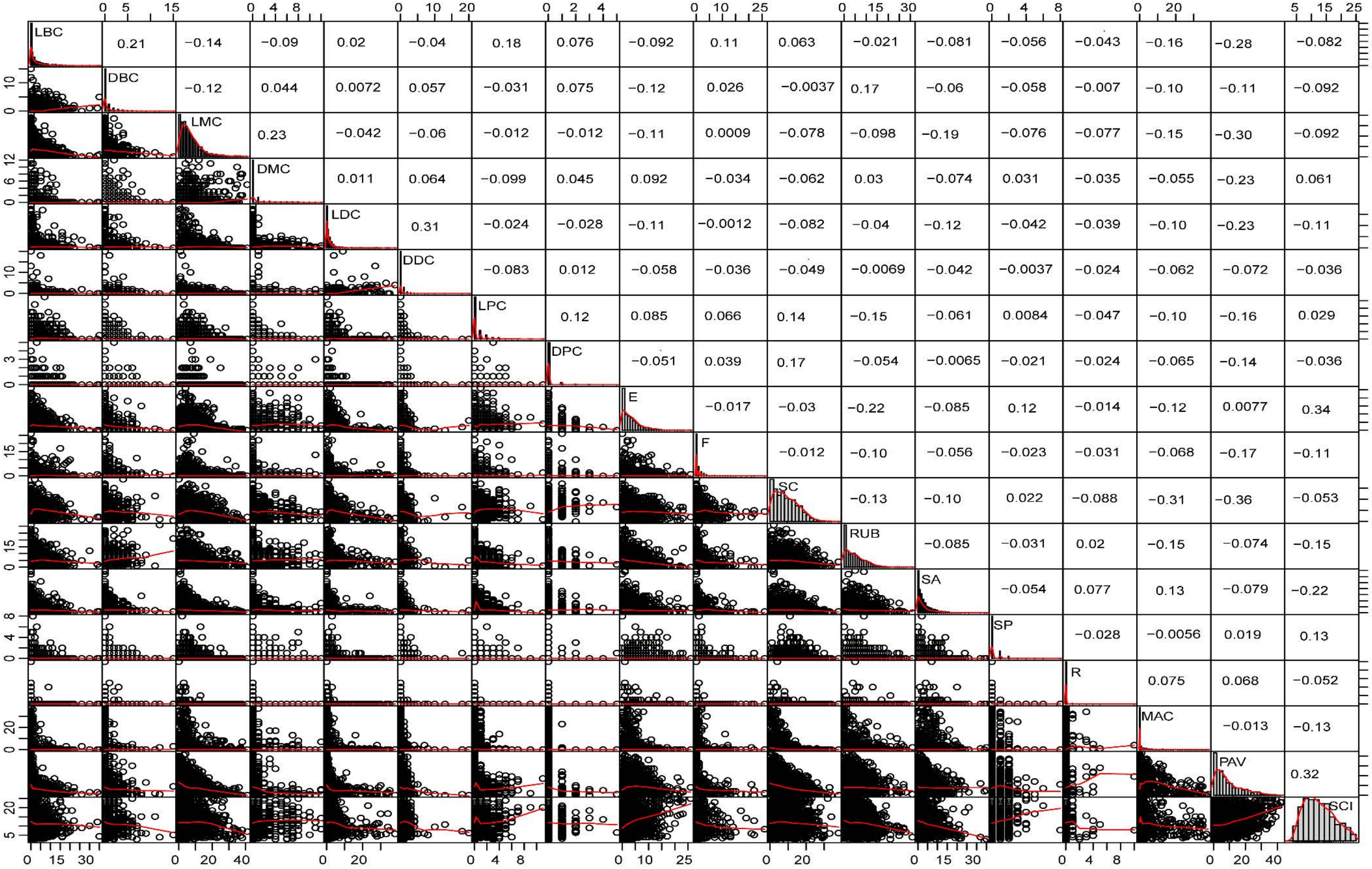


Figure S1: Pearson correlation coefficients for environmental predictor variables at the Palm Island group.

