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Effects of climate change and habitat degradation on Coral Trout (*Plectropomus* spp.)

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All experimental and field-based research was conducted in accordance with provisions and legislations of the State of Queensland and the Commonwealth of Australia, and was permitted and authorised by relevant Australian Government agencies and institutions, including the Great Barrier Reef Marine Park Authority (Permit No. G19/41916.1), and the James Cook University Animal Ethics Committee (Ethics Application No. A2755).

Abbreviations

AIMS	Australian Institute of Marine Science
BIA	Bioelectrical Impedance Analysis
BRT	Boosted Regression Trees
CRFFF	Coral Reef Fin Fish Fishery
DAF	Department of Agriculture and Fisheries, Queensland Government
FL	Fork Length
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
HV	Hepatocyte Vacuolation
JCU	James Cook University
KUD	Kernel Utilisation Distributions
LTMP	Long-term Monitoring Program (AIMS)
LRFFT	Live Reef Food Fish Trade
NTMR	No-Take Marine Reserves
RLF	Reef Line Fishery (formerly CRFFF)

Executive Summary

Fishes are at considerable risk from changing environmental conditions because they are, for most part, unable to regulate their body temperature. Exposure to relatively high temperatures may compromise critical biological functions, resulting in reduced performance, fitness and ultimately survival. Larger and more mobile fishes (including many major fisheries target species) may however, move between habitats to exploit natural environmental gradients and thereby moderate their exposure to extreme temperatures. Such behavioural thermoregulation may provide resilience to changing environmental conditions among wild fish stock, but may nonetheless impact on the capacity to catch such species. To test these ideas, coral reef scientists from James Cook University (JCU) and the Australian Institute of Marine Science (AIMS), collaborated with fish physiologists from Deakin University, and also fisheries managers from the Queensland Government, Department of Agriculture and Fisheries (DAF). This project uses pioneering studies to establish how fishes respond to changing environmental and habitat conditions, explicitly considering the capacity for fishes to actually move or moderate their activity to minimise adverse effects of high and increasing water temperatures. Extensive analyses of new and existing data were also undertaken to explicitly test for changes in the abundance, biomass and catches of Coral Trout following major disturbances and changing habitat condition across the GBR.

Background

Coral Trout (mainly, the Common Coral Trout, *Plectropomus leopardus*) are critical in sustaining the Queensland Reef Line Fishery (RLF), and are also important target species for recreational, charter and indigenous fishery sectors on Australia's Great Barrier Reef (GBR) and other coastal waters. Experimental studies on the temperature sensitivity of Coral Trout have suggested that population viability of Coral Trout, and the sustainability of relevant fisheries, may be undermined by climate change and reef degradation. More specifically, Coral Trout in the northern GBR are already exposed to maximum summertime temperatures that exceed their apparent thermal optima (27–30°C). Climate induced coral bleaching has also contributed to extensive coral loss and habitat degradation in the northern GBR, which is likely to impact on recruitment success, but also prey availability and physiological condition of adult Coral Trout. This builds on previous experimental studies to explicitly test how Coral Trout are responding to changing environmental and habitat conditions.

Aims

The specific objectives of this study were to:

- i) Establish the capacity for thermoregulatory behaviour among Common Coral Trout (*Plectropomus leopardus*), as well as measuring their preferred temperature;
- ii) Test for changes in the distribution and behaviour of Coral Trout associated with seasonal and latitudinal variation in ocean temperatures;
- iii) Explore effects of severe coral loss and habitat degradation (caused by recent mass-bleaching) on the abundance, diet and physiological condition of large-bodied fishery species, especially Common Coral Trout; and
- iv) Test for long-term changes in abundance and catches of Coral Trout associated with reef-wide changes in habitat condition on the GBR.

Methods

To test for behavioural thermoregulation among Common Coral Trout (*P. leopardus*) we conducted three distinct studies, starting with an experimental test of thermal preferences in controlled, heterothermal environments; *P. leopardus* (n= 10, ~400 mm FL) were implanted with thermal loggers and then placed in the experimental arena to understand if or how these fishes utilise thermal refugia. This laboratory study was then complemented with field-based studies to test for seasonal and latitudinal variation in activity

and space use by *P. leopardus*, whereby fish might be expected to exploit natural gradients in thermal conditions to mediate exposure to supra-optimal (high) or sub-optimal (low) temperatures.

To explore potential effects of recent severe marine heatwaves (2016-2017) and corresponding coral loss Common Coral Trout (*Plectropomus leopardus*), surveys were conducted across a range of reefs (both severely and relatively unaffected by recent coral bleaching) to assess the relationships between the abundance of Coral Trout and local habitat conditions and the availability of potential reef-associated prey (damselfishes). Moreover, a total of 420 Coral Trout (mostly *P. leopardus*) were sampled across these reefs to test for changes in diet and condition, which may reveal sub-lethal and longer-term effects of environmental stress and habitat perturbations.

To test for spatiotemporal variation in the status of wild stocks and catches of Coral Trout relative to large-scale disturbances and associated changes in habitat condition on the GBR, long-term data from both commercial and charter logbook data was compiled and related to extensive and ongoing monitoring of Coral Trouts and habitat condition.

Key findings and Implications

This study shows that while Coral Trout (especially, *P. leopardus*) are sensitive to changes in temperature, they can withstand a wide range of temperatures and do not necessarily move among environments to seek out optimal thermal conditions. Critically, *P. leopardus* did not make effective use of thermal refugia to moderate thermal exposure in tank experiments. Moreover, Coral Trouts did not exhibit expected seasonal changes in depth distribution to moderate their exposure to seemingly supra-optimal summer-time temperature's. Rather, *P. leopardus* appear more likely to reduce movement and activity patterns, and thereby conserve energy, when subject to sub- (low) and supra-optimal (high) temperatures.

Densities and biomass of *P. leopardus* recorded in the aftermath of the recent mass bleaching of corals was found to vary within and among reefs, mostly with respect to depth. There was not however, significant or consistent variation in the density or abundance of *P. leopardus* relative to local coral cover. Similarly, there was considerable variation in the physiological condition of *P. leopardus* sampled in the aftermath of the bleaching, but this did not correspond with local coral cover. There was, however, evidence of changes in dietary composition for *P. leopardus* (based on stable isotope signatures) corresponding with local coral cover. This reflects the high dietary versatility of Common Coral Trout and likely, contributes to increased resilience to changes in habitat structure and associated prey communities.

When considering the diversity of major disturbances that have occurred across the GBR, the largest changes (declines) in abundance and biomass (and also catches) of Coral Trouts (*Plectropomus* spp. and also *Variola* spp.) were recorded in the aftermath storms, and especially cyclones. These data may suggest that Coral Trouts are more sensitive to changes in the physical structure (topographic complexity) of coral reef habitats rather than loss of live coral, though extensive coral loss caused by biological disturbances (e.g., coral bleaching and outbreaks of crown-of-thorns starfish) may ultimately lead to declines in topographic complexity. Critically, this study suggests that ongoing outbreaks of crown-of-thorns starfish influence standardised catch rates of Coral Trouts, even though there were limited apparent effects on the abundance or biomass of these fishes.

Recommendations

While the abundance, biomass, and standardised catches of *Plectropomus* spp. on the Australia's Great Barrier Reef were not clearly and consistently related to changing environmental and habitat conditions, ongoing climate change and corresponding degradation of reef habitats are expected to have significant long-term or progressive effects on wild stocks. Notably, Common Coral Trout (*Plectropomus leopardus*) do not appear to moderate their exposure to adverse thermal conditions, and will therefore, be directly affected by increasing ocean temperatures and severe marine heatwaves. This necessitates ongoing research and monitoring to ensure that potential effects of changing environmental and habitat conditions on wild stocks are readily detectable and revealed in a timely manner. Most critically, specific

research is needed to understand how catch rates of Coral Trouts relate to stock size and structure, and how this relationship is affected by changing environmental and habitat conditions. This is important given that behavioural changes may undermine fisheries sustainability (as well as the viability of commercial fisheries), and necessitate changes in fisheries management, even before major changes in stock size and structure become apparent.

Keywords

Behavioural thermoregulation; biomass; climate change; coral reefs; Common Coral Trout (*Plectropomus leopardus*); Coral Trouts; habitat degradation; movement.

1. Introduction

Climate change (defined herein as anthropogenic induced changes in environmental conditions, attributable to increasing atmospheric concentrations of CO₂ and other greenhouse gases) is widely regarded as the foremost threat to tropical marine species and ecosystems (e.g., Harley et al. 2006; Hoegh-Guldberg & Bruno 2010; Doney et al. 2011; Bruno et al. 2018). Most critically, escalating ocean temperatures and corresponding increases in the incidence and severity of marine heatwaves are having major negative effects on the oxygenation, productivity, biodiversity, structure and function of tropical marine ecosystems (Wernberg et al. 2013; Levin 2018; Oliver et al. 2019; Laufkötter et al. 2020). These changes are also undermining the goods and services derived from tropical marine ecosystems, including fisheries production (e.g., Bell et al. 2013; Asch et al. 2018; Smale et al. 2019; Duarte et al. 2020; Lam et al. 2020).

The projected effects of environmental change on marine fishes and fisheries vary greatly (e.g., Cheung et al. 2010; Bell et al. 2013; Barange et al. 2014; Blasiak et al. 2017; Free et al. 2019; Lotze et al. 2019; Lam et al. 2020) depending on what is considered the most pervasive driver of change. Effects also vary regionally, with habitat, fishery type, and primary target species. Global scale analyses of fisheries production have emphasised potentially large and widespread impacts of environmental change due deoxygenation and corresponding loss of productivity (Barange et al. 2014; Ramírez et al. 2017) and/ or the redistribution of species (e.g., Cheung et al. 2010). However, it is also apparent that direct physiological effects of changing environmental conditions affect the individual demography and population dynamics of fisheries target species (e.g., Cheung et al. 2013), with potentially major ramifications for fisheries production and sustainability. Moreover, climate change is having pronounced effects on key habitat-forming and foundation species (e.g., corals, Hughes et al. 2018; kelp, Ling et al. 2009, Wernberg et al. 2013), compounding upon other anthropogenic pressures and leading to marked shifts in the structure of critical marine habitats (He & Silliman 2019; Duarte et al. 2020). The sustained and ongoing degradation of marine habitats has far-reaching effects on habitat-associated species (Jones et al. 2004; Pratchett et al. 2008), though the relative contribution (or synergistic effects) of climate-induced degradation of habitats and other indirect effects are often considered minimal (e.g., Brander, 2010; Brown et al. 2021), especially compared to direct effects of changing environmental conditions on fisheries target species. However, habitat degradation is expected to be one of the most pervasive impacts of climate change on fisheries production within coral reef ecosystems (Hoegh-Guldberg et al. 2007; Graham et al. 2015; Rogers et al. 2018), especially given increasing extent and severity of climatic disturbances (e.g., Hughes et al. 2017, 2018).

1.1 Coral tout (*Plectropomus* spp.)

Coral Trout (*Plectropomus* spp.) are among the most important tropical fisheries species throughout the Indo-West Pacific region (Frisch et al. 2016). In particular, *Plectropomus* species are a major component of the live reef food fish trade (LRFFT) that mostly operates through Hong Kong, with up to 14,000 tonnes of live fish traded annually at an estimated value of US\$1 billion per year (Sadovy de Mitcheson et al. 2013). *Plectropomus* spp. are vulnerable to harvesting, and have been over-exploited in some regions (especially Southeast Asia and parts of the western Pacific) due to the access and proximity to LRFFT markets (Sadovy de Mitcheson et al. 2013). Vulnerability of Coral Trout to fishing is also apparent based on the beneficial effect of no-take marine reserves (e.g., Unsworth et al. 2007; Russ et al. 2008; Emslie et al. 2015), whereby the size, abundance and biomass are higher in no-take marine reserves (NTMRs) compared to areas where fishing is permitted. The resilience of Coral Trout to environmental and habitat disturbances is also demonstrably higher in areas that are closed to fishing (Williamson et al. 2014; Emslie et al. 2015).

Aside from their fisheries value, Coral Trout (*Plectropomus* spp.) are also ecologically important (Rizzari et al. 2014; Frisch et al. 2016). There are eight species of *Plectropomus* spp. that occur throughout the tropical Indo-Pacific and the Red Sea, inhabiting a range of shallow marine habitats and especially on coral reefs (Frisch et al. 2016). Densities of Coral Trout in undisturbed and unfished coral reef habitats can be very high (e.g., 240 fish.ha⁻¹; Kingsford 2009), and exert a major influence on the structure of prey species (e.g.,

Graham et al. 2003; Boaden & Kingsford 2015). Critically, localised depletion of Coral Trout, mostly due to over-fishing, has been linked to marked changes in the structure and function of coral reef assemblages (Boaden & Kingsford 2015). Studies on the diet of Coral Trout have revealed ontogenetic shifts in prey use (St John 1999; Wen et al. 2013) whereby newly settled fishes feed mostly on benthic invertebrates, but become increasingly piscivorous as they grow and mature.

On Australia's Great Barrier Reef (GBR), Coral Trout (mainly, the Common Coral Trout, *Plectropomus leopardus*) are critical in sustaining the commercial Reef Line Fishery (RLF). RLF catches are recorded daily in logbooks with no distinction made between the species of Coral Trouts, including *Plectropomus* spp. and *Variola* spp. (Fox et al. 2022). Over the last 5 years (2017-2021) the total retained catch averaged 1,002 tonnes, including 812 tonnes by the RLF. This represents a marked reduction from peak annual harvests, which exceeded 2,000 tonnes across all sectors, in 2001-2002, which is attributable to a wide range of management reforms (Fox et al. 2022). Stocks of *P. leopardus* on the GBR are considered to be stable (Leigh et al. 2014; Campbell et al. 2019;), although there is recognised uncertainty in stock assessment models and limited information on recreational catches (Frisch et al. 2016; Campbell et al. 2019). The latest stock assessment model for Common Coral Trout (which is based on an age-structured Stock Synthesis modelling framework) estimates that the stock level is at 60% of unfished biomass, having increased from 46% in 2011, partly due to sustained quota restrictions to rebuild stocks (Fox et al. 2022). There is also growing concern regarding the impacts of climate change (Fox et al. 2022). In particular, increasing ocean temperatures and significant recent habitat degradation may increase vulnerability of *Plectropomus* spp. (and other reef-associated fishery species) to exploitation and undermine fisheries sustainability (Pratchett et al. 2017).

Previous experimental studies showed that individual performance (e.g., swimming speed and food intake) of *P. leopardus* declines with increasing temperatures above 27-30°C (Pratchett et al. 2013; Johansen et al. 2014; Sun et al. 2015; Messmer et al. 2017). Fish exposed to $\geq 30^{\circ}\text{C}$ also experienced significant levels of mortality up to 13 days after exhaustive exercise stress (Clark et al. 2017). This is a concern as Coral Trout at many low latitude locations (including the northern GBR) are already regularly exposed to summer-time temperatures that are $>27^{\circ}\text{C}$, if not $>30^{\circ}\text{C}$ (Pratchett et al. 2017; Scott et al. 2019). However, these experiments provide limited insight into the extent to which elevated temperatures may compromise wild stocks of Coral Trout, because they do not allow for movement and behavioural modification that may regulate thermal exposure. It is expected, for example, that large mobile fishes could mediate effects of temporary (seasonal) exposure to elevated temperatures by moving to greater depths (e.g., Richards et al. 2012; Currey et al. 2015) or other thermal refuges, and/or reducing activity (Johansen et al. 2014). Resulting changes in the distribution and behaviour may, however, directly impact upon catchability (Currey et al. 2015; Tobin et al. 2010). Tobin et al. (2010) reported depressed catch rates of *P. leopardus* (but increased catches of another target species, *Lethrinus miniatus*) in the aftermath of major tropical cyclones. Depressed catch rates were attributed to metabolic suppression among Coral Trout due to increased advection of cooler waters on to the continental shelf (Tobin et al. 2010). Ongoing climate change (especially projected warming) may, therefore, lead to declines in catches of Coral Trout across many equatorial locations (which currently sustain the world's largest *Plectropomus* fisheries; Frisch et al. 2016), due to declines in catchability, regardless of changes in the size or structure of wild stocks (Pratchett et al. 2017).

Aside from direct effects of environmental change (e.g., increasing temperature; Johansen et al. 2014; ocean acidification, Munday et al. 2013), the distribution, abundance and fitness of Coral Trout may be affected by climate-induced changes in the biological and physical structure of coral reef habitats (Graham et al. 2006; Pratchett et al. 2008; Rogers et al. 2018). Coral reef habitats are particularly vulnerable to changing environmental conditions, and especially increasing temperatures, which cause widespread and significant coral bleaching and coral loss (e.g., Hughes et al. 2018; Section 1.2). Increasing incidence and severity of climate-induced mass coral bleaching is compounding pre-existing disturbances and pressures, leading to extensive coral loss, as well as declines in habitat and topographic complexity (Alvarez-Filip et al. 2009). Coral Trout, like many other coral reef fish (see Pratchett et al. 2008, 2017), often utilise live coral habitats at or soon after settlement (Light & Jones 1997; Leis & Carson-Ewart 1999; Kingsford 2009; Wen et al. 2013). Wen et al. (2013) demonstrated that juvenile Barcheek Coral Trout (*Plectropomus maculatus*)

preferentially settle to live corals, which likely provide shelter from predators, but also increase access to prey. Reliance on live corals is less clear for adult Coral Trout, though several studies have reported increased densities of Coral Trout in areas with high coral cover (Kingsford 1992, 2009; Connell & Kingsford 1998; Williamson et al. 2014). Williamson et al. (2014) documented inter-annual changes in the abundance of *P. maculatus* at the Keppel Islands, on the inshore GBR, which followed marked fluctuations in live coral cover.

The role of live coral in sustaining increased densities of Coral Trout is often ascribed to the increased abundance of reef-associated prey fishes (e.g., damselfishes) in coral rich habitats (Connell & Kingsford 1998; Williamson et al. 2014; Wen et al. 2016; Hempson et al. 2017). Coral Trout do however, feed on a wide range of prey fishes including large quantities of pelagic prey (Clupeidae and Engraulididae) in certain habitats and conditions (Kingsford 1992; St John 1999), and might be expected to increase intake of pelagic fishes to compensate for reductions in the availability of coral-dependent prey. If so, Coral Trout might be somewhat resilient to localised coral loss. Apparent changes in the diet of *P. maculatus* were documented using stable isotopes following extensive coral loss and habitat degradation at the Keppel Islands (Hempson et al. 2017). Hempson et al. (2017) showed that $\delta^{13}\text{C}$ signatures declined with habitat degradation, which were attributed to increasing intake of benthic feeding prey fishes (e.g., territorial damselfishes) as opposed to plankton feeding fishes (including many coral-dwelling damselfishes). These diet shifts were not however, sufficient to ameliorate declines in the abundance of *P. maculatus* following localised coral depletion (Hempson et al. 2017; see also Williamson et al. 2014; Wen et al. 2016). Declines in coral cover were, however, compounded by declines in habitat complexity (Williamson et al. 2014), such that it is unclear what mechanism might be responsible for declines in abundance of Coral Trout in the aftermath of major disturbances and habitat degradation.

1.2 Australia's Great Barrier Reef Marine Park (GBRMP)

The iconic Great Barrier Reef (GBR) stretches 2300 kilometres along the north-east coast of Queensland. It comprises several thousand individual coral reefs, several hundred islands, plus a multitude of other habitats such as seagrass beds, mangroves, mesophotic reefs and inter-reefal habitats such as sponge gardens, *Halimeda* banks and lagoon floor (Pratchett et al. 2019). The Great Barrier Reef Marine Park (GBRMP) was established in 1975 to preserve the ecological importance of the region, later formally recognised by World Heritage Listing in 1981. The foundational management strategy for the statutory body, the Great Barrier Reef Marine Park Authority (GBRMPA), has been the implementation of a multi-use marine park, which permits a wide range of activities throughout the Park, including tourism, traditional owner custom, fishing and research. Much of the fishing and research activities within the GBRMP are focused on coral reefs.

Regular monitoring of coral reefs by the Australian Institute of Marine Science (AIMS) began in the 1980s using broad-scale manta tow surveys to assess the spatial extent of large-scale disturbances (Miller et al. 2019; Emslie et al. 2020), especially reef-wide population irruptions (or outbreaks) of crown-of-thorns starfish (CoTS). This program was continued through the 1980's and then expanded in 1992 into the Long Term Monitoring Program (LTMP) to include surveys of fixed sites in a standard reef slope habitat on 46 coral reefs spread across the continental shelf in five latitudinal bands. Surveys of fixed sites quantified the abundance and diversity of fish and benthic assemblages. They were conducted annually until 2005 and biennially thereafter to accommodate a monitoring program dedicated to examining the effects of the 2004 re-zoning of the GBRMP under the Representative Areas Program (RAP). These surveys were conducted biennially in the years in between the LTMP surveys on fixed sites at 56 reef pairs (one inside a no-take marine reserve, the other open to fishing) from 15°S to 24°S. These data have been used in many publications describing the spatiotemporal patterns in reef fish abundance and diversity (e.g., Emslie et al. 2010, 2012, 2017, 2019; Cheal et al. 2012), the effectiveness of the 2004 re-zoning of the GBRMP (Emslie et al. 2015), and the effects of habitat degradation on reef fishes (e.g., Cheal et al. 2008, 2017; Wilson et al. 2009; Emslie et al. 2011, 2014).

Coral cover on the GBR has fluctuated over time (Osborne et al. 2011; De'ath et al. 2012; Mellin et al. 2019), with periods of pronounced coral loss coinciding with large-scale disturbances and interspersed with periods of recovery, driven largely by increased abundance of *Acropora* spp. (Emslie et al. 2008; Johns et al.

2014). Up until 2012, pronounced episodes of coral loss were ascribed mostly to the periodic occurrence of severe tropical cyclones as well as recurrent population outbreaks of CoTS (Osborne et al. 2011; De'ath et al. 2012). Since that time, however, the occurrence and influence of climate-induced coral bleaching on the GBR has increased markedly, and is now among the foremost contributors to coral loss (Mellin et al. 2019).