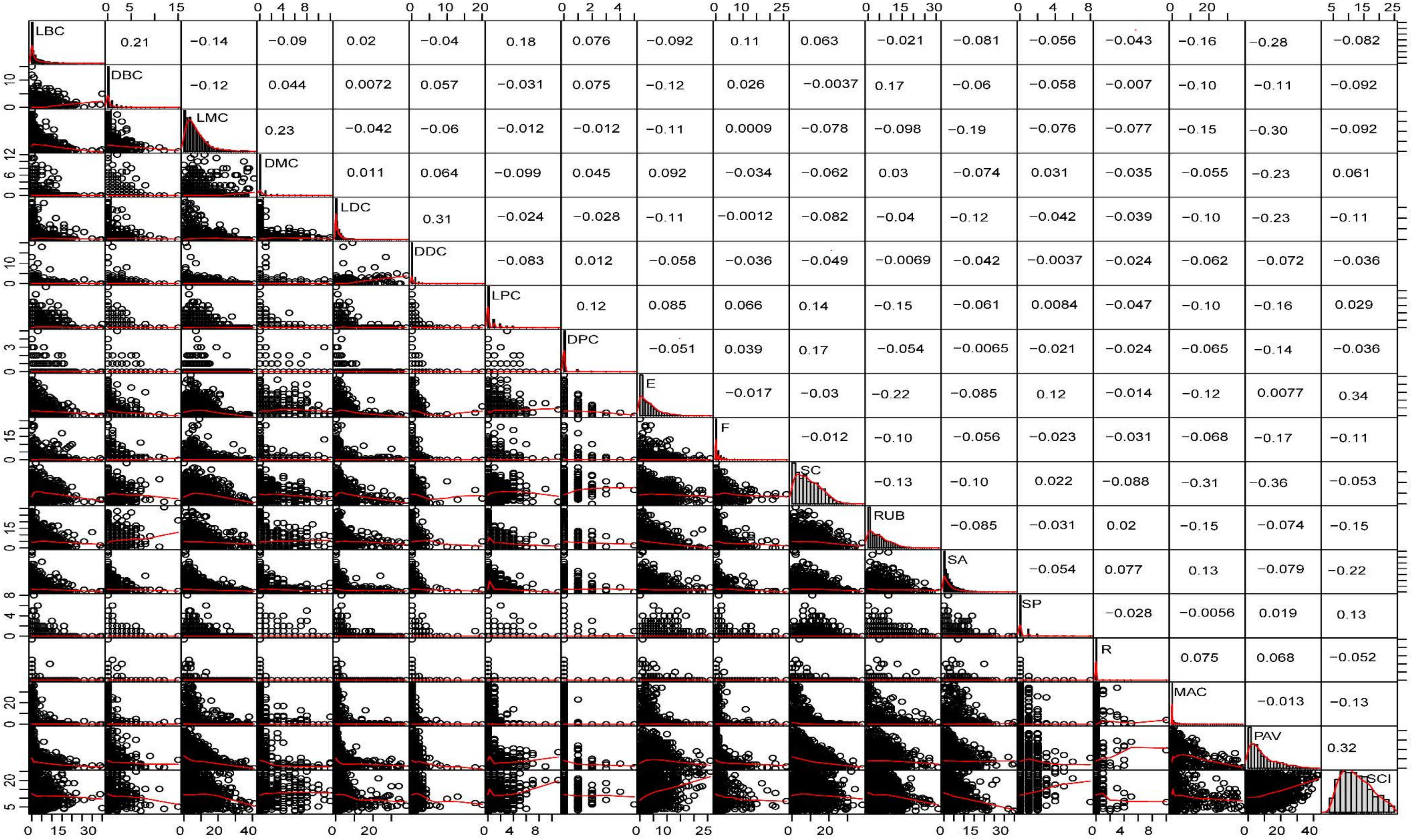


Figure S2: Pearson correlation coefficients for environmental predictor variables at the Whitsunday Island group.

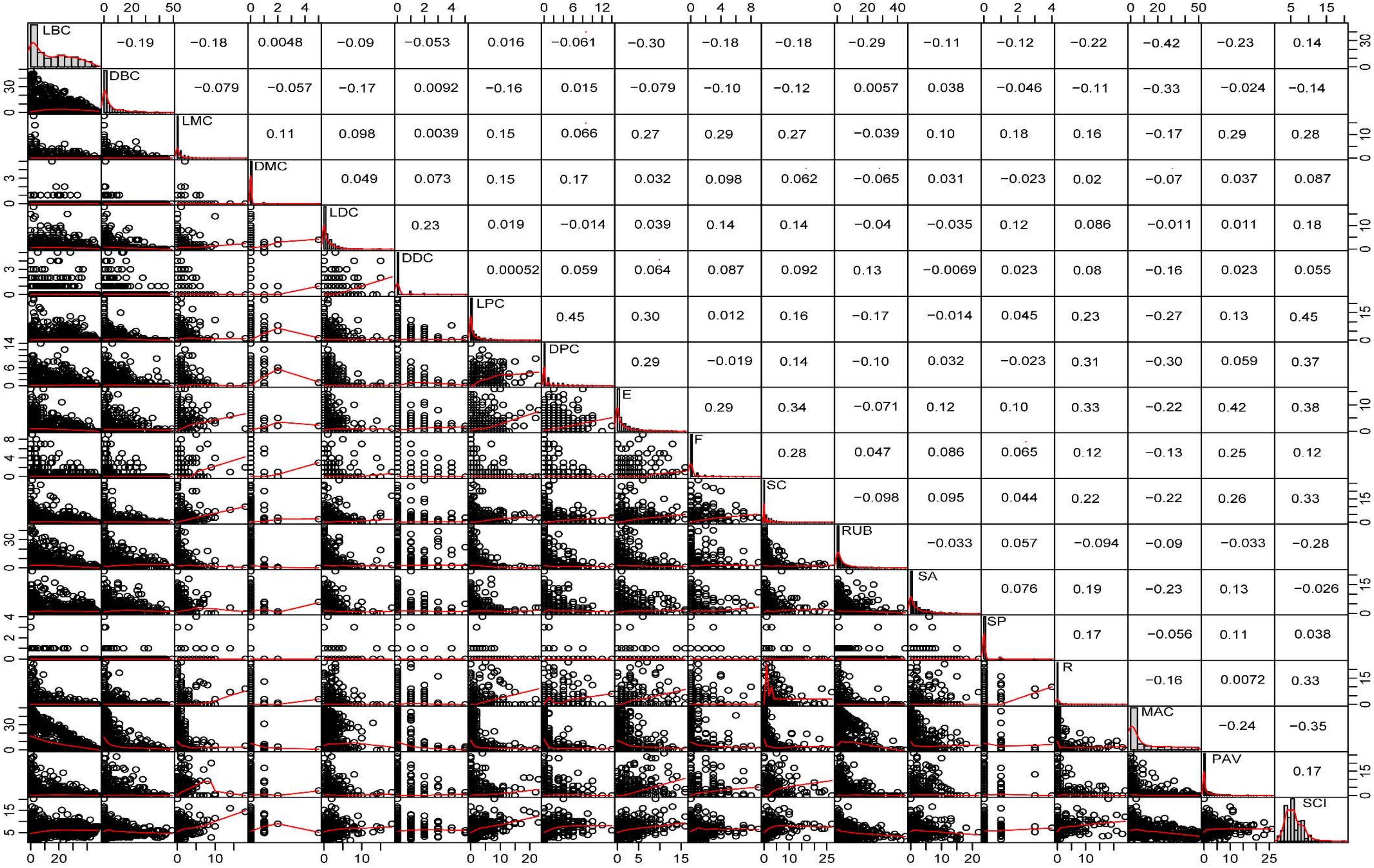


Figure S3: Pearson correlation coefficients for environmental predictor variables at the Keppel Island group.