The extent and severity of mass bleaching events on the GBR has been increasing since 1998, coinciding with increased maximum summertime temperatures (Hughes et al. 2017). In 2016, severe mass-bleaching (where >60% of coral bleached) occurred on nearly 50% of reefs, and up to 95% of bleached corals died at some reefs (Hughes et al. 2017). Very high levels of coral mortality across highly susceptible coral taxa (e.g., *Acropora* and *Seriatopora*) resulted in marked transformation in coral assemblages at these reefs (Hughes et al. 2018). Ecological impacts of the 2016 mass bleaching were further compounded by mass bleaching in the very next year (2017), representing the first recorded incidence of back-to-back mass bleaching on the GBR (Hughes et al. 2019a). Mass coral bleaching again occurred in 2020, representing the third major mass bleaching episode in just five years. The cumulative footprint of recent mass bleaching events on the GBR is very large (Dietzel et al. 2021), contributing to regional scale changes in the structure and function of coral reef assemblages (see Hughes et al. 2019b).

2. Objectives

The initial objectives that motivated this project were to:

- i) Establish the capacity for thermoregulatory behaviour among Common Coral Trout (*Plectropomus leopardus*), as well as measuring their preferred temperature;
- ii) Test for changes in the distribution and behaviour of Coral Trout associated with seasonal and latitudinal variation in ocean temperatures;
- iii) Explore effects of severe coral loss and habitat degradation (caused by recent mass-bleaching) on the abundance, diet and physiological condition of large-bodied fishery species, especially Common Coral Trout; and
- iv) Test for long-term changes in abundance and catches of Coral Trout associated with reef-wide changes in habitat condition on the GBR.

The specific research undertaken to address these objectives was organised into seven projects across three themes. Research was mostly focussed on the Common Coral Trout (*P. leopardus*), though it was not always possible to distinguish among different species of Coral Trouts. For example, fisheries catch for Coral Trouts includes all species of *Plectropomus* spp., and also *Variola* spp. The taxonomic breadth or focus of each study is therefore, made very clear.

1) Behavioural responses of Coral Trout that may mediate exposure to, and moderate effects of, high and increasing ocean temperatures - Fishes are at considerable risk from changing environmental conditions because they are, for the most part, unable to regulate their body temperature. Exposure to relatively high temperatures may compromise critical biological functions, resulting in reduced activity, movement and feeding in the short-term, as well as reduced performance, condition and fitness in the longer-term. Ongoing climate change and increases in ocean temperature may therefore, impose limits on the growth, if not survival, of fishes. Behavioural thermoregulation may however, allow some individuals, populations or species to mitigate the adverse impacts of changing environmental conditions. To test for behavioural thermoregulation among Common Coral Trout (*P. leopardus*) we conducted three distinct studies:

a) Experimental test of thermal preferences of Common Coral Trout (*Plectropomus leopardus*) in controlled, heterothermal environments - Current understanding of behavioural thermoregulation in aquatic ectotherms largely stems from “shuttle box” systems (e.g., Neill and Magnuson 1974; Nay et al. 2020), which are limited in their ecological relevance and their capacity to test large-bodied species. In contrast to the dynamically changing temperatures of shuttle boxes, the system presented here maintains static thermal refuges in an otherwise sub-optimal thermal environment. Common Coral Trout (*P. leopardus*; n= 10, ~400 mm FL) were implanted with thermal loggers and then placed in the experimental arena to understand if or how these fishes utilise thermal refugia.

b) Seasonal changes in depth distribution of commercially important fisheries species (including *P. leopardus*) corresponding with natural temperature gradients - Temperature generally declines with increasing water depth, and Coral Trout may move to deep water habitats during warmer months to moderate exposure to supra-optimal temperatures. To test this, Baited Remote Underwater Videos (BRUVs) were deployed over a broad depth gradient (13–71 m) at a submerged, offshore shoal in the northern Great Barrier Reef. BRUVs were deployed during two separate time periods (February and August 2017), to test for seasonal changes in depth distribution that might correspond with natural temperature gradients.

c) Latitudinal variation in activity patterns of *P. leopardus* - This study used acoustic telemetry to investigate spatial and temporal variation in space use (or home range) of Coral Trout from latitudinally distinct (northern and southern) locations on the Great Barrier Reef. Laboratory and field calibrations of tri-axial accelerometer transmitters were then used to assess the metabolic cost of movement and explore latitudinal differences in modes of activity and corresponding energy

budgets. Annual maximum waters temperatures differed between sites by approximately 2.5°C ranging from 19.9 to 27.4°C at the southern site and from 23.1 to 30.1°C at the northern site.

2) Effects of recent severe marine heatwaves (2016-2017) and corresponding coral loss Common Coral Trout (*P. leopardus*) - While some studies have shown that abundance of Coral Trout is affected by coral loss and habitat degradation (e.g., Williamson et al. 2014; Emslie et al. 2015; Hempson et al. 2017), the extent to which Coral Trout are reliant on live coral or specific habitat features is unclear (Brown et al. 2021). Given dietary flexibility (Kingsford 1992), adult Coral Trout may be resilient to moderate changes in habitat condition and associated declines in the availability of reef-associated prey. However, shifts in diet composition may nonetheless lead to declines in individual condition, with longer-term consequences for population replenishment, if not survivorship (e.g., Hempson et al. 2017). Extensive coral loss and habitat degradation across the northern GBR due to unprecedented coral bleaching in 2016-2017 (e.g., Hughes et al. 2017), provides an unparalleled opportunity to explore the effects of severe reef degradation on wild stocks of Coral Trout.

a) Variation in abundance and biomass of *P. leopardus* in the aftermath of mass-bleaching on the GBR - Surveys were conducted across a range of reefs (both severely and relatively unaffected by recent coral bleaching) to assess the relationships between the abundance of Coral Trout and local habitat conditions and the availability of potential reef-associated prey (damselfishes).

b) Variation in diet and condition of *P. leopardus* in the aftermath of mass-bleaching on the GBR - In addition to surveying Coral Trout across a broad range of reefs in the aftermath of the recent mass bleaching and mortality of corals (project 2a) a total of 420 Coral Trout (mostly *P. leopardus*) were sampled across 24 different reefs to test for changes in the diet (based on isotopic signatures in muscle tissue), and individual condition (based mainly on hepatocyte vacuolation which measures fat stores in the liver). Variation in the diet and condition of fish were related to environmental and habitat conditions at individual sites where fish were collected.

3) Spatiotemporal variation in wild stocks of Coral Trout relative to large-scale disturbances and associated changes in habitat condition on the Great Barrier Reef - Coral Trouts (mainly, *P. leopardus*) are critical in sustaining the Queensland Reef Line Fishery, and are also important target species for recreational, charter and indigenous fishery sectors on Australia's Great Barrier Reef (GBR) and other coastal waters. Recent research has suggested that the distribution, behaviour and population viability of Coral Trout are likely to change in response to recent and ongoing climate change and reef degradation (Munday et al. 2013; Johansen et al. 2015; Scott et al. 2017, 2019), especially in the northern GBR, with potentially important consequences for fisheries viability and sustainability. Specific analysis of catch-per-unit effort (CPUE) data and fishery-independent survey data to test for potential effects of recent (2016) heatwaves by Brown et al. (2021) suggest that catch rates of Coral Trout on the GBR are higher at increased temperature (either at lower latitudes or due to marine heatwaves), and Coral Trout are largely resilient to changes in habitat condition. Any such effects should be apparent based on longer-term datasets available for the entire GBR, but have not been tested.

a) Relate spatiotemporal variation in reported catches of Coral Trouts (based on commercial and charter logbook data) to habitat condition across the GBR - This project will test for long-term, reef-wide changes in catches of Coral Trout from commercial logbook data, extending back to 1991. Long-term changes in catches of Coral Trout will then be compared with spatial and temporal data on live coral cover and habitat condition from the AIMS Long Term Monitoring Program (LTMP). Analyses will be conducted across distinct regions, based on GBRMPA Bioregions (Leigh et al. 2014) and catch rates will be adjusted for the effects of tropical cyclones using methodology from FRDC 2013/020 (Courtney et al. 2015).

b) Explore changes in abundance and biomass of Coral Trouts associated with different types of large-scale disturbances that have contributed to coral loss and habitat degradation on the Great Barrier Reef - This project will test for changes in the size, abundance and biomass of Common Coral Trout (*P. leopardus*), based on underwater visual survey data from the AIMS LTMP, associated with different large-scale disturbances, including cyclones, population outbreaks of CoTS, and mass

coral bleaching. Temporal contrasts will also be undertaken separately for reefs that are open versus closed (i.e. within NTMRs) to fishing.

The methods and results relevant to each of the aforementioned projects will be presented sequentially under distinct sub-headings.

3. Methods

3.1(a) Experimental test of thermal preferences of Common Coral Trout (*Plectropomus leopardus*) in controlled, heterothermal environments

Most controlled studies examining behavioural thermoregulation in fishes have used dynamic “shuttle box” systems (Neill et al. 1972; Neill and Magnuson 1974; Nay et al. 2020; Christensen et al. 2021), whereby temperatures continually change and the animal is forced to move between interconnected chambers to avoid uncomfortable thermal conditions. These systems do not necessarily assess thermal preferences, nor do they effectively test an organism’s capacity to exploit thermal refugia. Shuttle box systems also have considerable constraints in terms of the size of individuals that can be tested (Christensen et al. 2021). To test for thermoregulation among *P. leopardus*, we therefore, exposed fish to static thermal refuges in an otherwise sub-optimal thermal environment.

Twenty-five Common Coral Trout (*P. leopardus*; fork length ~400 mm) were caught on the northern Great Barrier Reef, Australia, by commercial fishers in mid-June 2021 and transported to Deakin University Queenscliff Marine Science Centre, Queenscliff, Victoria. All fish were transported from the commercial holding facility in Cairns (AquaCairns) in a single 1 m³ shipping tank (~500 L of water, 19°C, with diffuser releasing pure oxygen). On arrival, fish were given a 2-3 min prophylactic freshwater bath before being distributed among two holding tanks (~1,000 L each, diameter 130 cm, water depth 75 cm). Water temperature of the holding tanks was initially set to 20°C and progressively warmed to 23°C over the following 24 h. Fish were provided with 600 mm lengths of PVC pipe (diameter 250 mm), in which they regularly sought shelter. Fish were fed to satiation every 2-3 days with a variety of food, including snapper (*Chrysophrys auratus*) and squid (*Sepioteuthis/Nototodarus* sp.).

Fish were allowed at least 3 weeks to habituate to the system, after which, 10 fish were selected and surgically implanted with an 8 mm passive integrated transponder (PIT) tag and thermal logger (iButton, Maxim). Individuals were anaesthetised using Aquic-S and a 20 mm incision was made ~40 mm anterior to the anus and just lateral to the ventral midline. The PIT tag was placed in the visceral cavity followed by the thermal logger, which had been cleaned and soaked in iodine solution for 24 h prior to the surgery. The incision was sutured and the fish was allowed to recover for ~10 min in a tub containing clean seawater and aeration prior to being placed back into its original holding tank. Fish were given at least 23 d to recover from the surgery and were only used in subsequent experiments once they had recommenced normal feeding.

To test for thermoregulation, fish with an iButton implanted were individually placed in a thermal preference arena for 2-4 days. The thermal preference arena was constructed using a large tank (diameter 335 cm, water depth 70 cm, volume ~6,170 L) containing five custom-built refuges/hides (Figure 1) that consisted of blue plastic tubs (L × W × H = 645 × 413 × 397 mm, with a lid) that enclosed a 700 mm length of 250 mm diameter PVC pipe (identical pipe to that positioned in holding tanks). Two of the five tubs contained a 3-kW heating system (elements positioned at the bottom of the tub), to control the water temperature within the respective refuge/hide. During trials, two refuges were maintained at 30-32°C, while the remainder of the refuges remained at ambient tank temperature which was maintained at 17.5-20.5°C across trials. These low temperatures were chosen to encourage use of the thermal refuges to increase body temperature towards the presumed optimum of ~27°C (Johansen et al., 2014; Pratchett et al., 2017). There existed a steep gradient of temperatures around the thermal refuges, whereby fish could access higher-than-ambient temperatures by positioning themselves beside or above the thermal refuges.

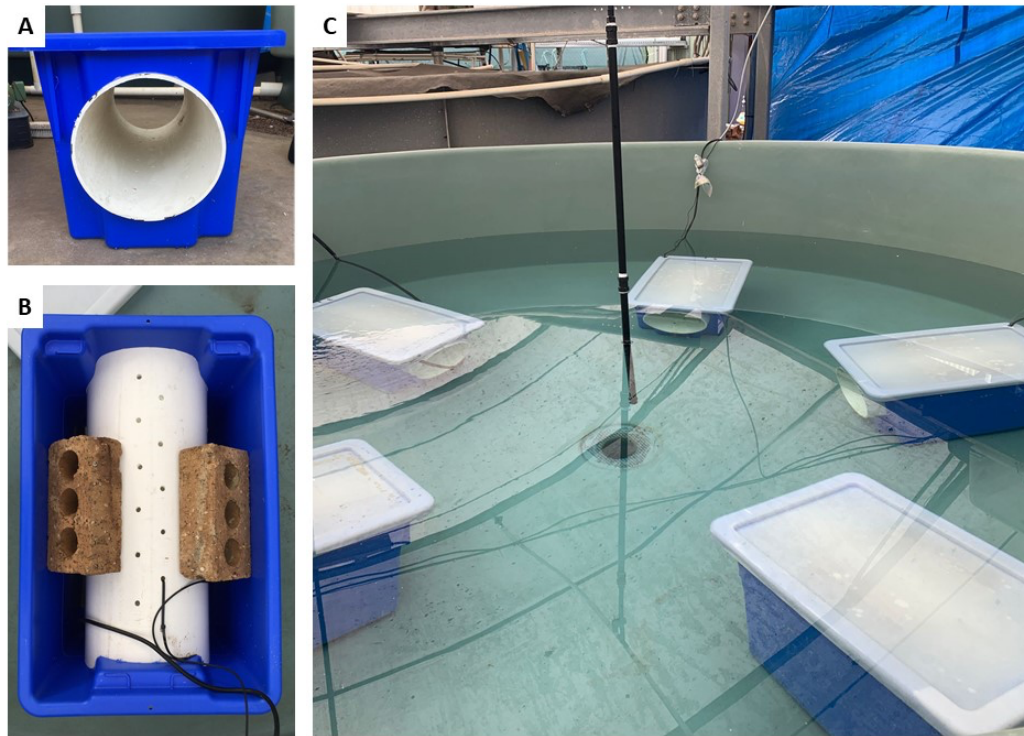


Figure 1. Thermal preference setup used for testing behavioural thermoregulation in Common Coral Trout (*Plectropomus leopardus*). Five custom-built refuges/hides (A,B) were placed in the experimental arena (C), though only two refuges heated the water ($\sim 31^{\circ}\text{C}$) above the ambient temperature ($17.5\text{--}20.5^{\circ}\text{C}$ across trials).

The body temperature of individual fish (measured from implanted iButtons) was compared to the ambient tank temperature (logged every 20 minute from an iButton within a non-heated refuge) at 3-minute intervals throughout the duration of the experiment. Ambient tank temperature was interpolated as required from the 20-min sampling frequency. Data from the first 30-minutes after fish were introduced to the thermal preference arena was excluded to allow thermal equilibration of the fish with the arena. Behavioural thermoregulation was considered to occur when the recorded body temperature was $\geq 0.5^{\circ}\text{C}$ above ambient tank temperature, indicating that the fish were making use of thermal refugia.

3.1(b) Seasonal changes in depth distribution of commercially important fisheries species (including *P. leopardus*) corresponding with natural temperature gradients

This study was conducted at Linden Bank (-16.296900° , 145.993066°), a submerged shoal (6.9 km long and 4.1 km wide) situated on the outer shelf edge of the northern GBR (Figure 2). The top of the bank is in 13–15 m of water and slopes gradually to ~ 70 m (Figure 2). Baited remote underwater videos (BRUVs) were deployed across a broad range of depths (13–71 m). Each BRUV unit (Figure 3) consisted of a Sony Mini-DV handycam placed inside an underwater housing custom made from PVC pipe, which was mounted within a pyramid-shaped galvanised steel frame. A flexible bait arm made of rigid PVC conduit held a plastic mesh bait bag containing 1 kg of minced pilchards (*Sardinops* or *Sardinella* spp.) approximately 1 m in front of the camera (Figure 2).

Between 6–8 BRUVs were deployed simultaneously, separated by 150–200 m and left to soak for a minimum of 60 minutes before being retrieved. BRUVs were deployed over five days in summer ($n=86$) and three days in winter ($n=79$). All deployments were conducted during daylight hours (0700–1700). A temperature logger (Vemco Minilog-II-T) was attached to each BRUV to provide accurate and real time temperature profiles for each deployment.

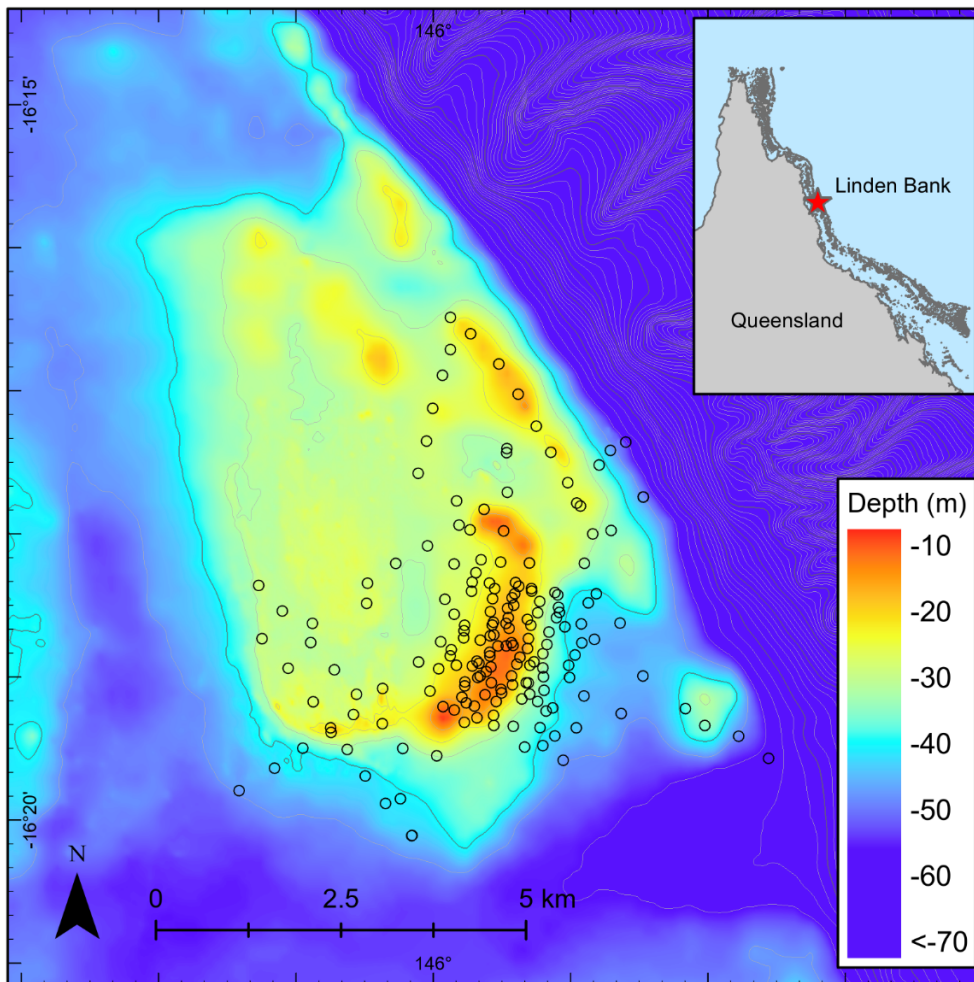


Figure 2. Map of Linden Bank and each BRUV deployment (circles). Bathymetric information from Geoscience Australia using the AusSeabed Marine Data Discovery Portal (<http://marine.ga.gov.au/#/>).

BRUV footage was analysed by two independent observers, who recorded the time on the sea-bed, time of first appearance of each species, and maximum abundance of each species (MaxN). MaxN is the maximum number of a fish species observed in a single frame of footage during one deployment (Willis et al. 2000), which eliminates the possibility of re-counting fishes swimming in and out of the field of view. All videos were analysed to their full length, which ranged from 60-70 minutes (average soak time of 64 min). All fishes (including *Plectropomus* species) were recorded.

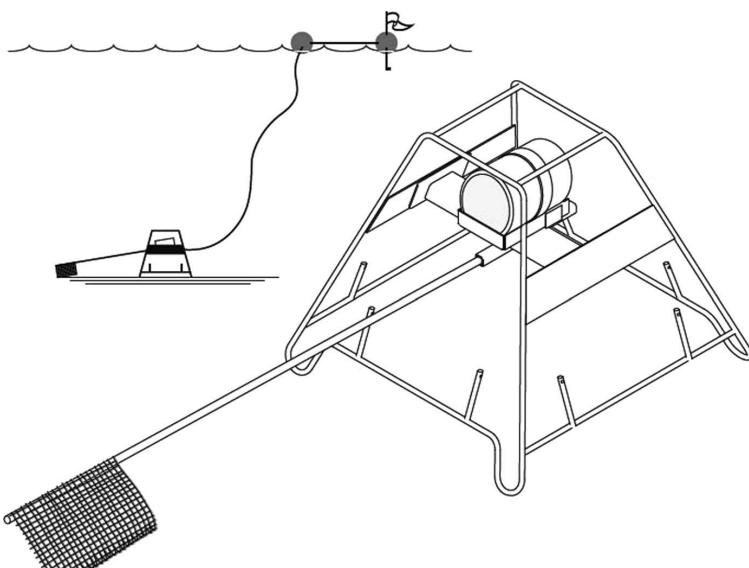


Figure 3. Depiction of the Baited Remote Underwater Video (BRUV) system (from Stowar et al. 2008) used to test for seasonal changes in the depth distribution of fishes (especially Coral Trout) corresponding with natural temperature gradients. To measure temperature, a temperature logger (Vemco Minilog-II-T) was attached to each BRUV

3.1(c) Latitudinal variation in activity patterns of *P. leopardus*

This study was conducted on Australia's Great Barrier Reef (GBR) at Opal Reef (16°14'20.77"S, 145°52'12.59"E) in the northern GBR (low-latitude location) and Heron Island Reef (23°25'57.86"S, 151°55'57.65"E) in the southern GBR (high-latitude location). The two study locations (Figure 4) are separated by approximately 1,000 km and seven degrees of latitude. At each location, the specific study sites were situated within no-take marine park zones and were chosen because they comprised similar fringing and patch reefs along depth gradients extending to ~25 m along the reef slope. Daily temperatures were recorded on four temperatures loggers (Vemco Minilog-II-T) attached to the receivers at approximately 7 m depth.

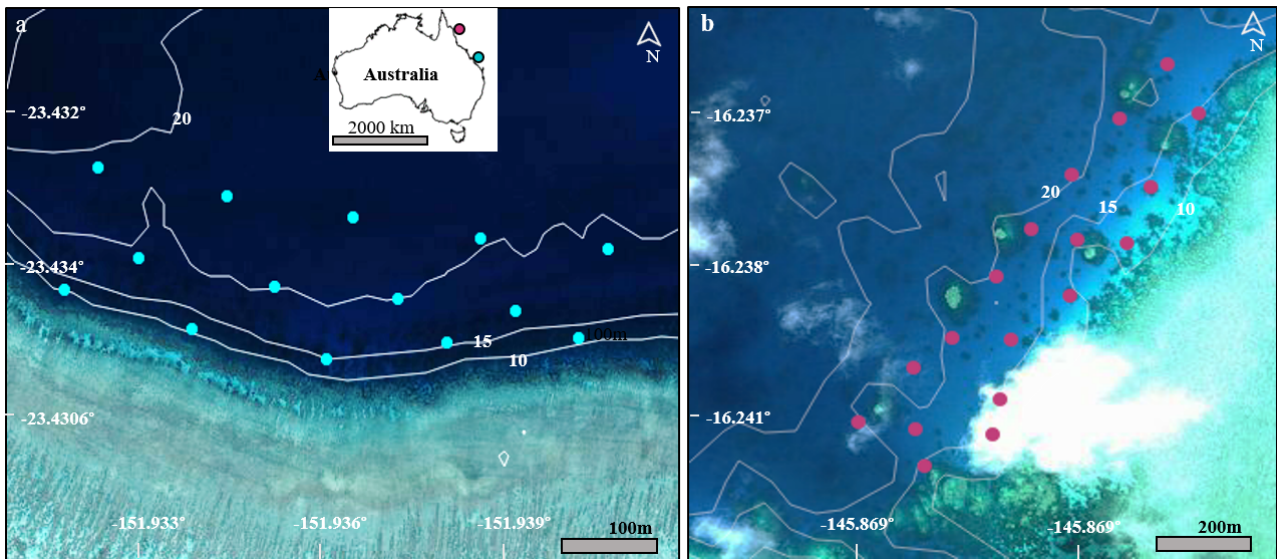


Figure 4. Aerial photographs of two distinct sites where acoustic arrays were established on Australia's Great Barrier Reef. The blue circles indicate the array at Heron Island Reef (a), Australia (high-latitude location) and the red circles indicate the array at Opal Reef (b) (low-latitude location). Each circle represents an acoustic receiver which were deployed in three lines parallel to the reef crest across a depth gradient from those closest to the reef (inner) to middle and outer receivers on the deeper reef slope.

To monitor movement and activity patterns of *P. leopardus*, acoustic tracking was undertaken using Vemco VR2W acoustic receivers (Vemco Ltd., Halifax, Canada). 14-18 receivers were established on the leeward side of both Opal Reef (low-latitude location) and Heron Island (high-latitude location) (Supporting Information Figure S1). Receivers were deployed in an identical arrangement, ~ 2 m above the substrate (reef or sand) using a chain and float mooring and set approximately 100 m apart in three lines (Figure 4). The maximum distance between adjacent receivers was ~ 120m based on receiver detection range estimates of 50-120 m, resulting in ~90% acoustic coverage of the area. Detection range at each site was factored into the study design and tested prior to the release of any transmitters (see Scott et al. 2019 for more detail). Acoustic receiver data were downloaded in May and September 2016.

At each location, 19 adult (>350 mm FL) *P. leopardus* were caught using barbless hooks, anesthetized in AQUI-S® (~ 30 L) diluted with seawater (1:10000), before a V13A-P transmitter (13 mm × 42 mm) was surgically implanted into the abdominal cavity. Each transmitter had a pressure (depth) and accelerometer (speed) sensor and was programmed to randomly emit a unique coded signal every 60-120 seconds, with an expected battery life of 349 days. Each fish was also fitted with an external dart tag (PDS; Hallprint®) in the dorsal musculature for external identification. Horizontal space use patterns of *P. leopardus* within and between locations were evaluated using 50% (core use area) and 95% (home range extent) kernel utilisation distributions (KUDs), calculated using the *adehabitat* package (Calenge 2006).

To describe and calibrate the relationship between activity (overall dynamic body acceleration), swim speed and metabolic rate, laboratory calibrations were undertaken using *P. leopardus* (n =13) caught at

Howie Reef (17°23'58.11"S, 146°22'58.23"E) and Peart Reef (17°29'17.63"S, 146°24'10.62"E) off Cairns on the Great Barrier Reef. Individuals ranged in Fork Length (FL) from 323-365 mm, and weighed between 380 - 622 g. All fish were transported to the Marine and Aquaculture Research Facility Unit (MARFU) at James Cook University within 72 hrs of capture. Upon arrival at MARFU, fish were tagged with a T-bar anchor tag to visually distinguish between individuals and placed randomly into three flow-through aquarium system tanks which were maintained at 24°C ± 0.1. This was the ambient water temperature from the location where they were caught. All tanks were held under natural 13-11 hrs light-dark regime and continuously supplied with filtered seawater (salinity 34ppt). All fish were fed one quarter of a *Nemipterus* spp. daily, however they did not necessarily eat every day. Fish were internally tagged with the V13 AP-H transmitters using standard surgical procedures (described above in section 2.0.2). Activity ($m.s^{-2}$) was determined by calculating the root mean square of triaxial acceleration (12.5 Hz) measured continuously. This calculation occurred on board the tag with a single activity value transmitted within a random period every 17 - 20 seconds. All data was transmitted to a Vemco VR2W acoustic receiver that was situated in the swim tunnel (there was no archival logging of data). Fish were allowed to recover from surgery for a minimum of 72 hrs and were fasted for 12 hrs before being introduced into the swimming respirometer. This recovery period (72 hrs) was considered a sufficient based on observation of fish behaviour. Of the 13 fish used for the swimming respirometry trials, only 9 yielded sufficient data to include in analysis.

Swimming respirometry trials were conducted in a 90L clear Loligo swim tunnel respirometer with a working section of 66 × 20 × 20 cm (width × length × depth). Oxygen levels in the respirometer were recorded using a contactless oxygen sensor (Firesting O2; PyroScience, Aachen, Germany) positioned at the end of the flow loop to record oxygen concentration continuously at 0.5 Hz. To calibrate the flow, a digital TAD W30 flow meter (Höntzsch, Waiblingen, Germany) was used within the working section of the respirometer to obtain a six-point calibration, ranging from 0 to 165 ± 0.5 $cm.s^{-1}$ (mean ± s.e.m). The maximum flow calibration is over five times the length of the fish per second, a speed unlikely to be reached by this species. Solid blocking effects of the fish were corrected by the respirometry software (AquaResp Swim / Python 3); the mean fish cross-sectional area was ~10% of the swim chamber cross-sectional area. To reduce bacterial growth in the system, the respirometer was bleached and rinsed with freshwater between each trial. This ensured that bacterial respiration rates ($\dot{M}O_2$) remained below 15% of the oxygen consumption at rest. Three $\dot{M}O_2$ determinations were run before and after each trial to measure bacterial respiration in the test chamber. The average of the background respiration rates were then subtracted from each $\dot{M}O_2$ measurement.

At the start of a trial, fish were placed in the swim tunnel and left to acclimate for 6-8 hrs at a swimming speed of 0.5 BL s^{-1} until their oxygen consumption rate stabilised. This speed corresponded to the lowest water flow necessary to ensure constant swimming and minimal spontaneous activity. To measure $\dot{M}O_2$ as a function of steady swimming speed (U), flow speed was increased incrementally by 0.25 BL s^{-1} every 30 min, following a standard critical swimming speed procedure (Steffensen et al. 1984). Within each level of swimming speed (i.e., 30 minutes), $\dot{M}O_2$ was measured for 5-minutes within each of three 10-minute cycles (flush; 240s, wait; 60s, measure; 300s). Based on the relationship between swimming speed and activity values in the swim tunnel, we then classified movements of *P. leopardus* in the wild into: i) low activity - <0.5 body lengths per second (bls) and <0.8 overall dynamic body acceleration (ODBA), ii) routine activity - >0.5 bls and >0.8 ODBA, and iii) burst activity - >1.75 bls and >1.22 ODBA. When performing burst swimming the pectoral fins were tucked away and the fish propelled itself forward using its caudal fin. *Plectropomus leopardus* are a relatively sedentary, ambush mesopredator and *in situ* observations and previous studies (Samoilys 1997; Zeller & Russ 1998; Scott et al. 2017) have shown that burst activity of *P. leopardus* take place within several seconds.

3.2(a) Variation in abundance and biomass of *P. leopardus* in the aftermath of mass-bleaching on the GBR

To test for variation in the abundance and biomass of Common Coral Trout (especially, *P. leopardus*) in the aftermath of severe marine heatwaves and extensive mass bleaching on the GBR (see Hughes et al. 2017, 2018), underwater visual censuses were conducted at a total of 35 reefs on the GBR during the period from 2019-2022 (Figure 5). Sampling was concentrated in the northern GBR (between Cairns and Princess

Charlotte Bay), where effects of severe marine heatwaves and corresponding mass coral bleaching in 2016 and 2017 were most pronounced (Hughes et al. 2017, 2018). All sampling was also conducted in February–March each year, to maximise detection of renewed bleaching. Sampling was restricted to mid-shelf and outer-shelf reefs (Figure 4), to focus sampling on *P. leopardus*, following Emslie et al. (2017). Notably, inshore reefs on the GBR tend to be dominated by *P. maculatus* (e.g., Williamson et al. 2014), whereas *P. leopardus* and also the Bluespotted Coral Trout (*Plectropomus laevis*) occur predominately on mid-shelf and outer-shelf reefs (Emslie et al. 2017).

At replicate sites within each reef, surveys were conducted within each of two different habitats, i) the reef crest (1–3m depth) and ii) the reef slope (9–10m depth), where three replicate 50m transects were run parallel to the depth contour with up to 10m between successive transects. Surveys of larger, motile and commercially important reef fishes (including *Plectropomus* spp.) were conducted within a 5m wide belt, while simultaneously deploying the transect tape. Smaller, site attached fishes (including damselfishes: family Pomacentridae) were then surveyed within a 2m wide belt along the length of the transect. Coral cover and benthic composition was assessed by recording the sessile organisms or substrate underlying uniformly spaced (50cm apart) points along the entire length of each transect. Corals were mostly identified to genus (using contemporary, molecular-based classifications for scleractinian corals), though data were pooled to family for some of the less common taxa (e.g., Merulinidae and Lobophyllidae). For survey points that did not intersect corals, the underlying substratum was categorised as either macroalgae (identified to genus), sponge, sand/ rubble or carbonate pavement.

Boosted regression trees (BRTs; Elith et al. 2008) were used to determine the relative influence of up to five predictor variables (Table 1) on the density and biomass of *P. leopardus*. Collinearity of predictor variables was examined using Pearson correlation to ensure highly correlated (>60%) variables were not used in the same model. BRTs have the ability to deal with some level of predictor variable correlation, but highly correlated variables may cause a false positive influence from one of the variables. The distribution of each response variable was determined through visual inspection of data and model testing, with the final models for *P. leopardus* density and biomass fit with Poisson and Laplace family error distributions, respectively (Table 2). A number of candidate BRT models of *P. leopardus* density and biomass with alternative predictor variables were run to determine the best performing model, with all noncorrelated predictor variables included in each initial model run. The best model for each response variable was determined by comparing the percent deviance explained by all candidate models ([mean total deviance — estimated cross validation deviance]/mean total deviance). The BRTs were run in R (R Core Team 2020) with *dismo* package and *gbm.step* function (Elith et al. 2008). BRT step encompasses automated cross-validation and tree optimization protocols. Model parameters were tested and selected to optimize best fit while maintaining ecological relevance (tree complexity, 3; learning rate, 0.01–0.001; bag fraction, 0.75; maximum trees, 10,000). Final BRT models were bootstrapped 100 times with the *ggPD_boot* function in the *ggBRT* package (Jouffray et al. 2019), to account for variability around observed patterns.

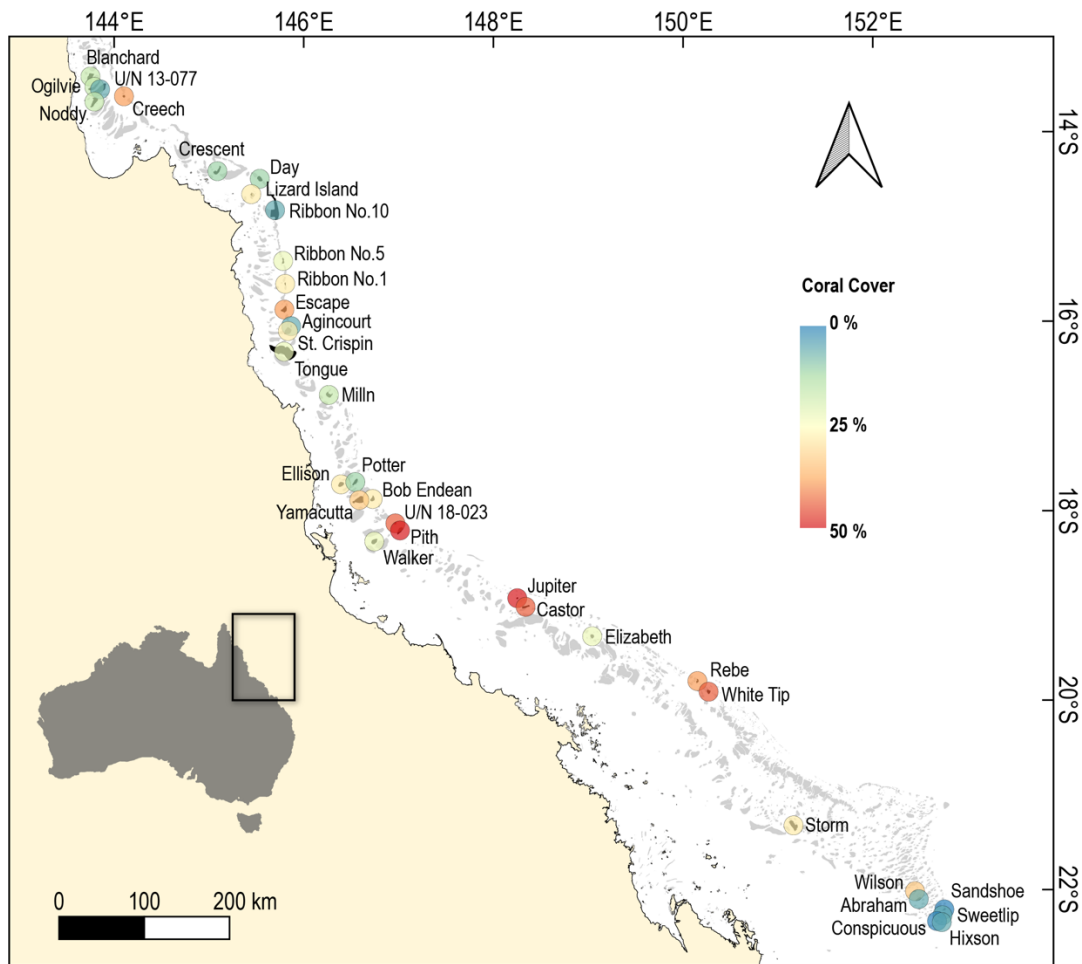


Figure 5. Map of the Great Barrier Reef, showing location of reefs ($n = 35$) surveyed in 2019–2022 to test for variation in abundance and biomass of Common Coral Trout (mainly, *P. leopardus*) relative to the contemporary condition of coral assemblages and reef habitats. Each reef is colour coded according to the average cover of hard (order Scleractinia) coral recorded during surveys.

Table 1. Details of predictor variables used in boosted regression trees to examine the relative influence of habitat variables on the density and biomass of Common Coral Trout (*P. leopardus*) in the Great Barrier Reef.

Predictor	Unit of measurement
Hard coral cover	% cover all hard (order Scleractinia) corals
Depth	metres
Pomacentrid density	abundance (count)
Structural complexity	Visually assessed on scale from 0 to 5 (Wilson et al. 2007)
Macroalgae cover	% cover

3.2(b) Variation in diet and condition of *P. leopardus* in the aftermath of mass-bleaching on the GBR

To assess spatiotemporal variation in the diet and condition of Common Coral Trout, replicate fishes were caught across a broad range of sites and reefs where underwater visual surveys were conducted (see Figure 5). Fish were predominantly caught using spear (on SCUBA) to avoid by-catch, though these samples were

supplemented using line caught fishes in some locations. All fishes were euthanised immediately post-capture, using pithing for larger individuals and cervical dislocation for smaller fishes. The main target species was *P. leopardus*, though all Coral Trouts were retained to maximise information obtained from each site and location. Also, it is sometimes difficult to ascertain the specific identity of *Plectropomus* species (as they often interbreed; van Herwerden et al. 2006) until post-capture. It was also both necessary and unavoidable to sacrifice fishes to derive critical information on their physiological condition, and feeding history, and only a very small sample (maximum 12 fish per site) were taken. The option of simply analysing the fish caught by the commercial fisheries sector was considered, but it was not possible or viable to segregate fish and thereby keep track of fish caught in specific sites, whereas a critical component of this study involves relating condition and feeding history of individual fish to the specific habitat condition where they are caught.

For each Common Coral Trout retained during this study, we recorded fork length (FL, in mm), standard length (SL, in mm) and overall body mass (Wt in g), we then visually examined stomach contents and recorded any identifiable prey items (mostly to family). The liver was removed in its entirety and snap frozen and then stored at -20°C for assessing hepatocyte vacuolation (HV), as the foremost measure of instantaneous physiological condition (explained below). A sample of the dorsal musculature (immediately below the dorsal fin) was also taken from each fish to be used for stable isotope analysis and snap frozen and stored at -20°C . Otoliths were removed from all fishes to provide information on age and growth. Age (years) was determined based on count of annuli on sectioned sagittal otoliths following Ferreira and Russ (1992). Further, we also measured individual otolith increments for all fishes to obtain a much better resolved information in individual growth history, following Adams and Williams (2001). In particular, we wanted to test whether the growth rate of Common Coral Trout was suppressed during severe marine heatwaves (e.g., in 2016 and 2017).

To test for inter-reef differences in dietary composition of *P. leopardus*, we used bulk stable isotope analysis of carbon and nitrogen. Variation in carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) signatures are expected to reflect long-term changes in predominant trophic pathways (e.g., Pinnegar & Polunin 2000), possibly associated with increased use of pelagic prey sources in degraded habitats. Information on diet was obtained by examining identifiable gut contents, though this provides very little insight into dietary composition for Common Coral Trout given the limited incidence and quantity of discernible prey items (e.g., St John 1999). Moreover, the relative abundance of different prey items in identifiable gut contents may be confounded by differential digestion rates (Hempson et al. 2017). For stable isotope analyses, small sections of muscle tissue (5mm maximum dimensions) were dissected from the retained sample then freeze-dried for 48 hours and ground using a ceramic mortar and pestle prior to analysis. Stable isotope analyses were conducted only using muscle tissue given relatively fast turnover ($\delta^{15}\text{N}$ half-life = 126 days) reported for *P. leopardus* (Matley et al. 2016a). Samples were subject to stable isotope analysis at James Cook University Cairns Stable Isotope Unit where C and N composition were determined using an elemental analyser with continuous flow isotope ratio mass spectrometry (EA/CF-IRMS) with a ECS 4010CHNSO elemental analyser (Costech Analytical Technologies Inc., Valencia, CA, USA). A Zero Blank autosampler (Costech Analytical Technologies Inc.) coupled with a ConFloIV interface (Thermo Fisher Scientific, Waltman, MA, USA) to a Thermo Fisher Scientific DeltaV^{PLUS} isotope ratio mass spectrometer were utilised. The C and N isotope ratios are expressed as parts per thousand (‰) relative to the VPDB standard. Standard error of the instrument's measurements were $\pm 0.1 \delta^{13}\text{C}$ and $\pm 0.1 \delta^{15}\text{N}$.

Physiological condition of *P. leopardus* was quantified using hepatocyte vacuolation (HV: the proportion of intracellular vacuoles in cross sections of the liver), following Pratchett et al. (2004). Livers were partially thawed, weighed and then sectioned (where necessary) prior to histological preparation. Liver samples from each fish were then placed in individual histology cassettes and fixed in 10% calcium-buffered formalin (FAACC) for a minimum of 1-week. After fixing, liver samples were dehydrated in a graded ethanol series and embedded in paraffin wax before being sectioned (5 μm thick) and mounted on glass slides. Mounted sections were then stained using Mayer's hematoxylin and eosin to emphasize hepatocyte vacuoles. Stained sections were then viewed using HD Lite capture camera (Scientific Instrument and Optical Sales) attached to a high-power microscope ($\times 40$ magnification) and the proportion of vacuoles was quantified using a 8×8 grid projected onto the image displayed on HD lite retina display using

IsCapture software (Informer Technologies Inc.). The number of points (out of 64) that intersected hepatocyte vacuoles was counted and then scaled to provide a percentage. Three estimates of hepatocyte vacuolation were recorded for each section (in haphazardly selected, non-overlapping areas of the liver that were fully enclosed by the recording grid) by each of two different observers, giving a total of six estimates for each fish. Replicate sections were also prepared for a sub-sample ($n = 6$) of fishes, which were independently scored to test for consistency.

Physiological condition was also measured for a sub-sample of *P. leopardus* (in 2020) using electrical phase angle, following Champion et al. (2020). Phase angle is a measure of resistance and reactance, which scales with body condition, and has been linked to variation in the nutritional status of individual fishes (Cox & Hartman 2005). All bioelectrical impedance analysis (BIA) measurements were taken using the Seafood Analytics Certified Quality Reader (CQ Foods Inc., <https://www.certifiedqualityfoods.com>). Measurements were taken using larger stainless probes along the dorsal musculature within 90 minutes of capture. All fishes were however, placed in commercial chiller box filled with a minimum of 30 litres of seawater and set to 4.0°C, for a minimum of 30 minutes to standardise measurements of BIA, which can vary with temperature (e.g., Champion et al. 2020).