Appendix 2.2: Relative Influence (%) of Predictor Variables on Wrasse Density from Boosted Regression Tree Analyses

Location	Species	LBC	DBC	LMC	DMC	DDC	LDC	LPC	DPC	E	F	SC	RUB	SP	SA	PAV	R	MAC	SCI	EX
Palm Island Group	*Anampses spp.*	23.2 (+)	2 (+)	0.7 (+)	1 (w)	0 (nr)	0.7 (+)	2.2 (+)	5.3 (+)	27.7 (v)	0.1 (v)	3.2 (+)	0.9 (+)	0 (nr)	0.6 (nr)	27 (-)	0 (nr)	0 (^)	1.9 (w)	3.3 (+)
	Bodianus spp.	7.2 (-)	1.2 (v)	8.6 (-)	1.9 (+)	0.3 (-)	6.6 (+)	0.6 (-)	0.4 (+)	5.7 (+)	2.6 (^)	8.5 (+)	6.9 (-)	2.1 (nr)	13.7 (-)	10.3 (+)	0 (nr)	0.6 (v)	18.2 (+)	4.5 (+)
	C. fasciatus	7.2 (-)	1.5 (-)	5.4 (-)	2.2 (-)	0 (nr)	1.5 (-)	0.7 (-)	0.2 (-)	9.6 (^)	2 (-)	12.1 (+)	6.5 (^)	0.8 (-)	10.1 (-)	8 (+)	0 (nr)	4.5 (+)	14.9 (+)	12.8 (-)
	E. insidiator	3.9 (-)	1.2 (-)	4.4 (+)	1.2 (+)	0.1 (nr)	5.3 (^)	0.4 (nr)	1.3 (+)	4.7 (+)	6.2 (+)	16.9 (+)	7.1 (w)	0.6 (nr)	15.3 (-)	7.1 (w)	0 (nr)	1 (^)	19 (+)	4.3 (-)
	H. fasciatus	2.6 (-)	1.1 (^)	5.1 (-)	0.4 (+)	0.2 (nr)	8.7 (+)	2.3 (+)	0 (nr)	3.7 (^)	6 (+)	7.8 (+)	15.2 (-)	0.3 (-)	20.1 (-)	7.3 (+)	0 (nr)	4.8 (+)	11.1 (+)	3.2 (+)
	H. melapterus	5.4 (w)	3.5 (+)	6.9 (v)	2.3 (-)	0.3 (+)	4.1 (v)	0.5 (-)	2.3 (+)	6.2 (-)	2.7 (+)	9.3 (+)	13.6 (-)	1.5 (-)	8 (v)	6.6 (+)	0 (nr)	4.7 (w)	18 (+)	3.9 (-)
	Halichoeres spp.	2.6 (+)	2.1 (+)	11.9 (-)	0.4 (-)	0.2 (-)	3.9 (-)	0.6 (^)	0.1 (nr)	4.3 (-)	2.8 (-)	5.9 (+)	11.4 (+)	2.2 (^)	23.7 (+)	7.8 (^)	0 (nr)	2.9 (v)	12.7 (w)	4.4 (+)
	Labroides spp.	7.3 (-)	4.5 (^)	5.4 (w)	5.8 (+)	2 (+)	5.3 (v)	0.6 (w)	1.6 (+)	2.6 (+)	1.9 (+)	11.6 (+)	10.5 (-)	4.7 (+)	6.9 (-)	11.3 (w)	0 (nr)	1.8 (-)	11.3 (+)	4.8 (-)
	O. digramma	4.6 (-)	2.8 (+)	5.5 (^)	0.2 (nr)	0.2 (nr)	1.4 (nr)	1.9 (-)	0.4 (-)	4.7 (-)	4.7 (+)	27 (+)	4.5 (w)	0.8 (-)	10.3 (-)	12.6 (w)	0 (nr)	1.3 (+)	14.3 (+)	2.8 (+)
	Stethojulis spp.	12.7 (^)	1.6 (^)	2 (v)	0.8 (w)	0.8 (+)	3 (+)	13.4 (-)	0 (nr)	8.2 (-)	0.9 (-)	8.5 (+)	5.4 (+)	9.8 (+)	4.7 (^)	14.9 (+)	0 (nr)	0.1 (+)	12 (-)	1.3 (-)
	Thalassoma spp.	3 (v)	5.3 (+)	4 (w)	0.9 (-)	0.1 (-)	2.5 (v)	0.3 (nr)	2.5 (+)	3.4 (-)	0.8 (+)	9.1 (^)	14.8 (-)	0.6 (-)	8.3 (-)	10.7 (+)	0 (nr)	1.2 (w)	20.7 (+)	11.9 (-)
Whitsunday Island Group	*Anampses spp.*	22.1 (+)	6 (+)	3.7 (-)	0.1 (nr)	1 (+)	12 (^)	0.5 (nr)	0 (nr)	3.6 (+)	25.2 (+)	11.8 (^)	0.5 (nr)	0 (nr)	0.8 (-)	1.7 (+)	0 (nr)	0.1 (-)	6.5 (-)	4.3 (+)
	Bodianus spp.	2.5 (w)	1.7 (+)	9.4 (-)	4.2 (+)	0.2 (nr)	1.8 (-)	3.6 (+)	0.2 (+)	16.4 (+)	1.5 (+)	13.3 (+)	8 (+)	1 (+)	8.3 (-)	7 (-)	0.1 (+)	2.9 (-)	15.4 (+)	2.5 (v)