3.3(a) Relate spatiotemporal variation in reported catches of Coral Trouts (based on commercial and charter logbook data) to habitat condition across the GBR

To explore spatiotemporal variation in reported catches of Coral Trouts on the GBR, this study used Queensland commercial and charter fishery logbook database maintained by the Department of Agriculture and Fisheries (DAF), for the RLF, calendar years 1988-2020. A commercial logbook data record provided the retained catch for one primary vessel. A primary vessel generally has several dories or “tenders” attached to it, and the day’s catch is combined over all the dories. The number of dories is recorded. Similarly, a charter logbook record generally provided both the retained and released catch for the vessel, and the catches were combined over all the charter guests. The number of guests are recorded.

Locations were divided into eleven regions, denoted Cape York, Lockhart, Princess Charlotte Bay, Cooktown, Cairns, Townsville, Bowen, Storm Cay Outer, Storm Cay Inner, Swains and Capricorn–Bunker (Figure 6). They were based on the Bioregions defined by the Representative Area Program of the Great Barrier Reef Marine Park Authority (GBRMPA 2009).

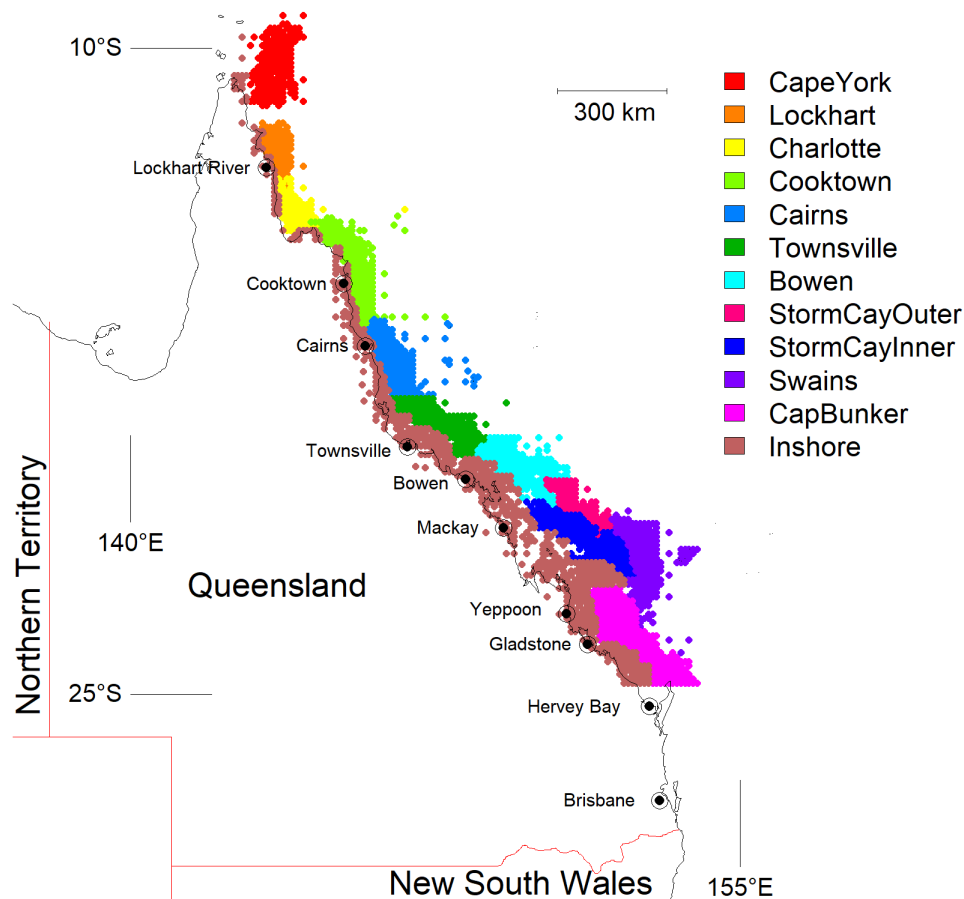


Figure 6. Regions used in the analysis of fishery and monitoring data, with locations of commercial fishery logbook catches of Coral Trout that were reported by at least five separate primary vessels.

The first five regions of the GBR, from Cape York to Cairns, were thought to be most at risk of coral bleaching events related to ocean warming. Commercial harvests around Storm Cay were high and could support separate catch-rate analyses for the Storm Cay Outer and Storm Cay Inner regions; it was believed that the inner region may be more susceptible to run-off from land. Regions from Townsville south experience tropical cyclones that can have major effects on fishery catch rates (see section 4.3(a) below).

Analysis of the data (relating daily catch rates from commercial and charter logbook data to coral cover data for the relevant year and reef from AIMS LTMP) was undertaken using generalised linear models (GLMs) in the software *R* (R Core Team 2021). For the commercial logbook data, the dependent variable was daily catch in kg taken by a primary vessel. The explanatory variables were year (calendar year, defined as a categorical variable), month (categorical variable), Bioregion, primary vessel, number of dories used by the primary vessel, and the presence of other species in the day's harvest that are positively or negatively associated with catches of Coral Trout. For charter logbook data, the dependent variable was the daily number of fish, retained and released combined, caught by a primary vessel. The explanatory variables were year (categorical), month (categorical), Bioregion, primary vessel, number of fishing guests, and presence of positively and negatively associated species. For the coral-cover data (both manta-tow and underwater visual survey), the dependent variable was the fraction of hard coral cover observed over a transect of a site. The explanatory variables were year (categorical) and reef.

Each of the above data sets was analysed separately for each region. The year coefficients were used to create a time series representing the expected value of the dependent variable under standard settings of the other explanatory variables. The analyses took the form of quasi-Poisson GLMs with log link function for Coral Trout abundance, and quasi-binomial GLMs with logit link function for coral cover. The range of the coral cover measurement was between zero (no coral) and 1 (completely covered with hard coral), which made the quasi-binomial GLM appropriate.

The crown of thorns starfish (CoTS, *Acanthaster cf. solaris*) data set contained reef-specific abundance of CoTS as a categorical measure with three levels: Absent, Incipient and Outbreak. We classified regions according to the highest observed CoTS category on any reef within the region. CoTS had to be absent from all surveyed reefs in the region for the region to be classified as Absent. Conversely, any reef classified as Outbreak was sufficient to classify the whole region as Outbreak. We note that the number of affected reefs in a region increases the longer an outbreak lasts, as starfish spread to more reefs.

Data on tropical cyclones and wave heights were used to determine cyclones that had major effects on coral and the coral-reef fishery on the GBR. The mechanism by which important tropical cyclones damage the GBR has been explained by Callaghan and Power (2011) and further investigated by a previous FRDC project 2013-2020 (Courtney et al. 2015). Large waves in the GBR are rare, due to the protection provided by the outer “barrier” reefs which prevent large waves from penetrating from offshore, but large waves are very destructive when they occur (Tobin et al. 2010). Large waves occur when cyclonic winds blow from south-east to north-west between the Swain Reefs and Townsville, along the fetch parallel to the coast and inshore of the barrier reefs. The dates of occurrence of cyclones, when correlated to wave heights, provide an objective list of important cyclones.

3.3(b) Relate spatiotemporal variation in abundance of Coral Trout (based on underwater visual surveys conducted as part of routine monitoring) to changing habitat condition on the GBR

AIMS LTMP has surveyed 103 reefs annually or biennially recording the abundance and length of Coral Trouts (*Plectropomus* spp. and *Variola* spp.) since 1997. Coral Trouts were surveyed in a standard reef slope habitat, usually the north-east flank of each reef, which provides consistency in the exposure related assemblage structure. Coral Trout were surveyed along five permanently marked 50x5m belt transects set at a depth of between 6-9m in each of three sites on each reef ($n=15$ transects reef⁻¹ year⁻¹). The start and finish of each transect are marked with metal stakes, with smaller metal rods spaced at approximately 10m intervals. An observer swam the transect with the transect tape unwound behind them, recording the abundance and length estimate of all species of Coral Trout encountered within the 5m belt.

To examine the effect of disturbances on Coral Trout, disturbance categorisation was based on quantitative data and observations during surveys. Each categorisation was based on distinctive effects on hard corals. For example, the local prevalence of CoTS and/ or conspicuous CoTS feeding scars were indicative of outbreaks of these coral-feeding starfish, while dislodged and overturned corals were considered indicative of storm damage. An analysis of AIMS LTMP data examined the effects of the acute disturbances (coral bleaching, CoTS, cyclones, coral disease, multiple, storms) on Coral Trout populations. Using AIMS LTMP fixed site surveys the analyses looked at change in Coral Trout abundance and biomass from before to after different disturbances. There was not adequate replication of each disturbance type in each of the eleven latitudinal sectors (see Figure 5) to enable a robust analysis of changes in each sector, so data was pooled to the GBR level for each disturbance type.

Changes in response variables were calculated as the difference between the year immediately preceding each individual disturbance event to the year following (i.e. highest to lowest). Changes were quantified using generalised linear mixed models in a Bayesian framework. Models were fitted separately for each of the response variables (Coral Trout abundance and Coral Trout biomass). Models had fixed terms of Time (before and after disturbance), Type of Disturbance, and Management Zone (open or closed to fishing). Random nested terms included Site and Transect nested within Reef. Coral Trout abundance was modelled against a zero-inflated negative binomial distribution with weakly informative priors, while Coral Trout biomass was modelled against a hurdle-gamma distribution with weakly informative priors.

4. Results

4.1(a) Experimental test of thermal preferences of Common Coral Trout (*Plectropomus leopardus*) in controlled, heterothermal environments

Fish in the thermal preference arena exhibited no signs of stress throughout the 2-4 d trial, with behaviours ranging from continuous, calm swimming (minutes-hours) to protracted stationary periods (minutes). Two of the four fish that were offered food in the thermal preference arena consumed the food, providing further evidence that fish were not overly stressed. Despite access to temperatures (in hides/ refuges) up to $\sim 31^{\circ}\text{C}$, and proven use of the refuges for transient periods, the fish chose not to warm themselves to their presumed optimum temperature of $\sim 27^{\circ}\text{C}$ (Figure 7). In fact, three of the ten fish maintained themselves at the ambient temperature of $17.5\text{--}20.5^{\circ}\text{C}$ for the entire trial and never spent any time with a thermal excess of $\geq 0.5^{\circ}\text{C}$ (Figure 7). Of the other seven fish, the thermal excess never exceeded 1.5°C , which represented a maximum body temperature of $\sim 21.5^{\circ}\text{C}$ (Figure 8). While there was some evidence of thermal detection and active behavioural thermoregulation in the present study (e.g., Figure 7B), the majority of fish began warming up at certain points but then moved away from the heat source (e.g., Figure 7F), suggesting that other motivations trumped thermoregulation.

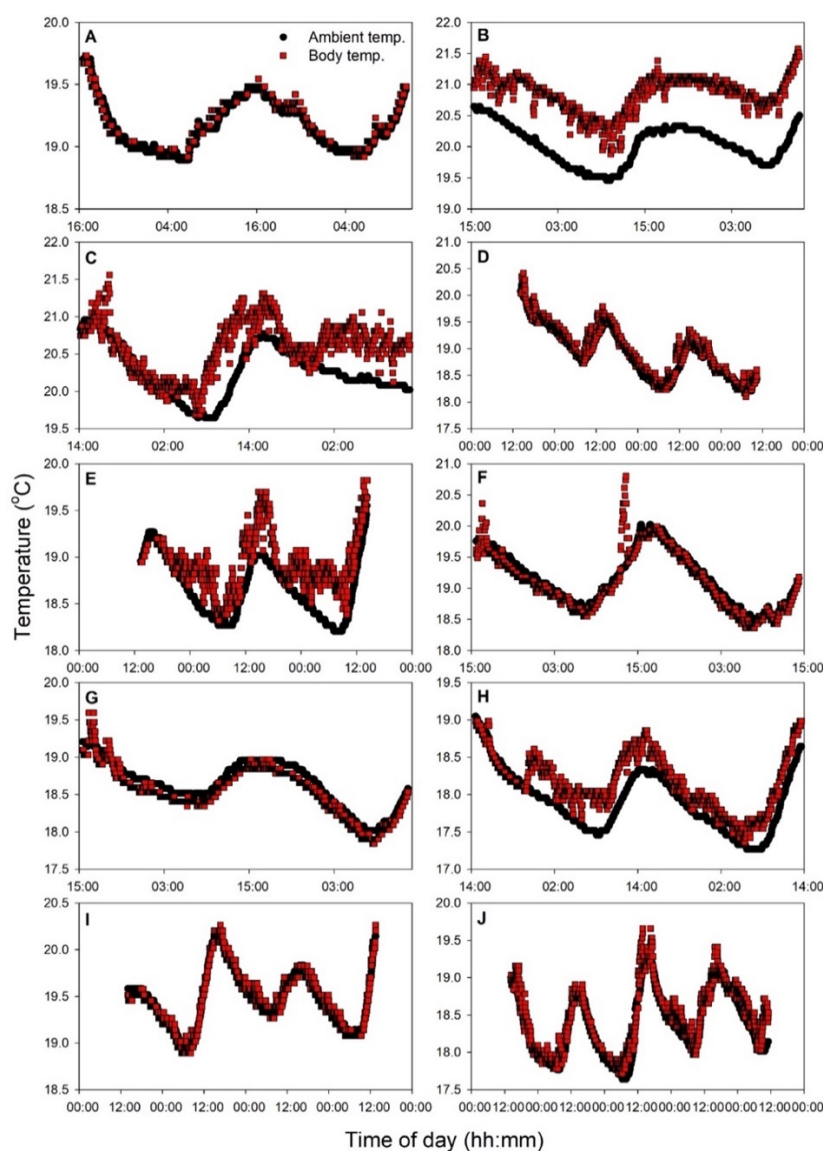


Figure 7. Ambient temperature of the thermal preference arena (black circles), which fluctuated due to daily temperature cycles, and corresponding body temperature (red squares) of individual Coral Trout. Each panel (A-J) shows data for a different fish ($n = 10$).

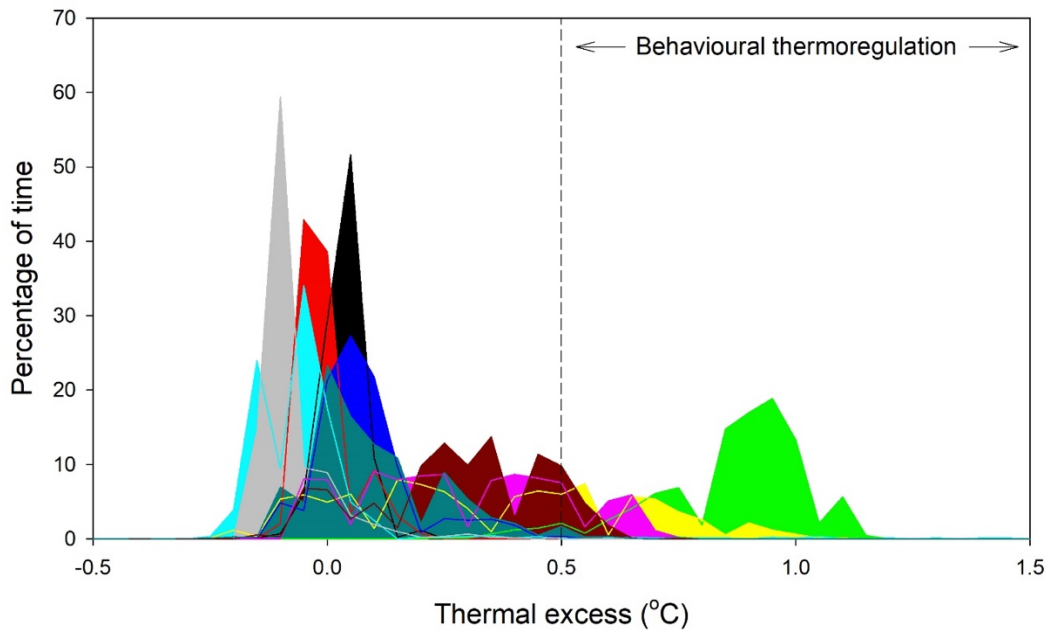


Figure 8. Frequency distribution of the thermal excess ($^{\circ}\text{C}$) of 10 different Coral Trout (different colours), calculated as the deviation in body temperature versus the ambient temperature of the thermal preference arena. Temperatures were measured every 3 min for 2-4 d, and the maximum possible thermal excess was $\sim 12^{\circ}\text{C}$.

4.1(b) Seasonal changes in depth distribution of commercially important fisheries species (including *P. leopardus*) corresponding with natural temperature gradients

A total of 165 BRUV deployments were undertaken at Linden Bank over five days in summer ($n=86$) and three days in winter ($n=79$) in 2017. The purpose of this study was to test for seasonal changes in the depth distribution of fishes (especially Coral Trout) associated with natural temperature gradients. However, temperature variability was minimal across the depth gradient examined (generally $<1^{\circ}\text{C}$). Notably, high summertime temperatures (29.5°C) were recorded to a depth of $>50\text{m}$, such that fishes would need to go below 60m to experience significant declines in temperature (Figure 9).

A total of 7381 (sum of MaxN) individual fishes, sharks and rays were identified, representing 356 species from 45 families. Species richness varied from 1-54 species per deployment. 122 species of fishes considered to be fisheries targets of the Queensland Line Fishery were observed on Linden Bank. Those included in the top 95% of Queensland catch data by weight were; *Plectropomus leopardus*, *Plectropomus laevis*, *Plectropomus areolatus*, *Variola albimarginata*, *Variola louti*, *Variola spp.*, *Lethrinus nebulosus*, *Lutjanus sebae*, *Caranx sexfasciatus*, *Caranx melampygus*, *Alectis indica*, *Carangoides spp.*, *Scomberomeros spp.*, *Lutjanus spp.*, *Choerodon spp.*, *Epinephelus spp.*, and *Siganus spp.*. Key shark species were also observed including; *Carcharhinus amblyrhynchos*, *Carcharhinus melanopterus*, *Galeocerdo cuvier*, *Triaenodon obesus*, *Sphyrna mokkaran*. These important fishery species were observed across all depths from 13-71 m and accounted for $\sim 27\%$ (1991 out of 7381) of all fishes observed. Overall, the relative abundance of all fisheries targeted species was fairly constant with depth across both sampling periods (Figure 10). However, for individual fisheries groups (*Plectropomus spp.*, Labrids, and Serranids) we documented higher relative abundances in shallower areas ($<40\text{ m}$), and fewer individuals at $>40\text{ m}$ depth (Figure 10). This decrease in relative abundance with depth was consistent between sampling periods.

The important fishery species were generally uncommon, but occurred across all depths from 10 to 70 m. For Coral Trout (*Plectropomus spp.*), there were seasonal differences in densities recorded in the shallow (10-19 m) and deepest ($>60\text{ m}$) reef habitats, though these did not conform with expectations that there would be greater abundance of mobile fishes at depth in summer versus winter. Rather, the highest densities of Coral Trout recorded at $>60\text{ m}$ depth occurred in winter, whereas the highest densities

recorded at 10-19 m depth occurred in summer. Overall, there was very limited evidence of seasonal differences in the depth distribution of fisheries target species (Figure 9).

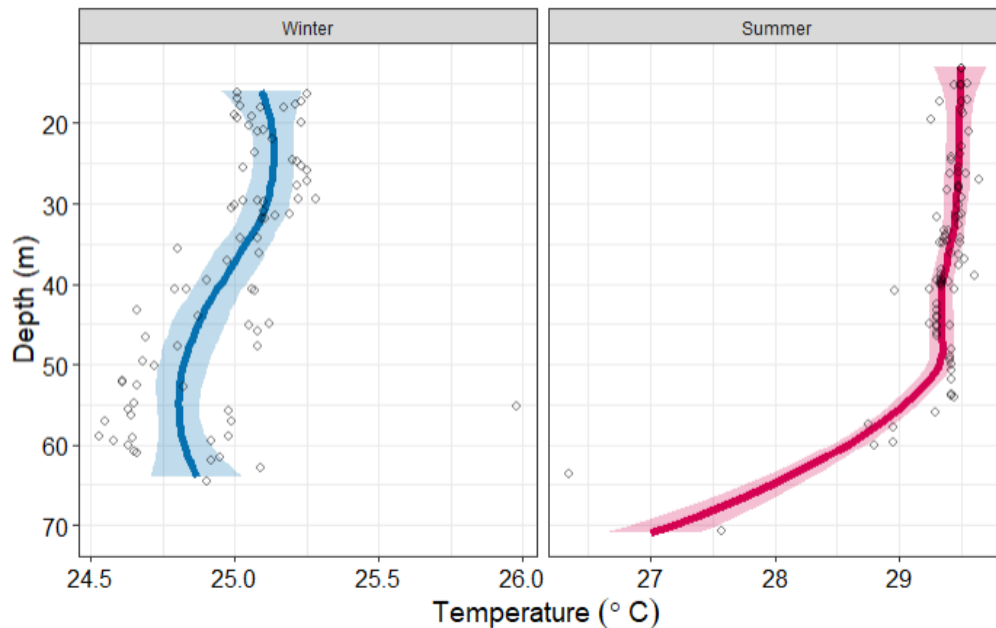


Figure 9. Depth variation in temperature (recorded using Vemco Minilog-II-T loggers attached to each BRUV) in summer (February) versus winter (August) at Linden Bank. Each point represents an average temperature recorded for each BRUV. The shaded ribbon represents the 95% confidence interval across each sampling period

While there was limited seasonal variation in depth distribution of fishes at Linden Bank, fish assemblages did vary significantly with depth. We found that shallow (13–30 m) areas were characterised by relatively higher abundances of typically reef-associated fishes (e.g. Acanthuridae, Chaetodontidae, Labridae, Pomacanthidae, and Pomacentridae), whereas the fish assemblage at greater depths (i.e. below 30 m) were dominated by species from Balistidae, Carangidae, Lethrinidae and Mullidae (Scott et al. 2022). Depth-related variation in the structure of fish assemblages is largely attributable to changes in the dominant habitat type; coral dominated reefs were the most prevalent habitat in shallow areas (< 32 m) and the associated fish assemblage tended to be comprised of smaller-bodied reef-associated fishes. Lower complexity, open sand or algal meadows and seawhip gardens dominated habitats in the upper-mesophotic zone (50–70 m) and were typified by mobile piscivores, and invertivores, as in previous studies (Asher et al. 2017; Williams et al. 2019).