	C. fasciatus	12.8 (+)	4.1 (+)	5.5 (-)	2.2 (+)	1.5 (-)	4.3 (+)	1.3 (-)	0.1 (nr)	3.6 (-)	3.5 (+)	10.2 (+)	10.4 (^)	0.4 (nr)	5.8 (+)	6.1 (-)	0 (nr)	7.6 (-)	14.9 (w)	5.8 (-)
	E. insidiator	8.3 (+)	3.7 (+)	5.5 (-)	1.1 (+)	0.6 (-)	10.6 (+)	4.8 (+)	3.3 (^)	7.3 (-)	1.6 (-)	11 (+)	7.8 (+)	0.6 (nc)	5.1 (-)	6.7 (v)	0 (nr)	9.2 (-)	10.6 (+)	2.1 (+)
	H. fasciatus	19.1 (+)	10.8 (+)	3.3 (-)	1.4 (+)	0.4 (-)	2 (^)	2.1 (+)	0.1 (nr)	13.5 (+)	10.4 (+)	6.3 (+)	3.8 (v)	0.5 (nr)	6.1 (-)	7.6 (+)	0 (nr)	5 (-)	5 (+)	2.8 (+)
	H. melapterus	20.3 (+)	11.9 (+)	9.3 (-)	1.1 (+)	0.7 (-)	2.5 (+)	0.3 (-)	0.7 (+)	1.9 (w)	4.8 (+)	3.7 (+)	20 (+)	0.6 (-)	2.7 (-)	8.8 (+)	0.3 (+)	4.6 (-)	3.1 (+)	2.7 (-)
	Halichoeres spp.	15.3 (+)	1 (+)	13.1 (-)	0 (nr)	0 (nr)	0.8 (^)	1 (+)	0.3 (+)	2.3 (-)	0.9 (nr)	8.6 (+)	8 (+)	0.3 (nr)	19.4 (+)	2.3 (+)	2.5 (+)	5.6 (^)	17.4 (-)	1.2 (^)
	Labroides spp.	5.2 (+)	1.2 (^)	14.7 (w)	3 (-)	1.8 (+)	4.3 (+)	1.9 (v)	0.4 (-)	6.2 (+)	1.8 (-)	15.9 (+)	8.8 (v)	2.1 (-)	3.6 (-)	12.2 (^)	0.7 (+)	2.1 (-)	12.1 (-)	2.1 (^)
	O. digramma	17.2 (+)	3.5 (+)	8.3 (v)	0.6 (-)	0.3 (-)	7.1 (+)	2.1 (v)	2.1 (+)	7.7 (v)	3.8 (+)	9.4 (^)	5.8 (+)	0.4 (-)	6.4 (w)	5.7 (^)	0 (nr)	1.9 (-)	14.1 (-)	3.5 (+)
	Stethojulis spp.	5.3 (+)	0 (nr)	2 (w)	0 (nr)	0.1 (v)	10.2 (+)	2 (-)	0.2 (nr)	3.7 (-)	0.3 (^)	4.8 (+)	4.2 (+)	0.5 (nr)	4.7 (+)	1.8 (-)	0 (nr)	32 (w)	14 (-)	14.1 (+)
	Thalassoma spp.	3.9 (+)	1.7 (-)	8.6 (-)	7.6 (+)	1.2 (-)	10.4 (+)	1.3 (-)	1.3 (+)	7.5 (-)	2.3 (-)	7.2 (w)	7 (-)	0.9 (-)	5.7 (-)	10.8 (w)	0.1 (-)	6 (-)	13.4 (+)	3 (v)
Keppel Island Group	*Anampses spp.*	11.5 (+)	6.6 (+)	7.3 (-)	0 (nr)	15.6 (+)	6.6 (+)	1 (nr)	6.5 (+)	3.9 (+)	4.4 (+)	0.5 (nr)	2.8 (+)	0.1 (+)	16.4 (+)	0.4 (nr)	10.1 (-)	0.8 (-)	2.6 (+)	3.1 (nr)
	E. insidiator	8.3 (-)	3.9 (w)	2.7 (v)	4.3 (+)	1.8 (+)	4.7 (-)	9.6 (v)	3.8 (v)	6.9 (+)	14.3 (+)	2.6 (^)	4.3 (-)	0.2 (+)	4.2 (-)	7 (-)	4.3 (+)	3.8 (-)	8.3 (^)	5.1 (+)
	H. melapterus	9.6 (+)	8.6 (-)	2.2 (+)	1.2 (+)	0.9 (-)	2 (w)	8.5 (+)	3.3 (+)	4.1 (-)	3.4 (+)	2.6 (^)	8.5 (+)	1 (+)	5.3 (^)	6.3 (+)	1 (+)	11 (-)	13.9 (^)	6.5 (-)
	Halichoeres spp.	10.4 (w)	10.8 (-)	0.7 (+)	0.2 (+)	0.3 (+)	6.9 (^)	2.9 (^)	2.8 (^)	1.4 (-)	0.9 (v)	1 (v)	15.6 (+)	0.3 (+)	7.7 (+)	2.8 (-)	4.9 (+)	7.2 (+)	13.2 (-)	9.9 (-)
	Labroides spp.	9.4 (+)	4.9 (-)	3.9 (+)	0 (nr)	0.2 (nr)	9.4 (+)	3.7 (+)	2.2 (+)	7.8 (v)	3.6 (+)	2.6 (-)	3.4 (-)	0 (nr)	3.9 (+)	5.6 (+)	4 (+)	2.7 (-)	23.1 (+)	9.6 (-)
	Stethohjoulis spp.	3.4 (+)	8.2 (+)	0.3 (+)	0 (nr)	0.1 (+)	3.3 (+)	2.9 (+)	0 (nr)	1.9 (-)	0.2 (-)	0.7 (-)	9.9 (+)	0.8 (+)	3.1 (w)	2.3 (-)	2 (+)	34.1 (+)	17.8 (-)	8.9 (-)
	Thalassoma spp.	15.9 (^)	7.6 (v)	1.7 (+)	0.1 (+)	1 (+)	3.5 (+)	3.1 (+)	1.5 (-)	3.3 (v)	5.8 (+)	3.4 (+)	5.2 (w)	1.5 (+)	3.3 (-)	6.1 (+)	0.7 (+)	13.7 (v)	10.8 (^)	11.9 (-)

LBC = live branching corals, DBC = dead branching corals, LMC = live massive corals, DMC= dead massive corals, DDC = dead digitate corals, LDC = live digitate corals, LPC = live plating corals, DPC = dead plating corals, E = encrusting corals, F= foliose corals, SC=soft coral,

RUB = rubble, SP=sponge, SA=sand, PAV = pavement, R=rock, SP = sponge, MAC = macroalgae, SCI=Structural complexity index, EX= site exposure to prevailing wind & waves. Direction of relationship between response and predictor variables are indicated in parenthesis: (+) = increasing, (-) = decreasing, (^) = increase followed by decline, (v) = decline followed by increase, (w) = multiple increases and declines, (NC) = no change. For site exposure, direction of trend is from to “sheltered” to “exposed” (i.e., sheltered, semi-exposed, exposed).