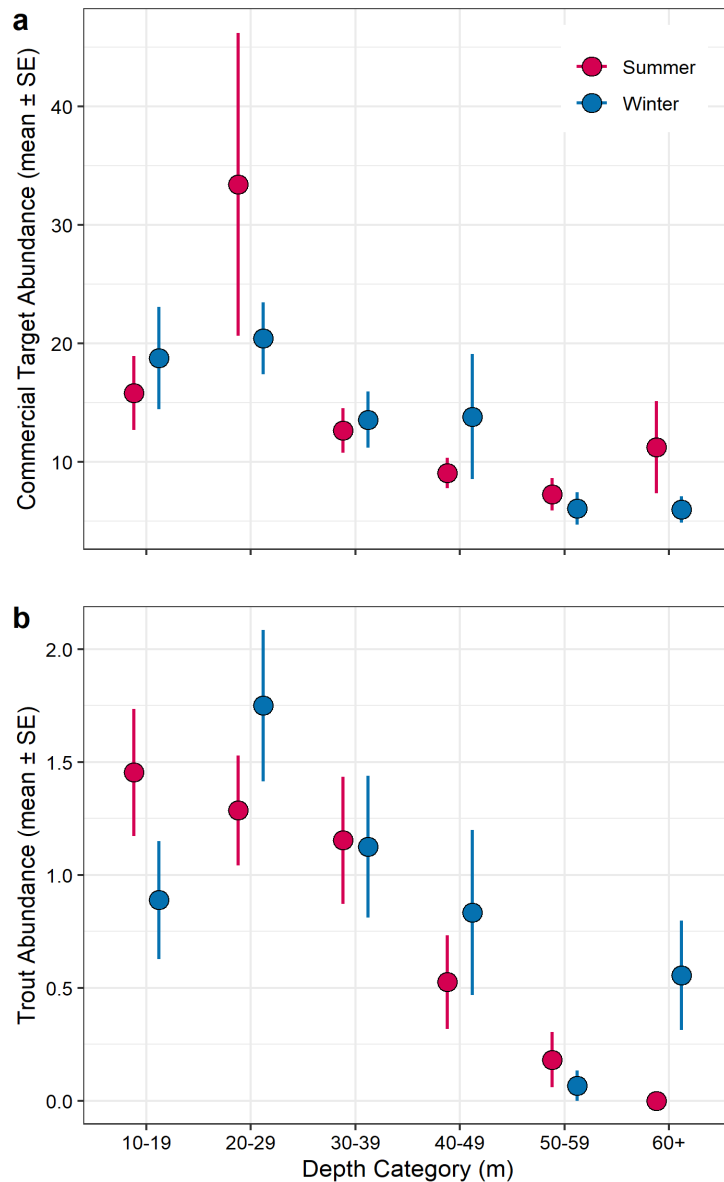


Figure 10. The mean (\pm SE) abundance of a) the top 95% commercial fisheries target species groups (Lethrinids, Carangids, Serranids, Siganids, Labrids) and b) Coral Trout only (*Plectropomus leopardus*, *Plectropomus laevis*, *Plectropomus areolatus*) by depth (pooled to 10-m depth classes).

4.1(c) Latitudinal variation in activity patterns of *P. leopardus*

Tagged *P. leopardus* ranged in size from 336-565 mm (average FL \pm SE = 431 \pm 13, n=18) at Opal Reef, and from 401-634 mm (average FL \pm SE = 543 \pm 13.20, n=18) at Heron Island. Although size structure differed between locations, the size of fish had no significant effect on core space use (50%KUD) or home range extent (95%KUD). Mean monthly residency indices varied between 0.7-1.0 (mean \pm SE = 0.87 \pm 0.01, n=36) indicating that *P. leopardus* were within range of the receivers approximately 87% of the detection period.

At Opal Reef (low-latitude location), monthly home range extent (95%KUD) was substantially different between summer and winter, though core use areas (50%KUD) did not differ throughout the year. Notably 95%KUD ranges contracted considerably between October 2015-April 2016 at Opal Reef, corresponding with higher (summer) temperatures (Figure 11). At Heron Island (high-latitude location), there was substantial variation in range use among individuals, but no significant variation in home range extent (95%KUD) or core use areas (50%KUD) throughout the year. The home range extent (95%KUD) of *P. leopardus* at Heron Island was higher at the peak of winter, but high variability in monthly space use masked any seasonal variation and temperature-dependent patterns in space use (Figure 11).

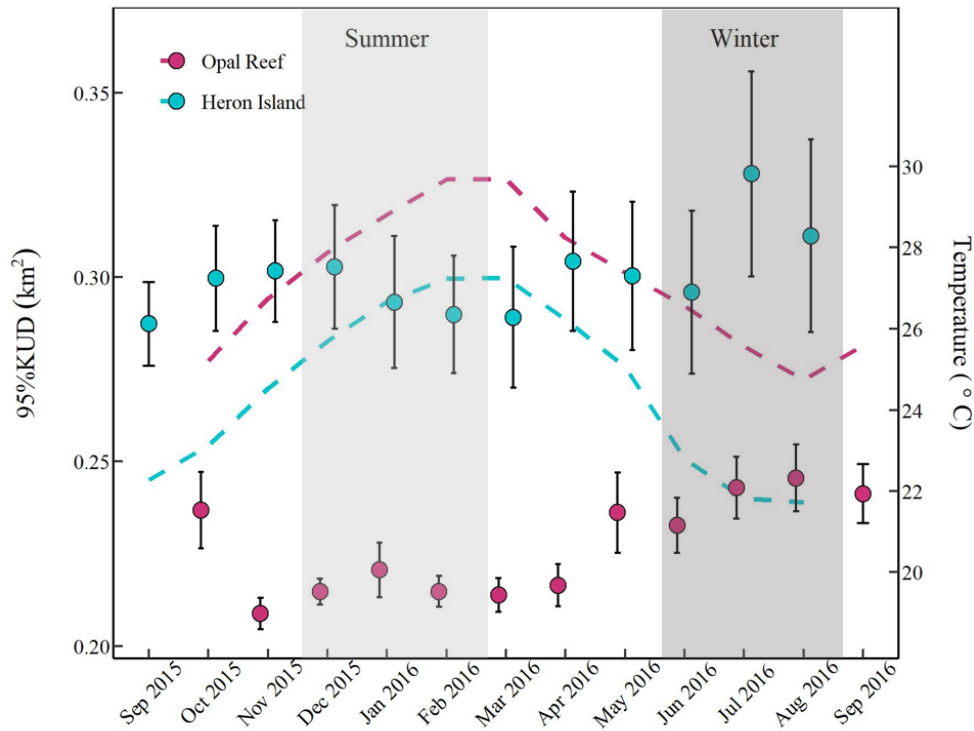


Figure 11. Mean (\pm SE) monthly 95% KUDs for Opal Reef (red) and Heron Island (blue) populations. Shaded regions represent summer (light-grey) and winter (dark-grey); dashed line colours represent the average monthly temperatures at each location. Annual maximum water temperatures over the course of the study differed by approximately 2.5°C, ranging from 19.9-27.4 °C at Heron Island (mean \pm SE = 24.5°C \pm 0.005), and 23.1-30.1°C at Opal Reef (mean \pm SE = 27.4°C \pm 0.003).

Average home range extent (95%KUD) for *P. leopardus* was substantially higher at Heron Island (0.32 km²), compared to at Opal Reef (0.23 km²). Taken together with seasonal variation, space use for *P. leopardus* appears to decline with increasing temperatures; Core space use (50%KUD) decreased from 0.13km² at 21°C to 0.02km² at 29.9°C, whilst home range extent (95%KUD) decreased from 0.49km² at 21°C to 0.19km² at 29.9°C (Figure 12).

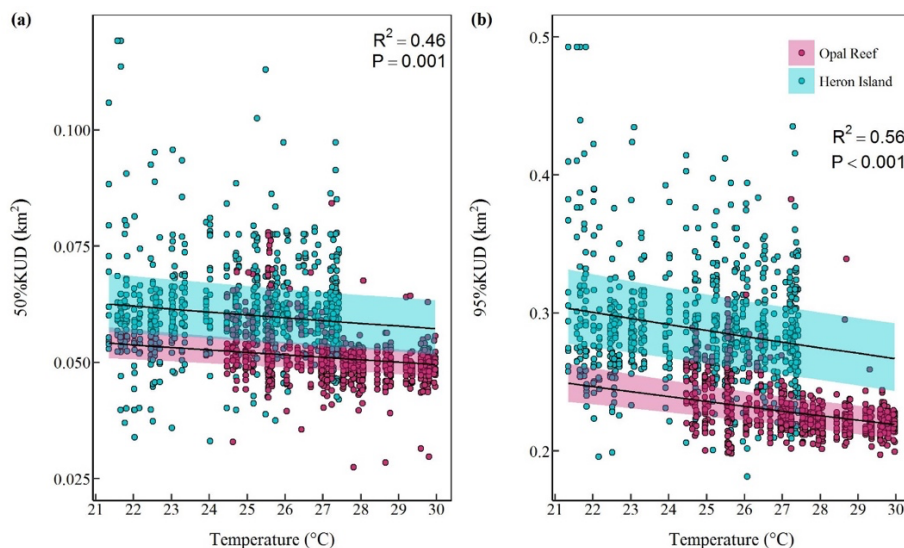


Figure 12. Plot of modelled values showing the influence of spatial and temporal variation in ambient temperature on a) core use (50%KUD) and b) home range extent (95%KUD) for Opal Reef (red) and Heron Island (blue).

Variation in space use of *P. leopardus* between the two locations (Opal Reef and Heron Island) were further reflected in the way that these fish partition their energy through alternative levels of activity at night

versus during the day (Figure 13). At Opal Reef (low-latitude), *P. leopardus* exhibited greater variation in activity levels between day (0600-1800) versus night (1800-0600), whereas activity levels were fairly constant between night and day at Heron Island (high-latitude). At both locations, burst swimming (which is most likely to occur when foraging) increased with increasing temperature, but the occurrence of burst swimming was higher during the day at Opal Reef compared with Heron Island. If these heightened levels of activity correspond with feeding, *P. leopardus* from Opal appear to forage more during the day than individuals at Heron, but then at night spend the majority of their time (> 80%) resting.

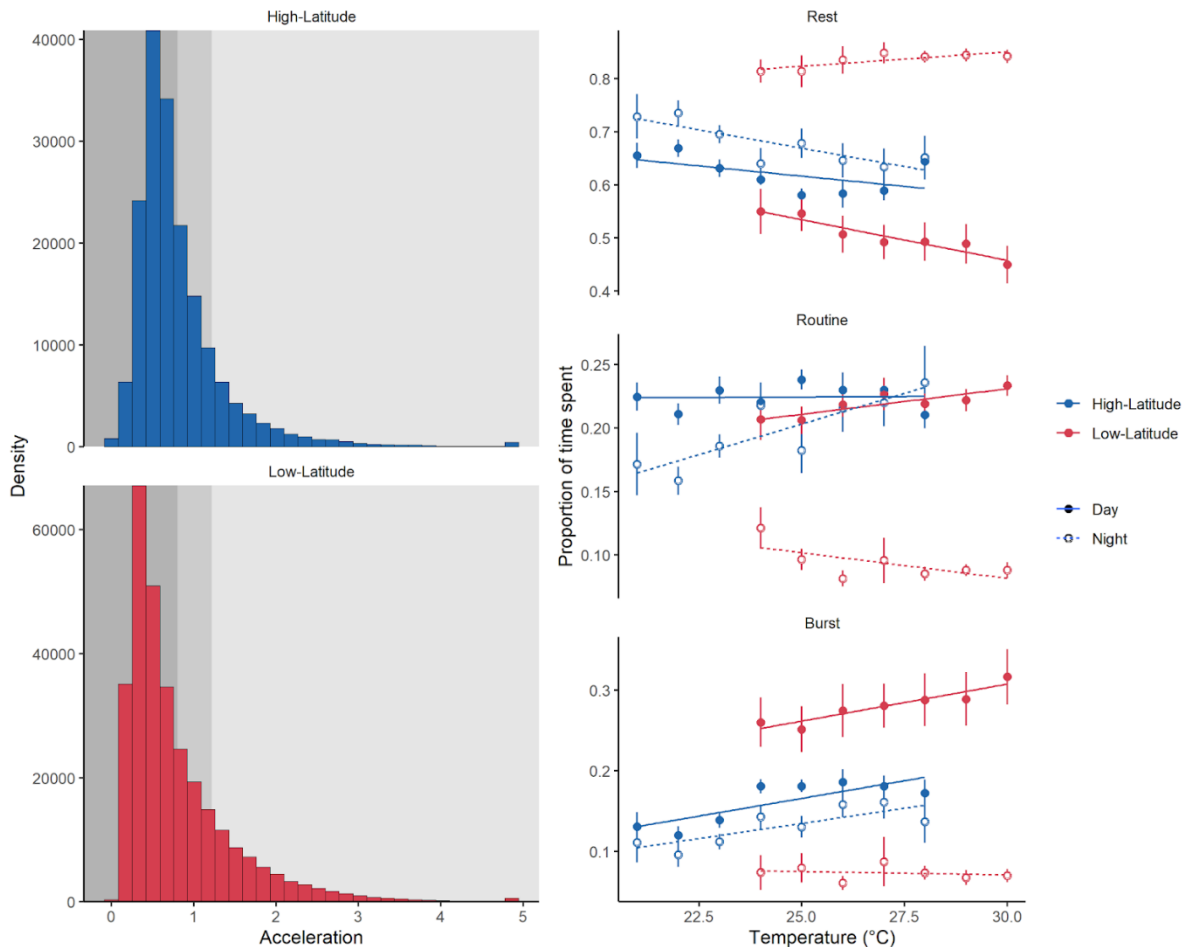


Figure 13. Histograms of raw activity data showing the relative frequency of movements for wild *P. leopardus* at Heron (high-latitude; blue) and Opal (low-latitude; red), corresponding with resting (dark grey), routine swimming (grey) and burst activity (light grey). Also shown are diurnal changes (day: 0600-1800 and night: 1800-0600) in levels of activity across the range of temperatures experienced in their environment (i.e. Heron Island 21 - 28°C and Opal Reef 24 - 30°C).

4.2(a) Variation in abundance and biomass of *P. leopardus* in the aftermath of mass-bleaching on the GBR

In situ transect-based visual surveys (n=492 transects) recording all conspicuous fish species (especially Coral Trout) as well as accounting for habitat condition (especially coral cover and complexity) were conducted at a total of 73 sites across 35 different reefs. Repeat surveys (in 2020 and 2021) were conducted at a limited number of reefs (Day, Escape, and Yamacutta) though the majority of reefs (and sites) were surveyed only once in 2019, 2020, 2021 or 2022.

Average cover of hard (order Scleractinia) corals was 24.16% (± 0.78 SE) across all zones, sites and reefs, but varied markedly among reefs (Figure 14; see also Figure 5). Average coral cover was low (<10%) on a number of reefs in both the northern (including U/N Reef 13-077, Ribbon Reef 10, Agincourt) and southern GBR (e.g., Abraham Reef and Hixson Reef). Reefs with low coral cover in the northern GBR were intentionally selected due to severe impacts of marine heatwaves in 2016 and 2017, such that coral

depletion was largely caused by high mortality following extensive bleaching. Coral cover was generally low (<20%) across most reefs surveyed in the northern and far northern section (Figure 14), reflecting widespread and pervasive effects of recent bleaching (Hughes et al. 2017). There were however, differences in the extent of coral mortality and rates of recovery post-bleaching, such that there were occasional reefs (e.g., Creech Reef and Escape Reef) in the northern GBR with coral cover >30%. Moreover, average coral cover increased on reefs that were surveyed in successive years (2020-2021) in the northern GBR, at Day Reef (12.16% to 17.58%) at Escape Reef (34.8% to 38.0%). In the southern reefs (e.g., Abraham Reef and Hixson Reef), very low coral cover (<10%) was due to significant and ongoing outbreaks of CoTS. These CoTS outbreaks were however, largely restricted to the reefs in the south-east section of the Swains, and mean coral cover was otherwise high (up to 48.33% \pm 3.53 SE at Jupiter Reef) at reefs in the central and southern GBR (Figure 14). In all, average reef-level coral cover ranged from 3.00-48.33%, and varied both within and among regions, providing a good opportunity to test whether the abundance and/ or biomass of Coral Trout varies with respect to coral cover and habitat condition.

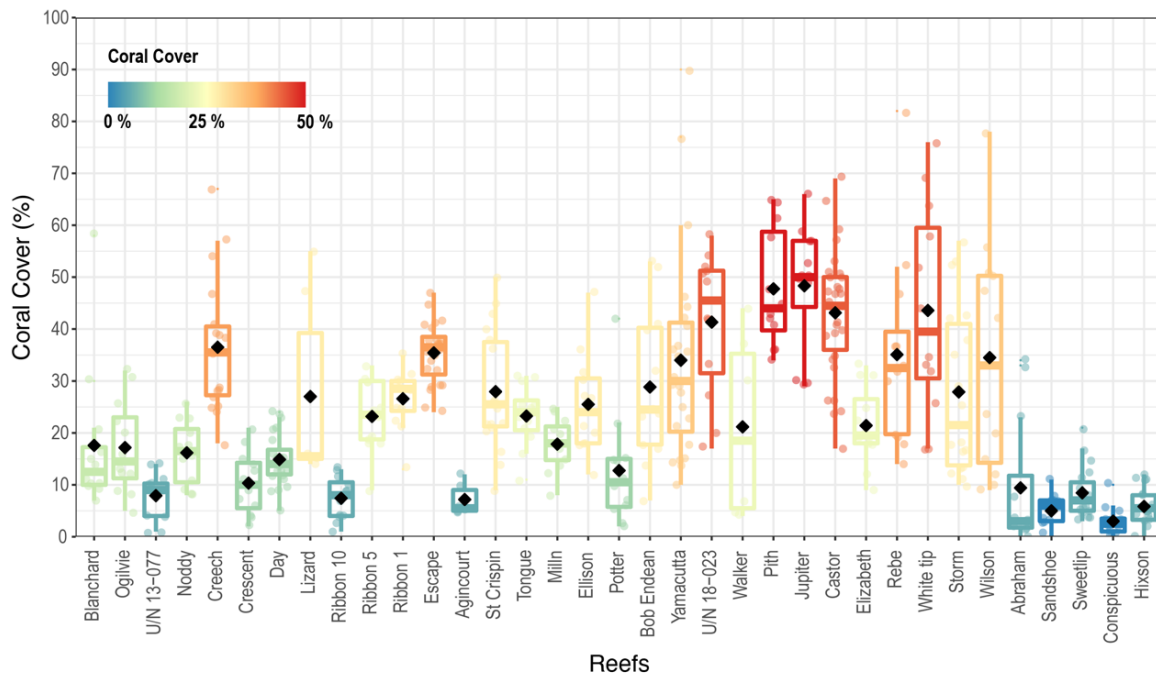


Figure 14. Box-plot inter-reef variation in cover (5) of hard (order Scleractinia) corals. Lowest coral cover (where average coral cover was <10%) was recorded at reefs in both the northern and southern GBR, though causes of coral depletion were very different (bleaching versus CoTS) between these regions.

A total of 488 Coral Trout were recorded during surveys conducted in 2019-2022. Counts were overwhelmingly dominated (87.1%) by *P. leopardus* (n=425), with only limited numbers of *P. laevis* (n = 61), *P. maculatus* (n = 1) and *P. aereolatus* (n = 1) recorded on transects. All subsequent analysis only included data for *P. leopardus*. The overarching density of *P. leopardus* was 0.91 (\pm 0.06 SE) fish per 250m², but varied greatly between depth zones, sites and reefs (Figure 16). Higher densities of *P. leopardus* (1.17 fish per 250m²) were recorded on the reef slope compared to the reef crest (0.66 fish per 250m²). Densities of *P. leopardus* recorded at individual reefs ranged from 0.0 fish per 250m² (where no Common Coral Trout were recorded on transects at either Milln, Pith, or Bob Endean Reefs, up to 3.58 (\pm 0.85 SE) fish per 250m² at Wilson Reef (Figure 15) located in the southern (Swains) section of GBR (see Figure 5). Inter-reef variation in densities corresponded closely with inter-reef variation in the biomass of Common Coral Trout (*P. leopardus*), showing that biomass recorded was largely influenced by densities of Coral Trout. The biomass of Coral Trout recorded at reefs in the southern GBR, was however, disproportionate to density (Figure 16), reflecting the generally larger size of Coral Trout recorded at these reefs.

Density and biomass of Common Coral Trout (*P. leopardus*) were generally higher on reefs in the southern GBR, regardless of hard coral cover recorded across the reefs surveyed (Figure 16). Notably, reefs in the southern-most section of the Swains (e.g., Conspicuous and Sandshoe Reefs) had the lowest hard coral cover, but highest biomass of Common Coral Trout. Also, in the northern GBR, reefs with low coral cover

(<10%: U/N Reef 13-077) did not have noticeably lower density or biomass of Common Coral Trout compared to comparable reefs with higher coral cover.