Appendix 2.3: Species Assumed to be Predators of Juvenile and/ or Adult Wrasses at the Palm, Whitsunday, and Keppel Islands

Genus	Species	Genus	Species
Lutjanidae	*Lutjanus argentimaculatus* *L. carponatatus* *L. fuviflamma* *L. kasmira* *L. lemniscatus* *L. lutjanus* *L. monostigma* *L. quinqueliniatus* *L. rivulatus* *L. russeli* *L. seabae* *L. vitta*	Lethrinidae	*Lethrinus atkinsoni* *L. laticaudis* *L. lentjan* *L. miniatus* *L. nebulosis* *L. olivaceus* *L. obsoletus* *L. ornatus*
Epinephelidae	*Epinephelus coeruleopunctatus* *E. coides* *E. corallicola* *E. fasciatus* *E. fuscoguttus* *E. lanceolatus* *E. hexagonatus* *E. merra* *E. ongu* *E. quoyanus* *Plectropomus laevis* *P. maculatus* *P. leopardus*		

Appendix 2.4: Optimal (within ΔAICc ≤ 2) Generalised Additive Mixed Models (GAMMs) Estimating Effects of NTMR Status, Time (duration of protection), Predator Density, and Cover of Benthos on Density of Wrasses at the Palm, Whitsunday, and Keppel Islands.

Taxa-specific top models shown in bold.

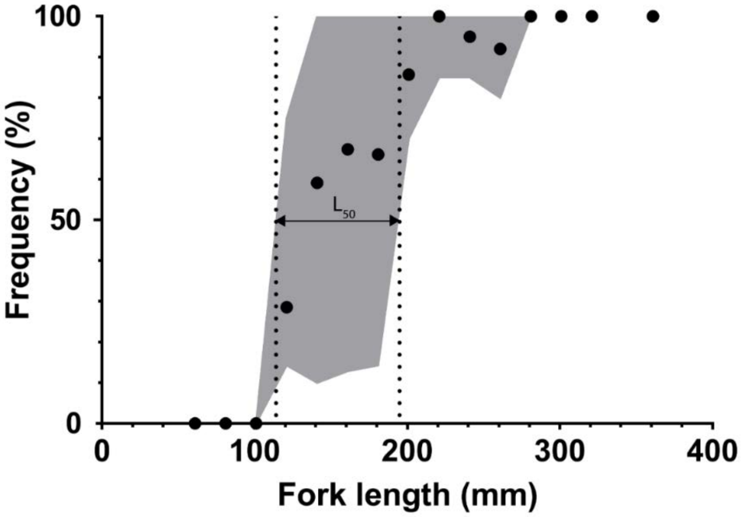
Location	Species	Model	AICc	ΔAICc	wAICc
Palm Island group	***Anampses spp.***	**time+pavement+exposure**	**266.652**	**0**	**0.197**
	Anampses spp.	pavement+status+exposure	266.937	0.285	0.171
	Anampses spp.	sand+pavement+exposure	267.243	0.592	0.147
	Anampses spp.	pavement+exposure	267.749	1.098	0.114
	Bodianus spp.	**time+exposure+live.branching.coral.by.exposure**	**1291.697**	**0**	**0.87**
	C.fasciatus	**exposure+time.by.exposure+sand.by.exposure**	**2003.771**	**0**	**0.351**
	C.fasciatus	SCI+exposure+time.by.exposure	2004.377	0.607	0.259
	C.fasciatus	status+soft.coral.by.status+SCI.by.status	2004.437	0.666	0.251
	E. insidiator	**soft.coral+sand+SCI**	**1584.249**	**0**	**0.94**
	H. fasciatus	**sand+exposure+live.branching.coral.by.exposure**	**837.957**	**0**	**0.765**
	H. melapterus	**encrusting+exposure+SCI.by.exposure**	**1397.244**	**0**	**0.313**
	H. melapterus	exposure+SCI.by.exposure+predatordensity.by.exposure	1398.336	1.093	0.181
	H. melapterus	status+exposure+SCI.by.exposure	1398.806	1.563	0.143
	Halichoeres spp.	**exposure+time.by.exposure+SCI.by.exposure**	**2426.123**	**0**	**0.493**
	Halichoeres spp.	time+exposure+SCI.by.exposure	2427.407	1.284	0.26
	Labroides spp.	**exposure+time.by.exposure+SCI.by.exposure**	**2309.285**	**0**	**0.969**
	O. digramma	**soft.coral+sand+SCI**	**1091.082**	**0**	**0.301**
	O. digramma	sand+exposure+SCI.by.exposure	1092.293	1.212	0.164
	O. digramma	soft.coral+sand	1092.964	1.883	0.117
	O. digramma	soft.coral+rubble+sand	1092.981	1.899	0.116
	Stethojulis spp.	**SCI**	**289.853**	**0**	**0.063**
	Stethojulis spp.	SCI+exposure	290.490	0.637	0.046
	Stethojulis spp.	encrusting+SCI	290.803	0.95	0.039
	Stethojulis spp.	sand+SCI	291.184	1.331	0.032
	Stethojulis spp.	null	291.555	1.703	0.027

	Stethojulis spp.	exposure	291.666	1.813	0.025
	Thalassoma spp.	**time+status+SCI.by.status**	**2914.307**	**0**	**0.986**
Whitsunday Island group	***Anampses spp.***	**exposure+live.branching.coral.by.exposure+SCI.by.exposure**	**1292.917**	**0**	**0.607**
	Bodianus spp.	**SCI+status+soft.coral.by.status**	**3163.278**	**0**	**0.42**
	Bodianus spp.	status+soft.coral.by.status+SCI.by.status	3163.559	0.281	0.365
	C. fasciatus	**live.branching.coral+predator.density+exposure**	**3960.945**	**0**	**0.729**
	E. insidiator	**time+soft.coral+sand**	**3246.214**	**0**	**0.25**
	E. insidiator	time+live.branching.coral+sand	3246.537	0.323	0.213
	E. insidiator	time+live.branching.coral+soft.coral	3246.633	0.418	0.203
	E. insidiator	sand+status+pavement.by.status	3246.851	0.637	0.182
	H. fasciatus	**sand+status**	**2301.889**	**0**	**0.179**
	H. fasciatus	soft.coral+sand+status	2302.985	1.095	0.103
	H. fasciatus	live.branching.coral+sand+status	2303.220	1.331	0.092
	H. melapterus	**live.branching.coral+status+rubble.by.status**	**3720.610**	**0**	**0.884**
	Halichoeres spp.	**live.massive.coral+sand+SCI**	**4694.043**	**0**	**0.999**
	Labroides spp.	**time+pavement**	**5505.813**	**0**	**0.244**
	Labroides spp.	soft.coral+status+SCI.by.status	5505.972	0.16	0.226
	Labroides spp.	pavement+status+SCI.by.status	5506.717	0.904	0.156
	O. digramma	**live.branching.coral+live.digitate.coral+status**	**2427.566**	**0**	**0.191**
	O. digramma	time+live.branching.coral+live.digitate.coral	2427.578	0.012	0.19
	O. digramma	live.digitate.coral+status+live.branching.coral.by.status	2428.193	0.627	0.139
	O. digramma	SCI+status+live.branching.coral.by.status	2428.429	0.864	0.124
	O. digramma	live.branching.coral+SCI+status	2429.060	1.494	0.09
	O. digramma	time+live.branching.coral+SCI	2429.152	1.586	0.086
	Stethojulis spp.	**time+pavement+SCI**	**1197.335**	**0**	**0.997**
	Thalassoma spp.	**time+pavement+SCI**	**7964.693**	**0**	**0.849**
Keppel Island group	***Anampses spp.***	**live.branching.coral+macroalgae+branching.dead**	**527.302**	**0**	**0.56**
	Anampses spp.	live.branching.coral+macroalgae+live.digitate.coral	527.924	0.621	0.41
	E. insidiator	**predator.density+status+exposure**	**445.541**	**0**	**0.45**
	H. melapterus	**time+macroalgae+predator.density**	**3076.158**	**0**	**0.898**
	Halichoeres spp.	**time+status+rubble.by.status**	**3352.025**	**0**	**0.914**
	Labroides spp.	**time+SCI+status**	**1291.927**	**0**	**0.936**
	Stethojulis spp.	**predator.density+exposure+macroalgae.by.exposure**	**2530.277**	**0**	**0.979**
	Thalassoma spp.	**live.branching.coral+predator.density**	**2468.411**	**0**	**0.999**

Appendix 3.1: Size-at-Sexual Maturity Estimates

Generalised size-at-maturity was determined following established techniques. Gonads from 589 wrasses (approximately evenly split across *H. melapterus, H.fascaitus, C.fasciatus, O. digramma*) were obtained from the Palm and Whitsunday Island groups from 2016 to 2018. Gonads were processed histologically and interpreted for sexual stages following West (1990). Individuals were classified as male, female or transitional (when degenerative vitellogenic ovaries were present with proliferating testis); females were classified as immature, mature active or mature resting.

Length at 50% female sexual maturity (L50) for each species examined was estimated by collating the proportional frequency of mature active and mature resting females in size class bins for all female samples. To generalise across species, proportional frequencies per size bin were then averaged across island groups. Mean proportional frequency for all species, at both locations was then plotted and fitted with shaded bands which represent the minimum and maximum values from species specific maturity curves (S4). To remain conservative, I used the upper limit of sexual maturation (approximately 20cm FL/ TL depending upon the species) as the cut-off between juvenile and mature subsets.



S4: Generalised maturity curve for *H. melapterus, H. fasciatus, C. fasciatus,* and *O. digramma* collected from the Palm and Whitsunday Island groups combined. Black data points represent mean proportional frequency per size bin for all species at both locations combined. Shaded band represents the minimum to maximum values from species-specific proportional frequencies for Palm and Whitsunday Island group.

Appendix 3.2: Environmental Disturbance History of Study Sites, 2007 – 2018

White bars denote years that sites were undisturbed, grey bars denote years when coral bleaching occurred, and black bars denote years when cyclones directly impacted reefs. Asterisks denote years of sampling.

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Palm Island group					■					▒	▒	
Years sampled	*		*			*		*		*		*
months sampled	Apr		Dec			Feb		Oct		Aug		Aug
Whitsunday Island group											■	
years sampled	*		*			*		*		*	*	*
months sampled	Oct/ Nov		Oct/ Nov			Oct/ Nov		Sept		Sept/ Oct	Nov/ Dec	Oct

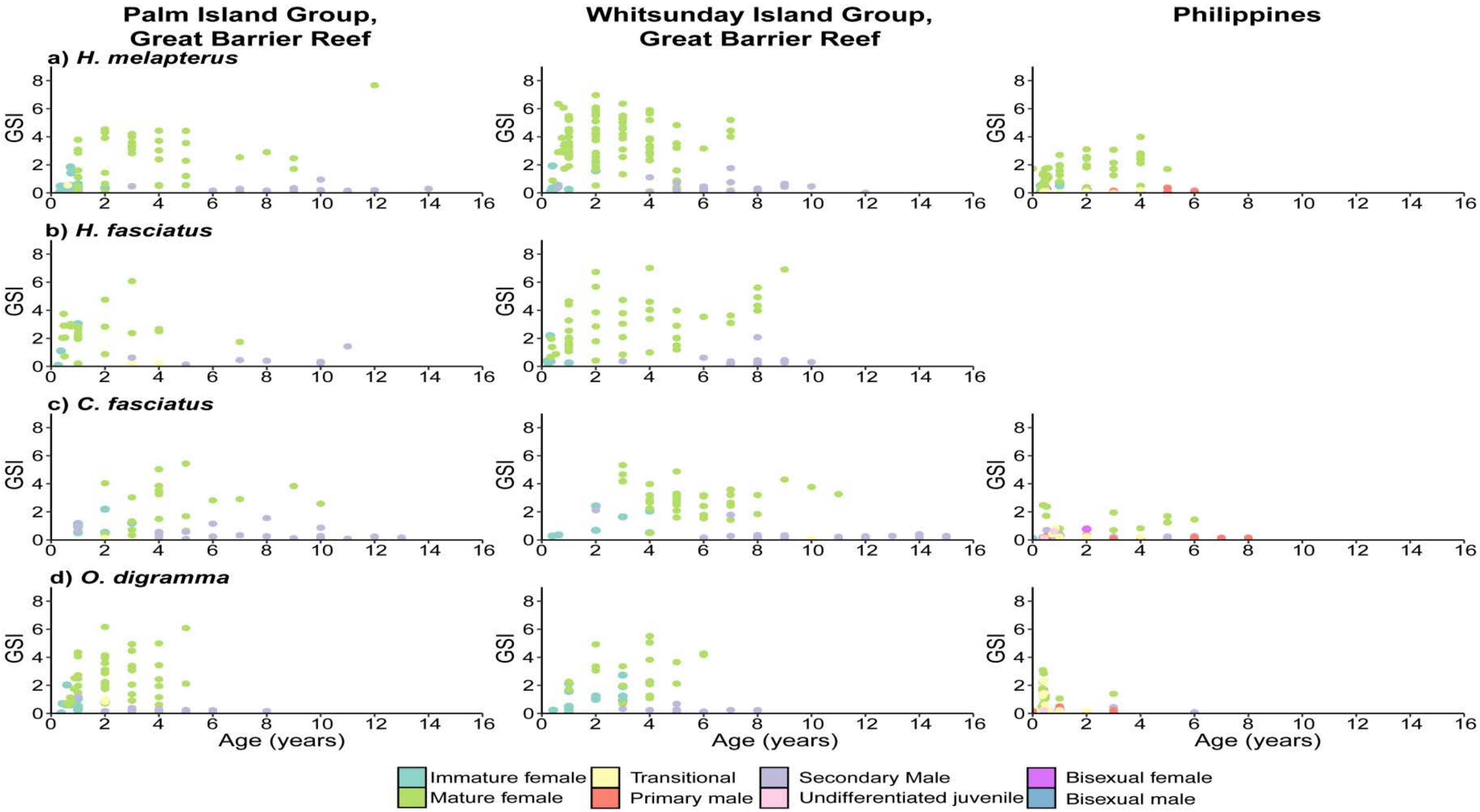
Appendix 3.3: Mean Species-Specific Total Body Weight used for Calculations of Wrasse Biomass