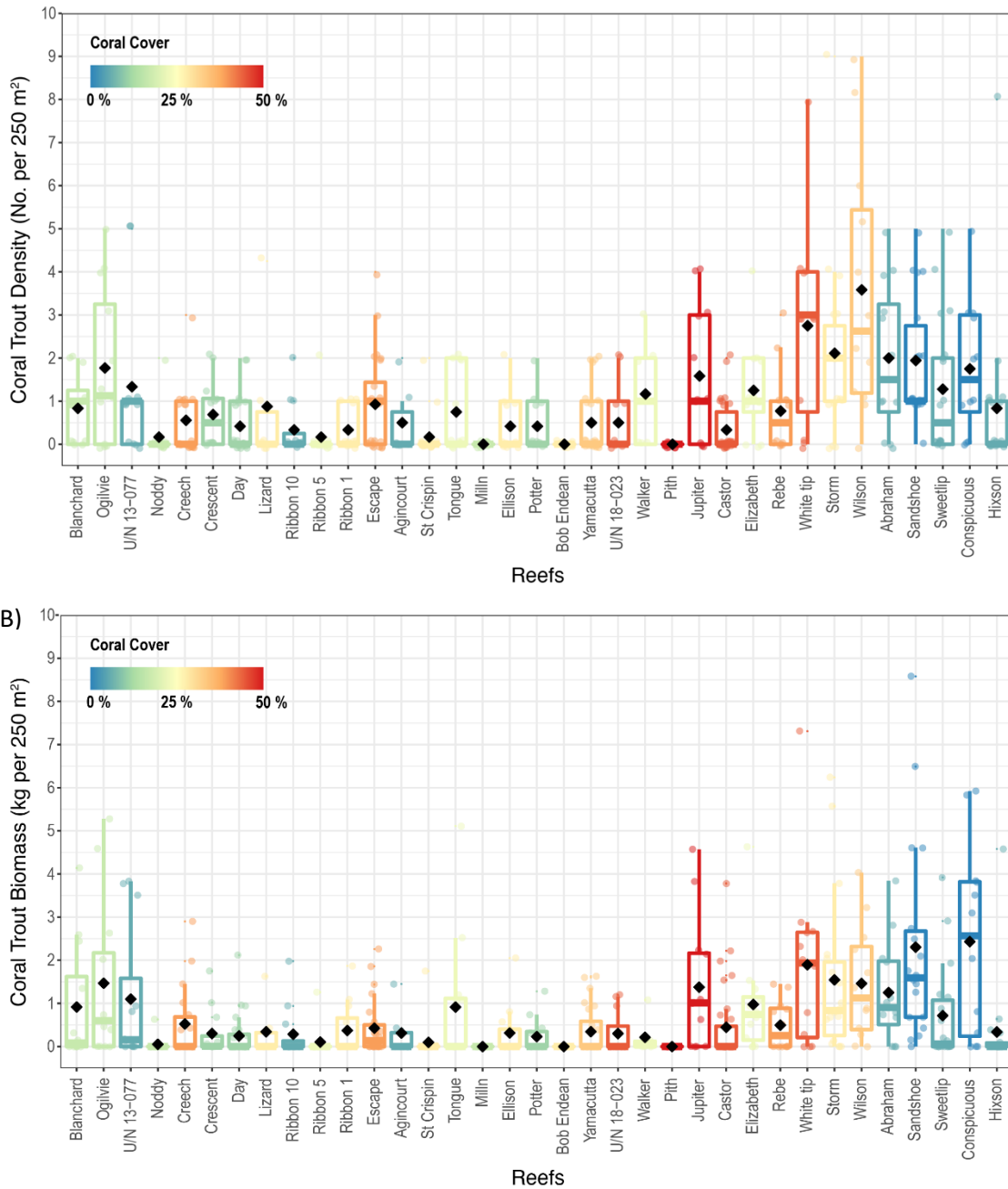


Figure 15. Box-plot of A) density and B) biomass for Common Coral Trout (*P. leopardus*), showing inter-reef variation among reefs surveyed along the GBR (2019-2022). Reefs are ordered according to latitude (see Figure 6) and box-plots for each reef are colour coded according to hard coral cover (see Figure 15).

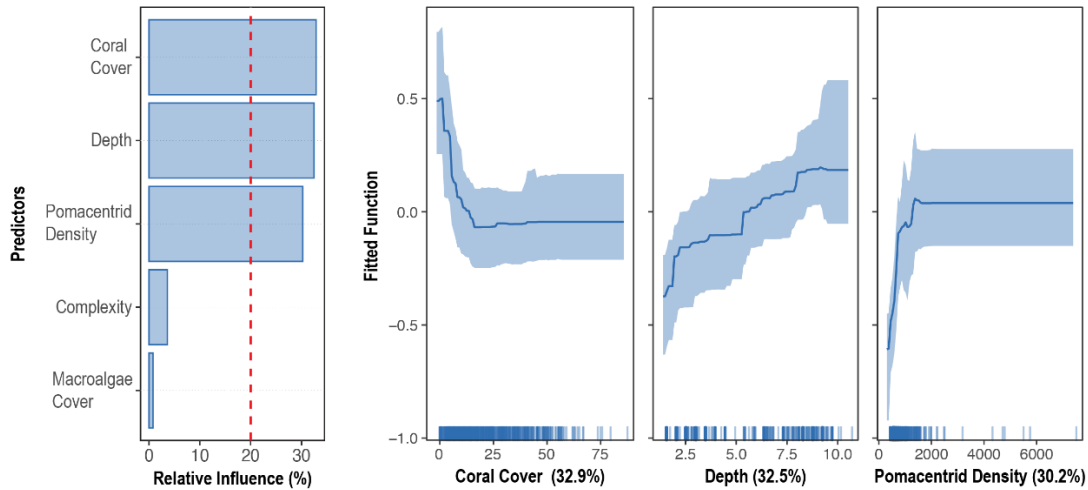
Boosted regression tree models used to relate variation in wild stocks of Common Coral Trout to spatiotemporal variation in habitat condition in the aftermath of mass bleaching on the GBR, revealed that variation in both i) density and ii) biomass were influenced by hard coral cover, but also varied with depth, habitat complexity, macroalgae cover and densities of pomacentrids (or damselfishes). These habitat variables collectively explained 17.04% of variation densities of *P. leopardus* and 24.37% of variation in biomass (Table 2), and the most influential variables were hard coral cover, depth and pomacentrid densities (Figure 16).

Table 2. Parameters of final boosted regression tree model for each response variable.

Response	Coral Trout density /250m ²	Coral Trout biomass /250m ²
Predictors	Hard coral cover, depth, pomacentrid density, complexity, macroalgae cover	Hard coral cover, pomacentrid density, depth, complexity, macroalgae cover
Distribution family	Poisson	Laplace
Learning rate	0.001	0.001
Tree complexity	3	3
Bag fraction	0.75	0.75
Optimal no. trees	1750	1000
Final no. variables	5	5
% cv explained	7.26	22.21
% explained	17.04	24.37
Residual deviance	1.55	0.65

While density and biomass of Common Coral Trout were shown to vary with respect to hard coral cover, the relationship was negative and varied mostly over low levels of coral cover (0-20%); density and biomass of Common Coral Trout were largely invariant with changes in coral cover from 20-80% (Figure 17). There was however, much greater variation in recorded biomass of *P. leopardus* at reefs with >50% coral cover compared to <50% coral cover (Figure 17). Similarly, variation in the density and biomass of Coral Trout was influenced by inter-reef variation in density of damselfishes (Pomacentridae), but only when there were very limited densities of these potential prey fishes. Depth appeared to have the most consistent and important influence, whereby both density and biomass of these fish increased with respect to the survey depth (Figure 17). There was minimal influence of either habitat complexity, nor the local cover of macroalgae, on recorded densities and biomass of *P. leopardus*.

(A) Coral Trout Density



(B) Coral Trout Biomass

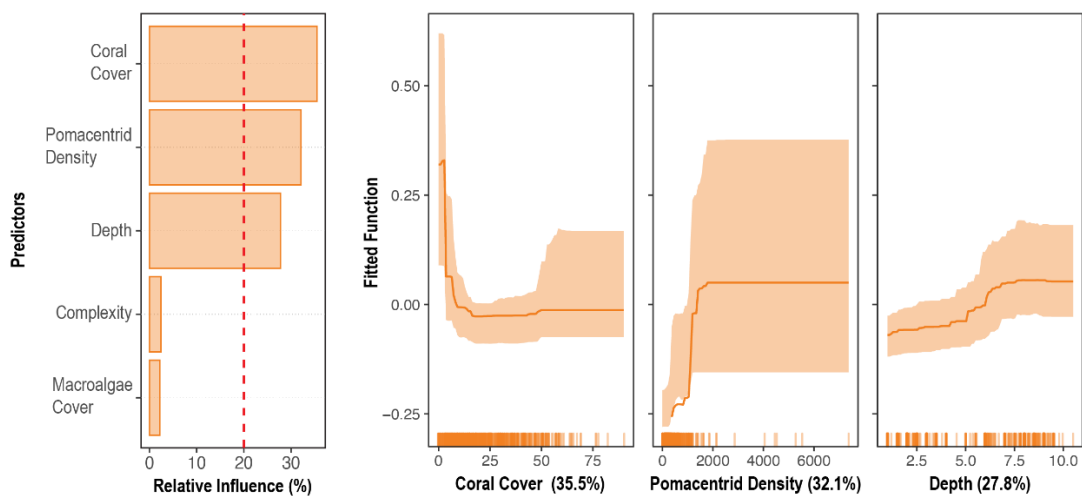


Figure 16. Variation in A) density and B) biomass for Common Coral Trout (*P. leopardus*) with coral cover, pomacentrid density and depth (which were the most influential variables), analysed using boosted regression trees.

4.2(b) Variation in diet and condition of *P. leopardus* in the aftermath of mass-bleaching on the GBR

A total of 418 Coral Trout (*Plectropomus* spp.), mostly *P. leopardus* ($n=407$) as well as small numbers of Passionfruit Coral Trout (*Plectropomus aereolatus*), *P. laevis*, and *P. maculatus*, were collected across 24 reefs on the GBR in summer (February-March) 2020 and 2021. Only *P. leopardus* were used in subsequent analyses and ranged in size from 110-781 mm (FL). The mean size and body mass of *P. leopardus* were 370 mm FL (± 4.7 SE) and 889 g (± 35.8 SE), respectively. Examination of the stomach contents for a subset of *P. leopardus* caught ($n = 225$), revealed that most were empty (67.1%) or unidentifiable (17.8%). For those fish with identifiable prey items in the stomach contents (34 out of 225 fish), most had consumed reef fishes (73.5%), and predominantly damselfishes (Pomacentridae) or wrasses (Labridae). Only 11.7% (4 out of 34 fish) had consumed pelagic prey fishes (Atherinidae and Engraulididae), while 14.7% had consumed invertebrate prey (mostly squid). These data reaffirm that Common Coral Trout predominantly feed on coral reef fishes (see Kingsford, 1992), though these data are biased towards fishes consumed during the day (within hours of capture) and may be confounded by differences in digestion, whereby reef fishes identified in the stomach contents were much larger than the pelagic fishes.

Stable isotope analyses revealed substantial inter-reef variation in the diet of *P. leopardus*. Average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for all *P. leopardus* sampled ($n=407$) were 10.52 and -14.85, respectively, but ranged from 9.08 to

11.71 and -16.33 to -12.77, among reefs. High variability in isotopic signals of *Plectropomus* spp. have been reported previously, even within a single reef (Matley et al. 2016a; Hempson et al. 2017), which is attributed to high levels of dietary flexibility and size-based differences in foraging behaviour. Inter-reef differences in stable isotope signatures may however, reveal systematic differences in the trophic structure and predominant prey types. Notably, there was a significant relationship between average coral cover and $\delta^{15}\text{N}$ ($R^2 = 0.213$, $F_{1,393} = 107.5$, $p < 0.001$), with a 0.025-unit increase in reported $\delta^{15}\text{N}$ for every unit increase in average coral cover. This suggests that *P. leopardus* are feeding at relatively lower trophic levels on reefs with low coral cover (see also Hempson et al. 2017), which may be attributable to trophic simplification in more degraded habitats, *sensu* Dobson et al. (2006). There was also significant relationship between average coral cover and $\delta^{13}\text{C}$ ($R^2 = 0.222$, $F_{1,393} = 113.4$, $p < 0.001$), with a -0.04 -unit increase in reported $\delta^{13}\text{C}$ for every unit increase in average coral cover. This infers that *P. leopardus* change their diet, increasingly feed on prey with more enriched $\delta^{13}\text{C}$ signatures, in more degraded habitats. On coral reefs, enriched sources of $\delta^{13}\text{C}$ are mostly considered to be of benthic origin (Fry et al. 1982, but see Fry et al. 1991), suggesting that there is increased reliance on reef-associated prey in degraded habitats. However, this may also reflect a shift in diet from planktivorous to benthic-feeding damselfishes (see Hempson et al. 2017).

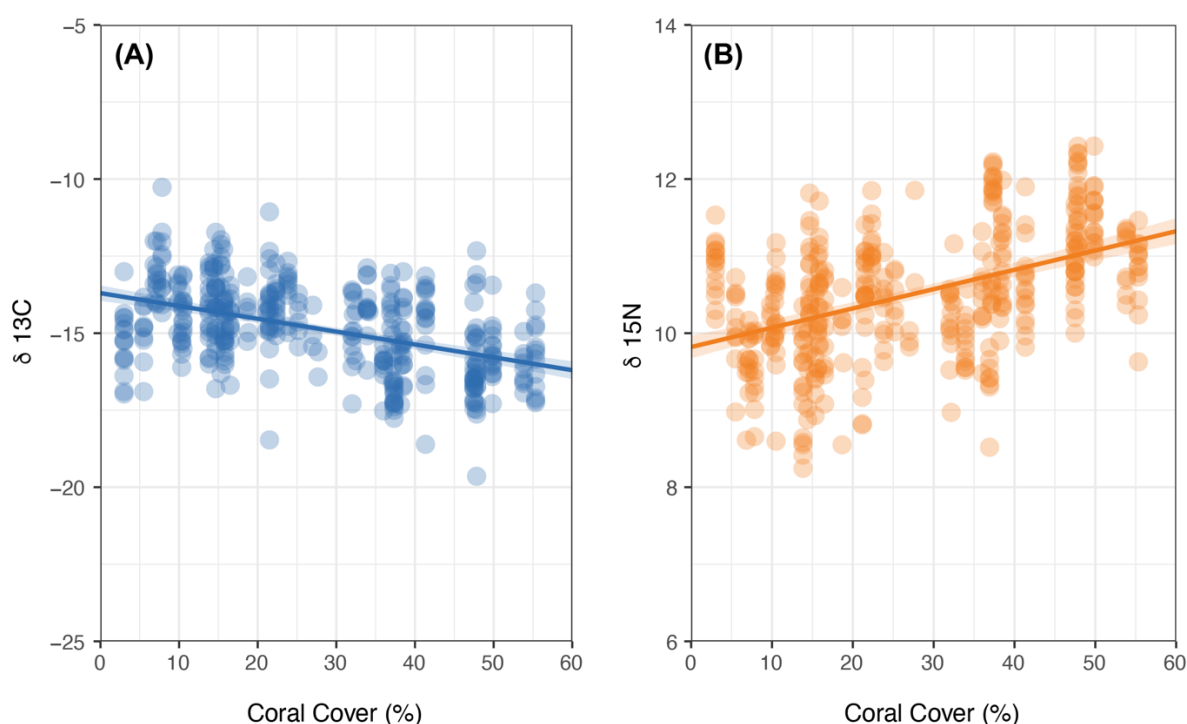


Figure 17. Variation in stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) signatures from muscle tissue of *Plectropomus leopardus* ($n=407$) relative to hard coral cover at sites where fish were caught.

Physiological condition of *P. leopardus*, inferred using hepatocyte vacuolation (HV), varied among individual fish, mostly in accordance with their size. Average HV recorded across all *P. leopardus* ($n=407$) was 3.98% (± 0.17 SE), and ranged from 0.0% to 23.89%. Condition (HV) was generally higher, but also more variable, among larger fishes; for fish that were $<200\text{mm}$ (TL) the average HV was 2.43% (0.53-7.36%), compared to 3.79% (0.00-23.89%) for fishes 200-400mm (TL) and 4.50% (0.00-18.24%) for fishes $>400\text{mm}$ (TL). Condition (HV) also varied spatially (e.g., among reefs) but did not relate to local coral cover. Overall, the best model to account for variation HV among *P. leopardus* included size of fish, though this model was not significantly better (AIC difference < 2) than models that included size and age, but also latitude of sampling locations (Table 3). Notably, average HV of *P. leopardus* was lowest on reefs in the northern GBR and tended to increase with increasing latitude, though average HV was also low at reefs in the southern GBR where coral cover had been depleted due to CoTS.

Physiological condition was also measured using bioelectrical impedance analysis (BIA) for a subset of *P. leopardus* ($n=233$) sampled in 2021. Average phase angle (PA) was 29.64° (± 0.22 SE), and ranged from

13.20-37.60°. The best model to explain individual variation in BIA included size and latitude of sampling locations (Table 3). However, spatial variation in BIA (among sites and reefs) did not correspond with local coral cover (Figure 18).

Table 3. Linear model selection results for (a) bioelectrical impedance analysis, BIA and (b) hepatocyte vacuolation, HV, predicted as a function of ‘Latitude’ (Reef), ‘Size’ (SL) and ‘Age’ and their interaction effects.

Model	df	LL	AIC	wAIC	Adj R ²
(a) log [HV+1]					
~ Size	3	-251.390	508.8	0.181	0.013
~ Size+ Age	4	-250.492	509.0	0.164	0.021
~ Latitude + Size + Age	5	-249.688	509.4	0.135	0.026
~ 1	2	-252.690	509.4	0.134	0.000
(b) BIA					
~ Latitude + Size	4	-548.556	1105.1	0.651	0.403
~ Latitude + Size + Age	5	-548.515	1107.0	0.249	0.403
~ Latitude + Size * Age	6	-548.429	1108.9	0.100	0.404
~ 1	2	-606.725	1217.4	0.000	0.000

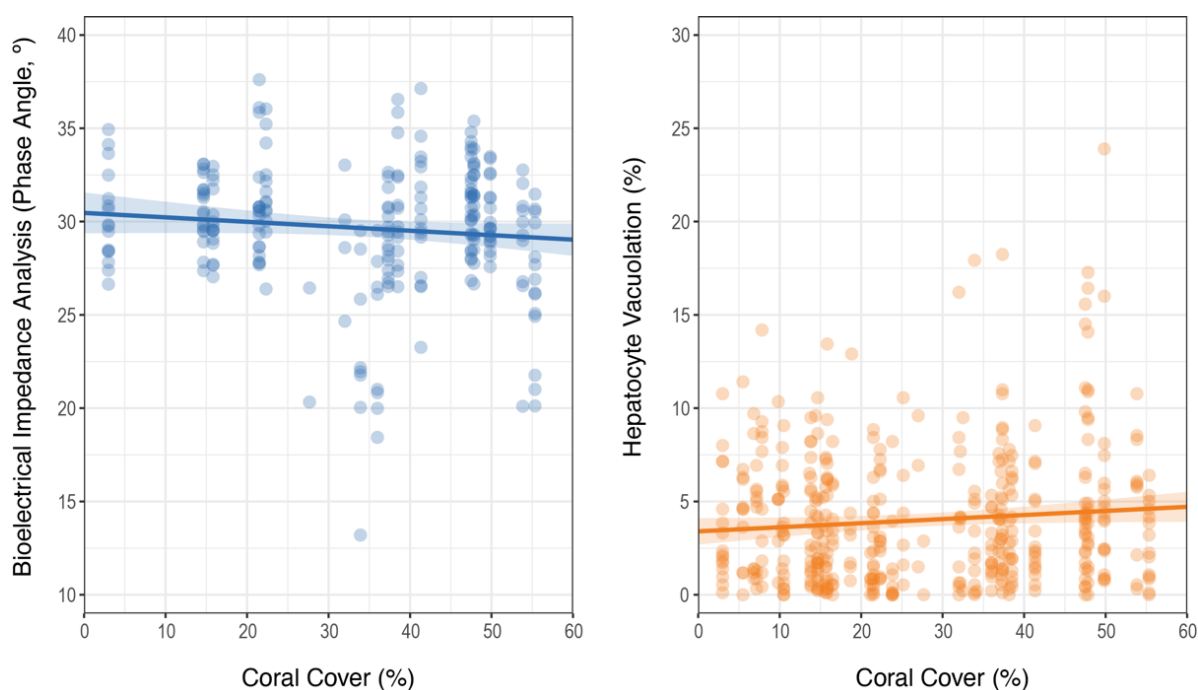


Figure 18. Variation in physiological condition, measured using A) bioelectrical impedance analysis (n = 233) and B) hepatocyte vacuolation (n=407) for *P. leopardus* relative to hard coral cover at sites where fish were caught.

While BIA measures different aspects of individual condition (overall impedance between fat and fat-free; Cox and Hartman 2005) relative to hepatocyte vacuolation (liver lipid stores), there was a positive, but very weak relationship between these two independent measures of physiological condition (Figure 19). Notably, there was considerable variation in BIA measurements of fishes with low HV. BIA of *P. leopardus* was however, significantly and positively correlated with Fulton’s K (a morphometric measure of overall body condition), though the relationship was very noisy (Figure 19).

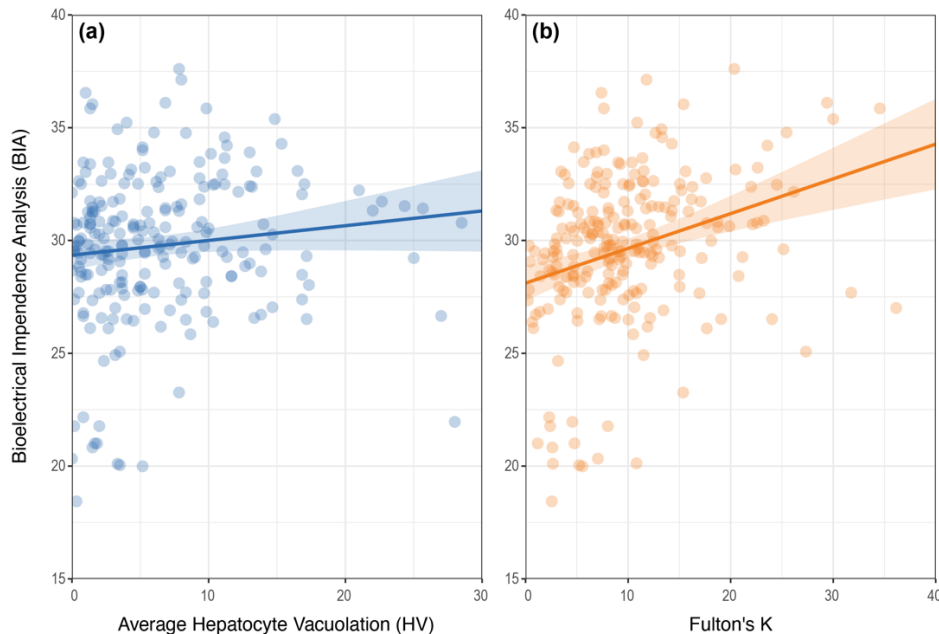


Figure 19. Variation in stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) signatures from muscle tissue of Common Coral Trout ($n = 407$) relative to hard coral cover at sites where fish were caught.

4.3(a) Relate spatiotemporal variation in reported catches of Coral Trout (based on commercial and charter logbook data) to habitat condition across the GBR

Our fishery-related conclusions are based mainly on the commercial fishery logbook and AIMS manta-tow data sources, as these contained the most data and were believed to produce the most precise estimates of Coral Trout abundance and coral cover. The charter fishery logbook and AIMS underwater visual survey databases contained lesser amounts of data and appeared to provide less precise results. Also, the charter fishery appeared to operate in water of greater depth than the depths associated with all the other data sets. Results from the charter fishery and underwater visual surveys were in broad agreement with the commercial logbook and manta-tow results, although the effects were less clear due to the lesser quantity of data.

There was no clear relationship between standardised catch rates for Coral Trout abundance and changes in coral cover (Figures 20-28), especially in the aftermath of severe marine heatwaves. Coral Trout abundance and coral cover both have strong relationships with major tropical cyclones. Coral cover also has a strong relationship with outbreaks of CoTS. Standardised catches of Coral Trout sometimes follows the same relationship with CoTS, but often catch rates appear to suppressed low even during the early onset of CoTS outbreak (when apparent impacts on coral cover are still minimal), and does not fall further during the CoTS outbreak (Figure 22). The strongest relationship between Coral Trout abundance and a CoTS outbreak was in the Swains region from 1988-2004 (Figure 27). During this period there were sustained declines in both standardised catches of Coral Trout catch rates in the commercial fishery and hard coral cover. Catch rates trended upwards when the outbreak ended, then were affected by major tropical cyclones for some years. They have trended up strongly in recent years (Figure 27).

Cyclones do not appear to have long-term negative effects, as catch rates and coral cover recover strongly within a few years (e.g., Figure 23), sometimes even in the presence of a CoTS outbreak (Figure 26). Obviously, it would be a major negative effect if a sequence of cyclones were ever strong enough to break the integrity of the outer “barrier” reefs which protect the GBR from cyclones coming from most directions. There is no evidence that such a break has happened to date, judging by the observation that most tropical cyclones, even severe ones, have little or no noticeable effect on Coral Trout catch rates and do not produce exceptionally large waves inside the GBR.

The most important tropical cyclones since the fishery logbook system began in 1988 are

- Cyclone Justin, 1997
- Cyclone Hamish, 2009
- Cyclone Ului, 2010
- Cyclone Yasi, 2011
- Cyclone Dylan, 2014.

Since 2014, the most important cyclone has been Debbie in 2017, whose waves, although of similar height to the above cyclones, had a shorter period. Debbie may have affected fishery catch rates in 2018, which were generally high in 2017 but fell in 2018.

Damage from cyclones generally occurs between Townsville and the southern end of the GBR. Although cyclones are common north of Townsville, the lack of long inshore fetches means that they do not produce waves of the sizes that damage the coral further south.

The Capricorn–Bunker region is not protected by barrier reefs and has little underlying complexity once surface coral is removed. It is less affected by either cyclones or CoTS than the other southern GBR regions.

In the Townsville region, coral cover had a strong relationship with CoTS during two CoTS outbreaks (1985–1991 and 2000–2007), and was greatly affected by Cyclone Yasi in 2011–2012 (see Figure 21). Judging from catch rates after 2015, the commercial Coral Trout catch rate in Townsville region may have fallen during the first outbreak. For unknown reasons it didn't rise much after 1991, then was affected by Cyclone Justin in 1997: it appears to have been already low during the second CoTS outbreak (2000–2007), and didn't fall further during the outbreak. The Coral Trout catch rate was then affected by cyclones for several years, and recovered strongly after 2015.

Similarly, in the Storm Cay Inner region, coral cover has been affected by the combination of a CoTS outbreak (2004–2014) and Cyclones Justin (1997), Hamish (2009), Ului (2010) and Yasi (2011) (see Figure 22). The commercial Coral Trout catch rate fell for unknown reasons prior to the CoTS outbreak and stayed low during the outbreak and cyclones. It recovered strongly after 2015.

In view of the results, it was not feasible either to adjust the DAF Coral Trout stock assessment model for long-term environmental change, or to define future scenarios that significantly differ from the current state of the GBR.

The main impact of this work on stock assessment of Coral Trout is that it is important to take account of crown of thorns starfish outbreaks, which was not considered prior to this project. The apparent effect of CoTS is especially strong in the Swains region, where both the coral cover and fishery catch rates continued to decline throughout the duration of an outbreak, and took many years to recover afterwards. The nature of the relationship with CoTS in other regions is more subtle. It appears that, through some unknown factor unrelated to cyclones, CoTS, coral cover or fishing, the health of reefs can already be depressed and Coral Trout catch rates can already be low before a CoTS outbreak takes hold. The catch rates then stay low through the outbreak and can recover afterwards.

Inclusion of the effects of tropical cyclones on stock assessments was attempted by Leigh et al. (2014, ch. 3) but had little success due to not appreciating the protective effect of the outer barrier reefs on the GBR. The methodology was greatly improved in Courtney et al. (2015, Appendix 7).

Currently, the best way to handle tropical cyclones in stock assessments is simply to omit catch-rate inputs for region–year combinations that have been found to be significantly affected by cyclones. These significant effects apply to the year of the cyclone and one or two years afterwards, once it has been established through wave-height data that the cyclone had a major effect in that region. Most cyclones, even severe ones, have negligible effects on wave heights, and wave-height data are critical to the detection of cyclones that have major effects.

An oceanographic model for the effect of cyclones that includes the protective effect of the outer barrier reefs, and can quantitatively predict the drop in fishery catch rates from the strength and direction of cyclonic winds and the GBR's geometry, does not to our knowledge currently exist.

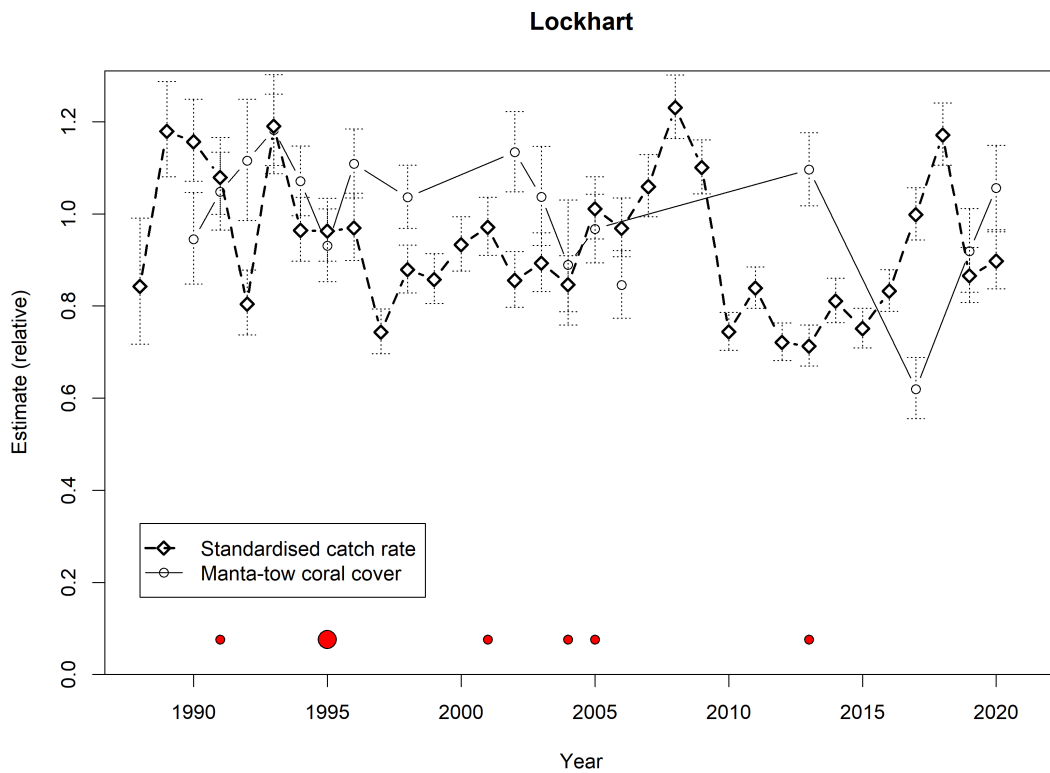


Figure 20. Time series of commercial fishery standardised catch rates and coral cover for the Lockhart region (see Figure 6 for map of regions), with 95% confidence limits. Red dots mark years of crown of thorns starfish outbreaks (small dot for “incipient”).

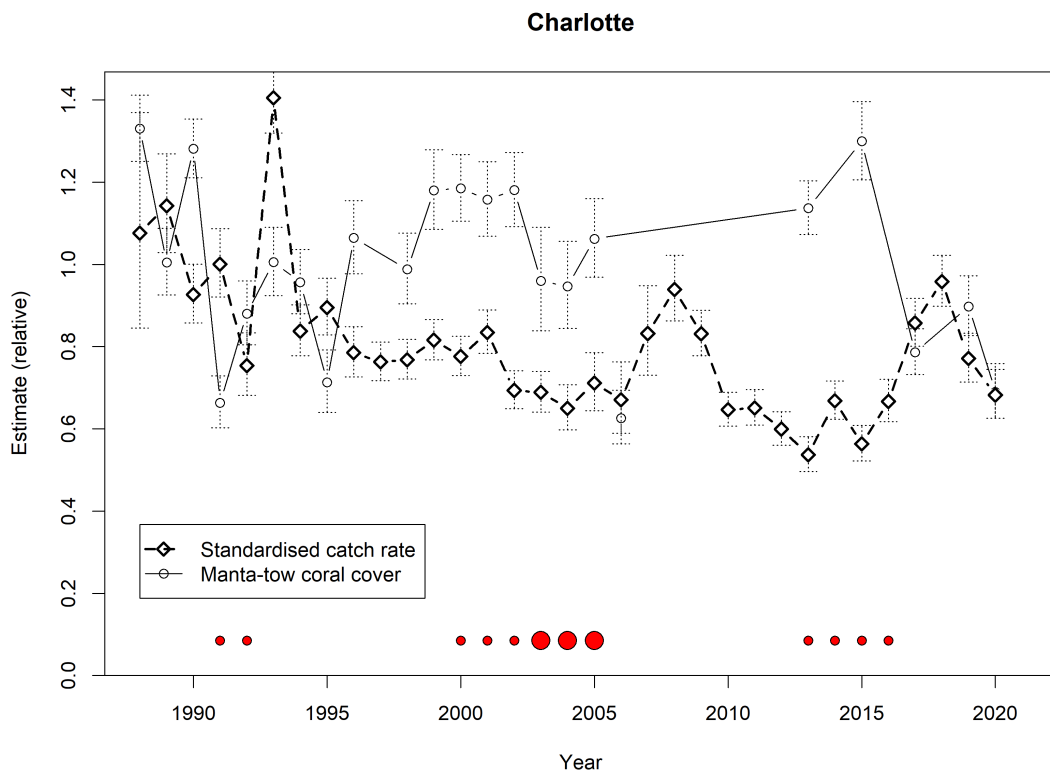


Figure 21. Time series of commercial fishery standardised catch rates and coral cover for the Princess Charlotte Bay region (see Figure 6 for map of regions), with 95% confidence limits. Red dots mark years of crown of thorns starfish outbreaks, as in Figure 20.

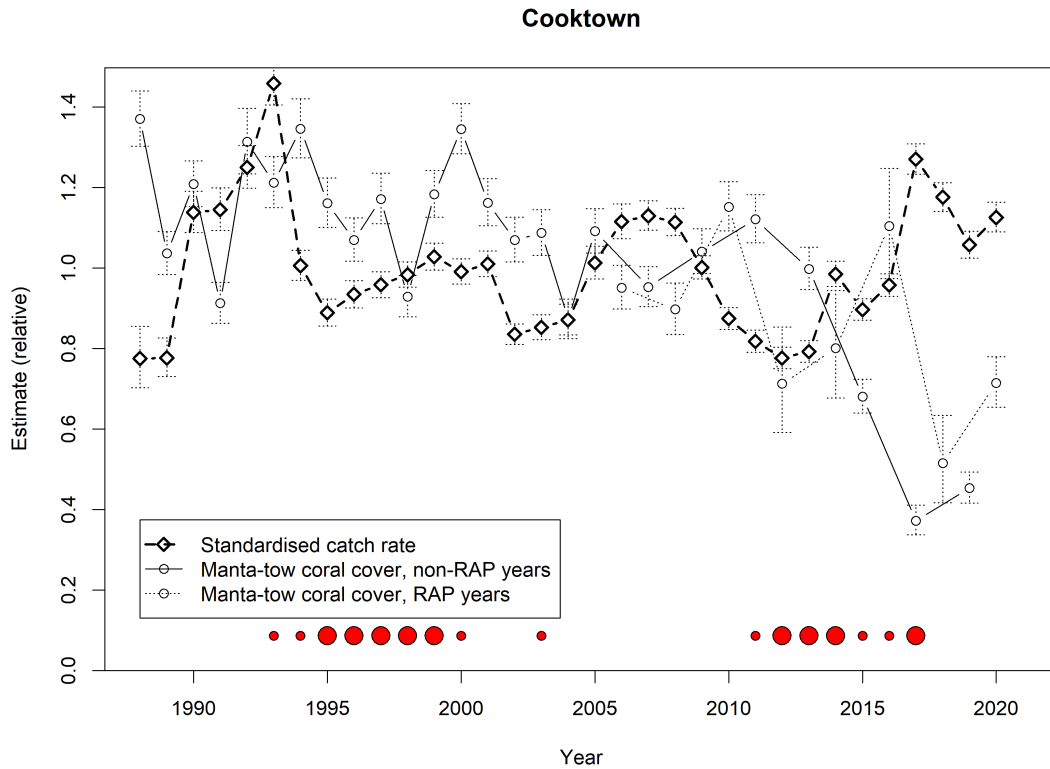


Figure 22. Time series of commercial fishery standardised catch rates and coral cover for the Cooktown region (see Figure 6 for map of regions), with 95% confidence limits. Red dots mark years of crown of thorns starfish outbreaks (small dot for "incipient"). The set of reefs that were sampled in even-numbered years changed from 2006 onwards after the introduction of Representative Area Protection (RAP) on the Great Barrier Reef; these reefs are shown as a separate time series.

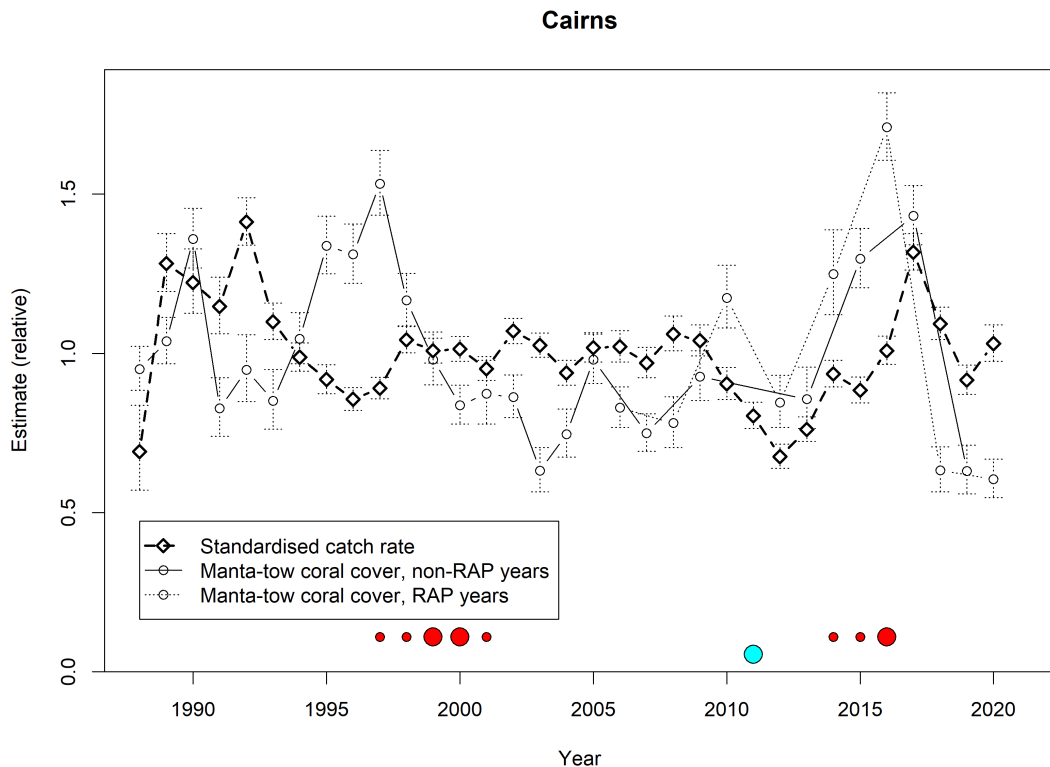


Figure 23. Time series of commercial fishery standardised catch rates and coral cover for the Cairns region (see Figure 6 for map of regions), with 95% confidence limits. Red dots mark years of crown of thorns starfish outbreaks (small dot for "incipient") and blue dots mark years of important tropical cyclones. The set of reefs that were sampled in even-numbered years changed from 2006 onwards after the introduction of Representative Area Protection (RAP) on the Great Barrier Reef; these reefs are shown as a separate time series.

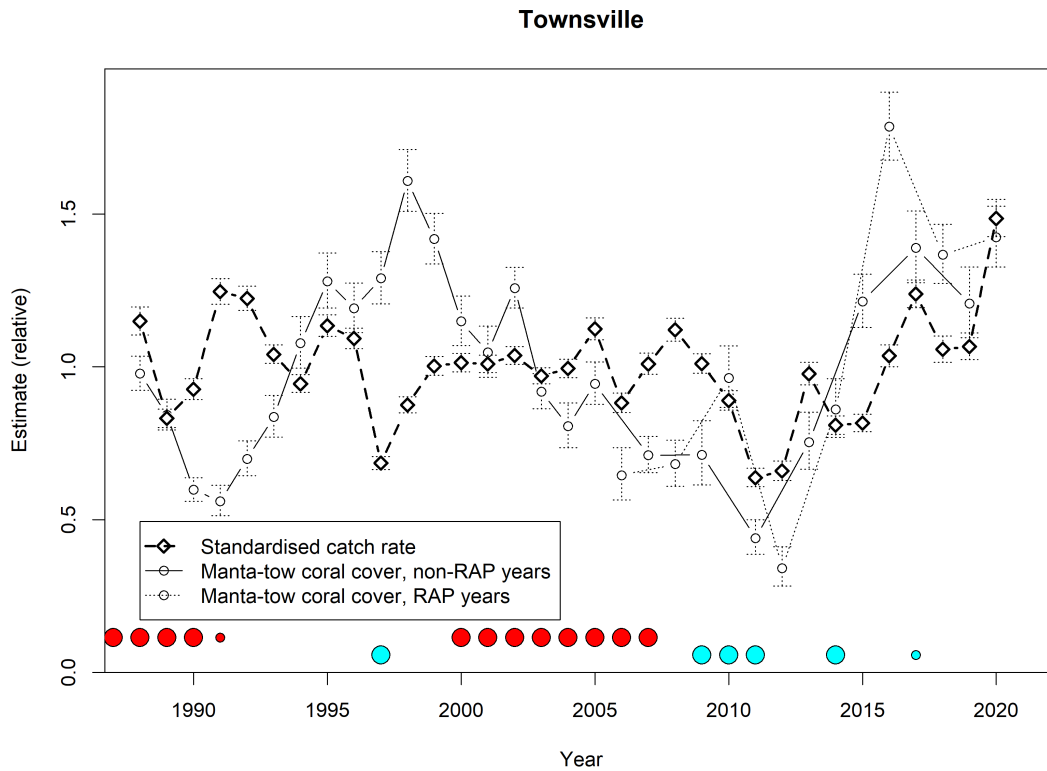


Figure 24. Time series of commercial fishery standardised catch rates and coral cover for the Townsville region (see Figure 6 for map of regions), with 95% confidence limits. Red dots mark years of crown of thorns starfish outbreaks (small dot for “incipient”) and blue dots mark years of important tropical cyclones (small dot for Cyclone Debbie which may or may not have been important). The set of reefs that were sampled in even-numbered years changed from 2006 onwards after the introduction of Representative Area Protection (RAP) on the Great Barrier Reef; these reefs are shown as a separate time series.

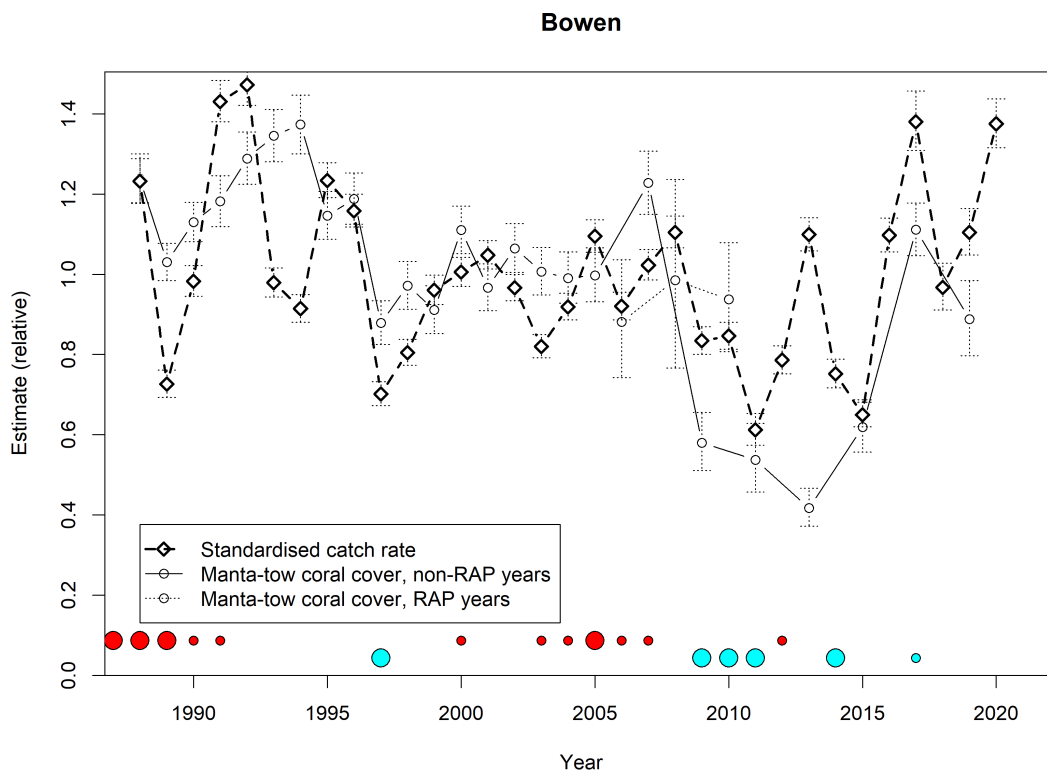


Figure 25. Time series of commercial fishery standardised catch rates and coral cover for the Bowen region (see Figure 6 for map of regions), with 95% confidence limits. Red dots, blue dots and dotted lines mark years of crown of thorns starfish outbreaks, important tropical cyclones and sampling under Representative Area Protection, as in Figure 24.