Species	**Midpoint of length category (cm)**	**Mean total body weight (g)**	**SE**
H. melapterus	15	71.64	2.42
	20	134.95	3.41
	25	255.64	7.99
	30	408.78	13.97
	40	606.23	15.62
H. fasciatus	15	82.93	3.23
	25	165.06	5.19
C. fasciatus	10	38.78	5.15
	25	78.21	2.41
	20	149.09	5.47
	25	260.71	7.72
O. digramma	15	67.39	2.68
	20	168.61	5.98

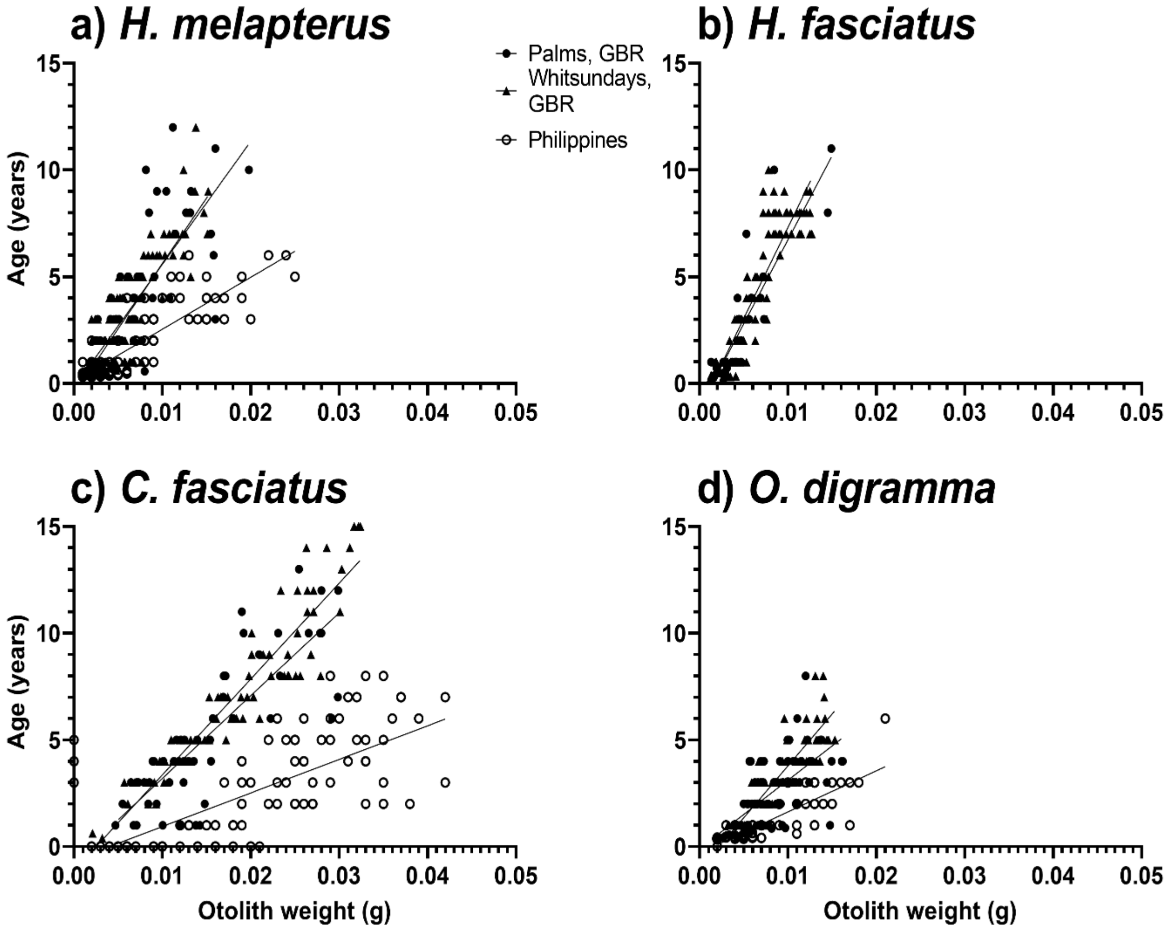
Appendix 4.1: Sex-structure of 20-individual subsample per species determined by reading all 3 histological sections or by reading the medial section alone, across one and two gonad lobes

Sex	Distal (D), medial (M) and proximal (P) histological sections	M section only	Error from reading M section only	Left Lobe	Right Lobe	Error from reading D, M, P sections from a single gonad lobe
Female	53	57	8%	53	53	0%
Male	21	21	0%	21	21	0%
Transitional	6	2	67%	6	6	0%

Appendix 4.2: Age vs. Gonadosomatic Indices of (a) *H. melapterus,* (b) *H. fasciatus,* (c) *C. fasciatus,* and (d) *O. digramma* Sampled from the Palm and Whitsunday Island groups, GBR and from Philippine Fish Markets



Appendix 5.1: Otolith Weight vs Age of (a) *H. melapterus,* (b) *H. fasciatus,* (c) *C. fasciatus,* and (d) *O. digramma* sampled from the Palm and Whitsunday Island groups, GBR and from Philippine Fish Markets



Appendix 5.2: ANCOVA and Tukey HSD Result Tables for Mortality Comparisons

Significance codes: 0 “***”, 0.001 “**”, 0.01 “*”, 0.05 (.), 0.1 “”, 1.

ANCOVA table: Mortality of *H. melapterus* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
Age	1	17.8984	17.8984	149.0356	1.57E-11	***
Location	2	0.5982	0.2991	2.4907	0.10492	
Age:Location	2	0.692	0.346	2.8809	0.07647	.
Residuals	23	2.7622	0.1201			

Tukey HSD table: Mortality of *H. melapterus* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	0.5305	0.2992	1.773	0.2002	
Whitsundays - Palms	0.6698	0.2707	2.474	0.0531	.
Whitsundays - Philippines	0.1393	0.3087	0.451	0.8941	

ANCOVA table: Mortality of *H. fasciatus* among Palm and Whitsunday reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
Age	1	0.9119	0.91191	2.286	0.15873	
Location	1	1.2902	1.2902	3.2343	0.09958	.
Age:Location	1	0.0427	0.04273	0.1071	0.74961	
Residuals	11	4.3881	0.39892			

Tukey HSD table: Mortality of *H. fasciatus* among Palm and Whitsunday reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Whitsundays - Palms	0.4704	0.6274	0.75	0.469	

ANCOVA table: Mortality of *C. fasciatus* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
Age	1	4.1453	4.1453	19.8174	0.0001239	***
Location	2	1.7532	0.8766	4.1907	0.0255795	*
Age:Location	2	2.0371	1.0185	4.8693	0.015318	*
Residuals	28	5.8569	0.2092			

Tukey HSD table: Mortality of *C. fasciatus* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	0.9384	0.4028	2.33	0.06777	.
Whitsundays - Palms	-0.4792	0.3781	-1.267	0.42453	
Whitsundays - Philippines	-1.4176	0.3726	-3.805	0.00191	**

ANCOVA table: Mortality of *O. digramma* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
Age	1	4.2362	4.2362	24.047	0.0004688	***
Location	2	1.2223	0.6112	3.4692	0.0678953	.
Age:Location	2	0.6165	0.3082	1.7498	0.2188805	
Residuals	11	1.9378	0.1762			

Tukey HSD table: Mortality of *O. digramma* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	0.5855	0.4643	1.261	0.444	
Whitsundays - Palms	-0.4683	0.4519	-1.036	0.57	
Whitsundays - Philippines	-1.0538	0.485	-2.173	0.12	

Appendix 5.3: ANCOVA and Tukey HSD Result Tables for Length-Weight and Body Condition Comparisons

Significance codes: 0 “***”, 0.001 “**”, 0.01 “*”, 0.05 (.), 0.1 “”, 1.

ANCOVA table: Length-Weight of *H. melapterus* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq.	Mean Sq.	F value	Pr(>F)	Sig.
log(tl)	1	293.199	293.199	33761.68	< 2.2e-16	***
Location	2	1.695	0.847	97.583	< 2.2e-16	***
log(tl):Location	2	0.8	0.4	46.04	< 2.2e-16	***
Residuals	303	2.631	0.009			

Tukey HSD table: Length-Weight of *H. melapterus* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	-1.2169	0.1853	-6.568	<1e-04	***
Whitsundays - Palms	0.388	0.2143	1.81	0.167	
Whitsundays - Philippines	1.605	0.2067	7.766	<1e-04	***

ANCOVA table: Length-Weight of *H. fasciatus* among Palm and Whitsunday reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
log(tl)	1	32.774	32.774	5043.08	<2e-16	***
Location	1	0.007	0.007	1.0291	0.3126	
log(tl):Location	1	0.005	0.005	0.7226	0.3971	
Residuals	111					

Tukey HSD table: Length-Weight of *H. fasciatus* among Palm and Whitsunday reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Whitsundays - Palms	-0.3414	0.4211	-0.811	0.419	

ANCOVA table: Length-Weight of *C. fasciatus* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
log(fl)	1	163.87	163.87	15795.14	< 2.2e-16	***
Location	2	0.45	0.225	21.706	2.47E-09	***
log(fl):Location	2	0.503	0.252	24.247	3.02E-10	***
Residuals	221	2.293	0.01			

Tukey HSD table: Length-Weight of *C. fasciatus* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	-1.8303	0.3375	-5.423	<1e-05	***
Whitsundays - Palms	-0.2023	0.4029	-0.502	0.869	
Whitsundays - Philippines	1.6279	0.3219	5.057	<1e-05	***

ANCOVA table: Length-Weight of *O. digramma* among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
log(tl)	1	105.397	105.397	11172.2	< 2.2e-16	***
Location	2	0.918	0.459	48.639	< 2.2e-16	***
log(tl):Location	2	0.217	0.109	11.513	1.80E-05	***
Residuals	211	1.991	0.009			

Tukey HSD table: Length-Weight of *O. digramma* among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	-0.7489	0.3575	-2.095	0.0931	.
Whitsundays - Palms	0.7943	0.3905	2.034	0.1064	
Whitsundays - Philippines	1.5432	0.3562	4.332	<1e-04	***

ANCOVA table: Generalized body-condition among Palm, Whitsunday, and Philippine reefs.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	Sig.
log(tl)	1	641.91	641.91	29335.63	< 2.2e-16	***
Location	2	3.3	1.65	75.398	< 2.2e-16	***
log(tl):Location	2	2.83	1.41	64.557	< 2.2e-16	***
Residuals	862	18.86	0.02			

Tukey HSD table: Generalized body-condition among Palm, Whitsunday, and Philippine reefs.

	Estimate	Std. Error	t value	Pr(>|t|)	Sig.
Philippines - Palms	-1.9912	0.2137	-9.319	<1e-05	***
Whitsundays - Palms	-0.2039	0.2385	-0.855	0.668	

Whitsundays - Philippines	1.7872	0.2162	8.267	<1e-05	***