StormCayInner

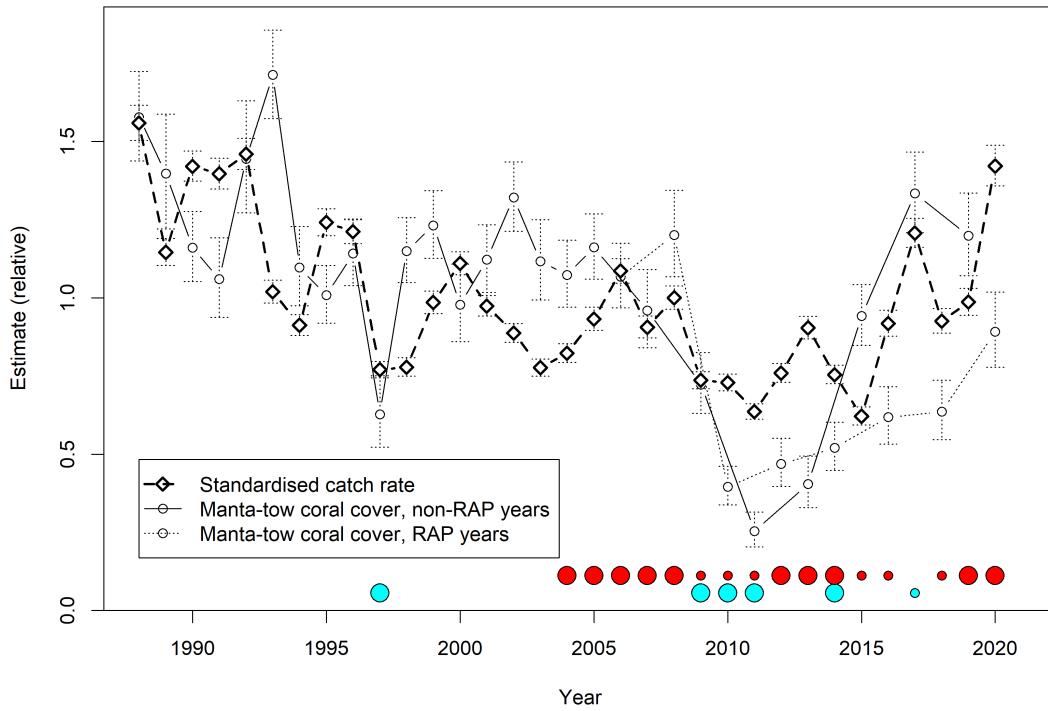


Figure 26. Time series of commercial fishery standardised catch rates and coral cover for the Storm Cay Inner region (see Figure 6 for map of regions), with 95% confidence limits. Red dots, blue dots and dotted lines mark years of crown of thorns starfish outbreaks, important tropical cyclones and sampling under Representative Area Protection, as in Figure 24.

Swains

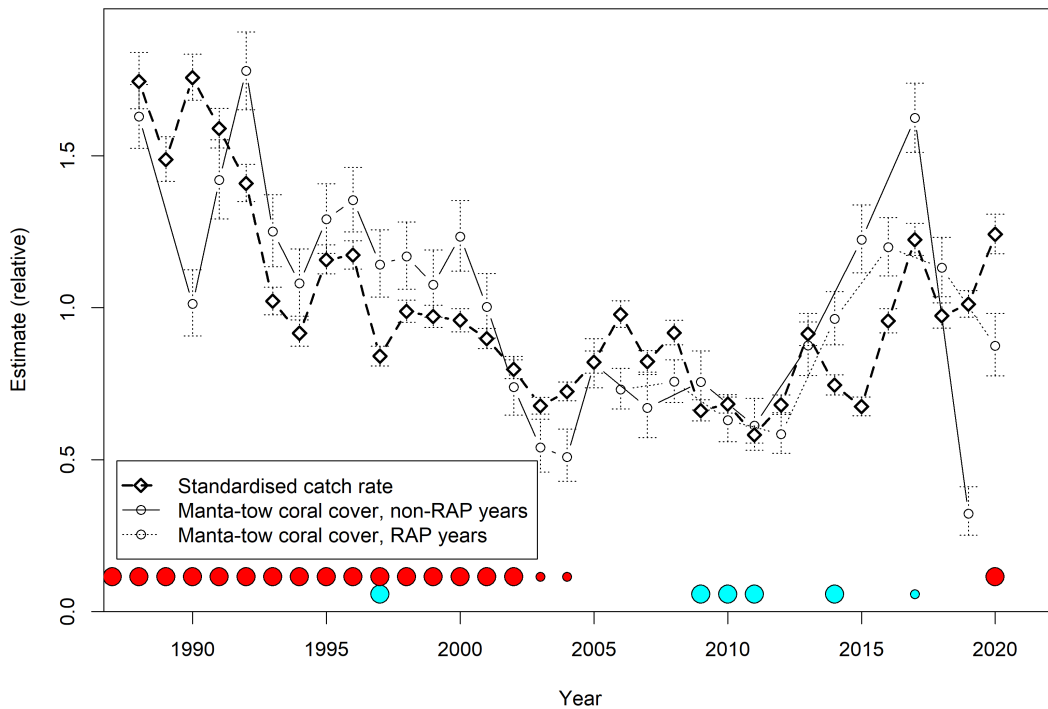


Figure 27. Time series of commercial fishery standardised catch rates and coral cover for the Swains region (see Figure 6 for map of regions), with 95% confidence limits. Red dots, blue dots and dotted lines mark years of crown of thorns starfish outbreaks, important tropical cyclones and sampling under Representative Area Protection, as in Figure 24.

CapBunker

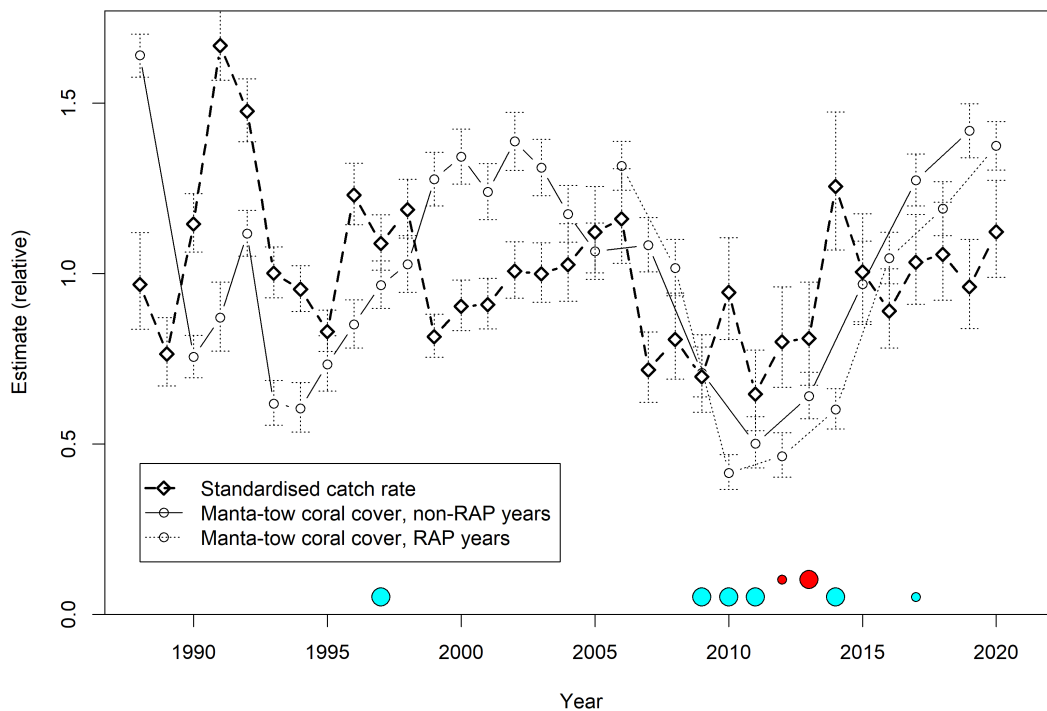


Figure 28. Time series of commercial fishery standardised catch rates and coral cover for the Capricorn–Bunker region (see Figure 6 for map of regions), with 95% confidence limits. Red dots, blue dots and dotted lines mark years of crown of thorns starfish outbreaks, important tropical cyclones and sampling under Representative Area Protection, as in Figure 24.

The generalised linear models for commercial and charter logbook data used the catch in one primary-vessel-day as the dependent variable. For the commercial sector the catch was the retained catch measured in kg, whereas for the charter sector it was the total catch (retained plus released), measured in number of fish. Charter fishers nearly always recorded both the retained and released catch, while commercial fishers generally recorded only the retained catch.

The explanatory variables included categorical variables for calendar year, month, fisher, region and the presence or absence of species commonly associated with Coral Trout. Additional, continuous explanatory variables were log of number of dories and log of number of crew for the commercial sector, and log of the number of fishing guests for the charter sector. Each commercial vessel carried a number of dories or “tenders” and employed a number of crew to catch the fish; zero numbers were replaced by 1, on the assumptions that a zero number of dories meant fishing from the primary vessel, and a zero number of crew meant fishing by the skipper only. Each charter vessel carried a number of guests who fished from the vessel.

The error distribution in all cases was quasi-Poisson. This is a straightforward model whose annual catch rates, in the absence of other explanatory variables, equal the common “raw” catch rate defined as total annual catch divided by total annual effort. The model can handle zero catches easily if required, but fishers generally appeared to catch Coral Trout whenever they targeted it, so logbook records with zero catches of Coral Trout were excluded from analysis. Plots of residuals against fitted values showed only small amounts of heteroscedasticity (whereby relative errors in the fit increased with catch size), implying that the quasi-Poisson model was adequate for the analysis and that no more complex model was needed.

Associated species, which were positively correlated with Coral Trout catches, comprised the following species groups:

- Trevally and Spanish mackerel for the commercial sector in Cape York, Lockhart, Princess Charlotte Bay and Cooktown regions
- Trevally, Spanish mackerel, deep-water tropical snappers and rocky-reef fish for the commercial sector in Cairns, Bowen, Storm Cay Inner and Swains regions

- Trevally, Spanish mackerel and rocky-reef fish for the commercial sector in Townsville region
- Trevally, Spanish mackerel and deep-water tropical snappers for the commercial sector in Storm Cay Outer region
- Spanish mackerel, deep-water tropical snappers and rocky-reef fish for the commercial sector in Capricorn–Bunker region
- Any tropical snapper or emperor for the charter sector in Cooktown, Townsville, Bowen and Storm Cay Outer regions
- No associated species for the charter sector in Cairns region
- Any tropical snapper or emperor, and rocky-reef fish for the charter sector in Storm Cay Inner and Swains regions
- Rocky-reef fish for the Capricorn–Bunker region.

For the commercial fishery, deep-water tropical snappers comprised gold-band snapper (CAAB species code 37346002), ruby snapper (37346014), sharp-tooth snapper (37346019), rosy jobfish (37346032), small-tooth jobfish (37346036), flame snapper (37346038) and unspecified jobfish (37346901) for the commercial fishery. Rocky-reef fish comprised pearl perch (37320003) and snapper (37353001). Charter data were not analysed in the far northern regions due to scarcity of logbook data there.

The observation that the relatively shallow-water taxa of trevally and Spanish mackerel were positively associated with Coral Trout in the commercial sector but not in the charter sector imply that the charter sector targets Coral Trout in deeper water than that commercial sector. Most commercial Coral Trout fishing takes place on precise “hangs” at the ends of coral gutters, where Coral Trout wait for prey to expose themselves. Fishers, operating individually, use view buckets and target fish that they can see. The charter fishing process appears to be quite different. It is not feasible to fix a large group of guests on a single hang, and in any case the process used by commercial fishers may demand more fishing skill charter guests possess. Charter guests appear to target Coral Trout that they cannot see in deeper water.

The AIMS data on coral cover are from shallow water, down to approximately ten metres depth. Therefore it is to be expected that charter catch rates will have less correlation with coral cover than commercial catch rates.

4.3(b) Relate spatiotemporal variation in abundance of Coral Trout (based on underwater visual surveys conducted as part of routine monitoring) to changing habitat condition on the GBR

Surveys recorded 127 individual disturbances on 78 reefs. Disturbances caused variable coral loss both among disturbance types, but also among reefs for each disturbance type (Table 4). The duration of each disturbance was in part a function of the sampling design and logistical considerations, in that some reefs were not able to be surveyed in some years due to adverse weather e.g., storm with a duration of 4 years, means that the After survey was delayed (Table 4). In contrast, some CoTS outbreaks and multiple disturbances continued for several years where consecutive disturbances impacted a reef (e.g. several years of coral disease followed by CoTS outbreaks).

Average modelled coral loss varied between management zones (open and closed to fishing) for six out of the seven disturbance types (Figure **Error! Reference source not found.**). Loss were greater on reefs closed to fishing for CoTS and coral disease, while greater coral loss occurred on reefs open to fishing for cyclones, multiple disturbances and storms (Figure **Error! Reference source not found.**).

Table 4. Number, impact and duration of disturbances recorded in this study.

Disturbance	Number of events	Number of Reefs impacted	Absolute % coral loss (min - max)	Interval Before – After (years)
Bleaching	16	16	0.17 - 23.1	1 - 3
COTS	28	25	5.0 – 65.4	1 - 7
Cyclone	28	25	4.7 – 54.6	1 - 2
Disease	5	4	5.0 – 13.5	1 - 2
Multiple	34	28	5.1 - 73.8	1 - 14
Storm	25	21	5.6 – 76.2	1 - 4
Unknown	2	2	7.2 – 11.6	1 - 2

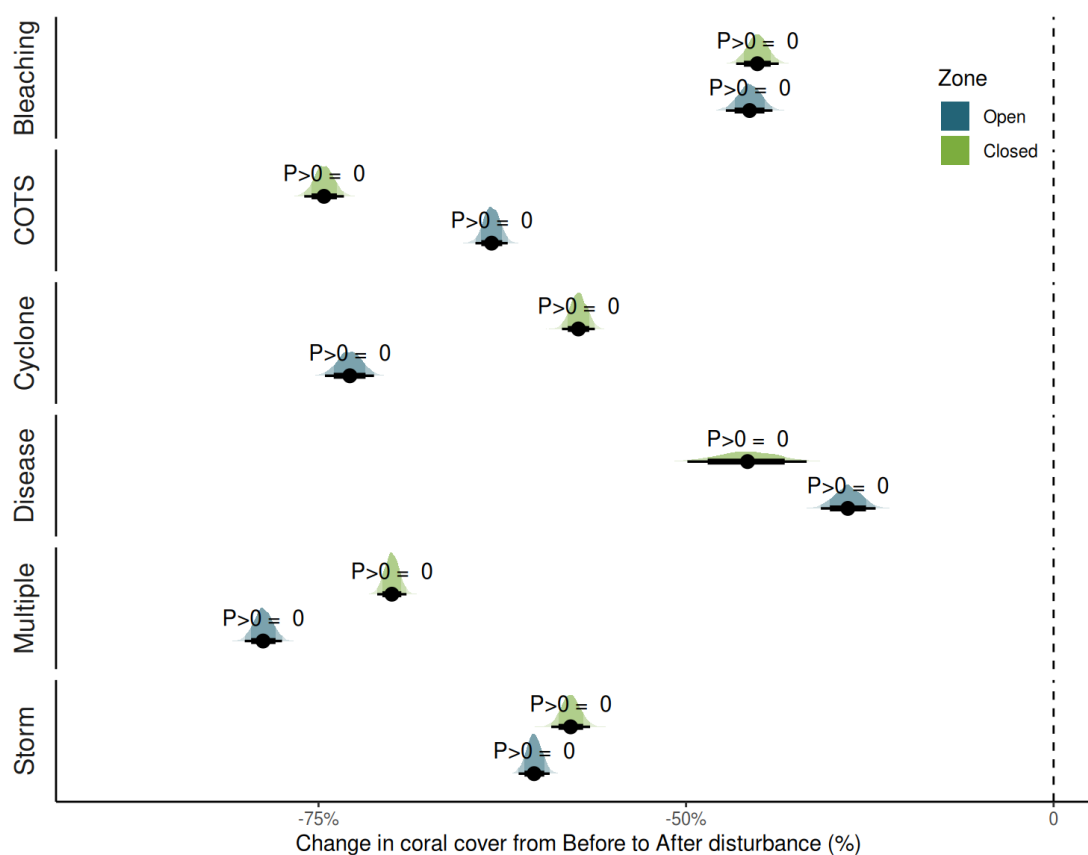


Figure 29. Change in percent hard coral cover from before to after disturbances on the Great Barrier Reef. Data are effect sizes from Bayesian hierarchical generalised linear mixed models and are expressed as a percent change of the abundance prior to disturbance. Colours represent management zone: blue denotes reefs open to fishing, and green denotes reefs inside no-take marine reserves. $P > 0$ is the posterior probability that the change in percent hard coral cover is positive (i.e., coral cover is increasing after disturbance).

The response of Coral Trout abundance to disturbances was variable with some differences between management zones (Figure 30). Coral Trout abundance declined after cyclones and storms and coral bleaching on reefs open to fishing, but there was no change in abundance on reefs in no-take marine reserves (Figure 30). There was strong evidence of declines in trout abundance following multiple disturbances in both no-take marine reserves and reefs open to fishing (Figure 30).

The response of Coral Trout biomass to acute disturbances was dependent on management zone. Coral Trout biomass on reefs in areas open to fishing declined for all disturbances except coral disease, where there was no change (Figure 31). Conversely, Coral Trout biomass increased or remained unchanged following all disturbances (Figure 31). Most notably, Coral Trout biomass inside no-take marine reserves increased substantially following coral bleaching events and non-cyclonic storms (Figure 31). The changes in biomass reflect shifts in the length distribution of Coral Trout, which varied between zones open and closed to fishing for different disturbances. For example, the increase in trout biomass following bleaching events and sub-cyclonic storms was due to an increase in the size of trout rather than an increase in abundance (Figure 32). Conversely, losses in trout biomass following most disturbances resulted from a decrease in average size of trout, coupled with losses in abundance following disturbances (Figure 32).

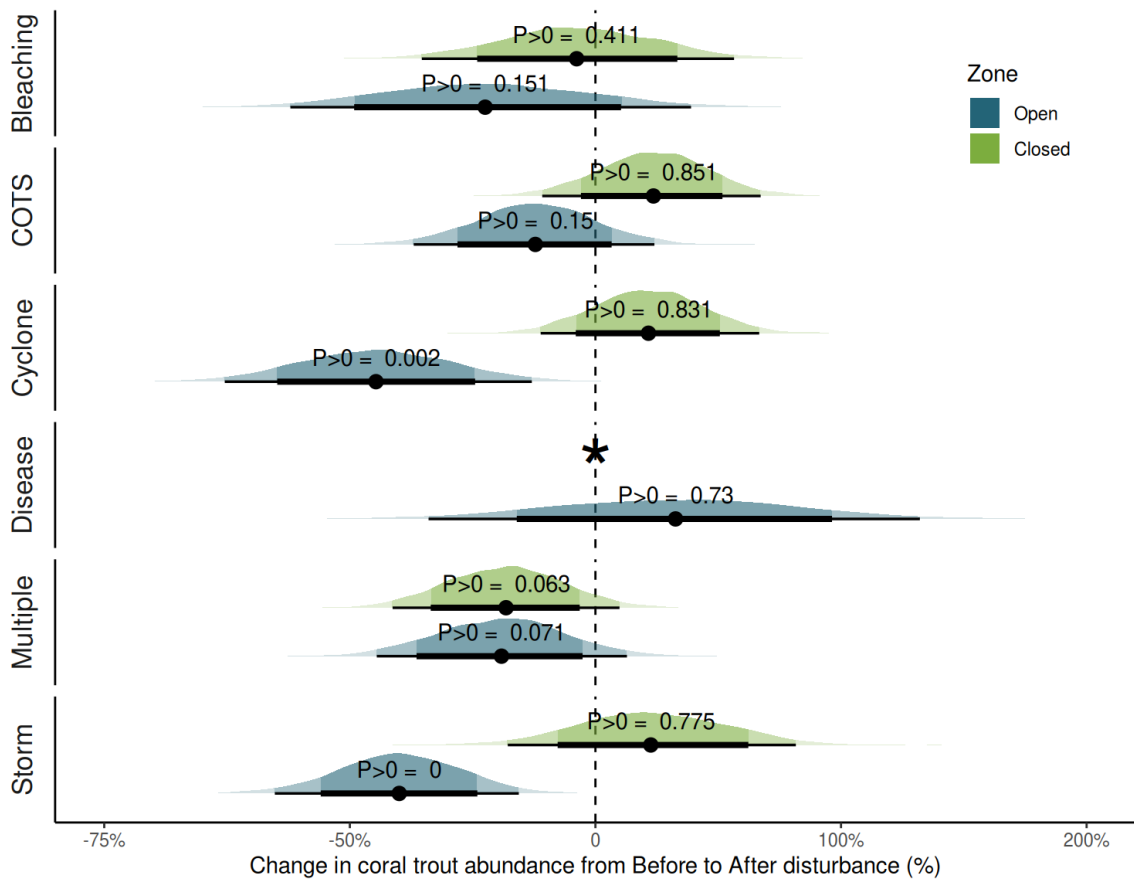


Figure 30. Change in Coral Trout abundance following acute disturbances on the Great Barrier Reef. Data are effect sizes from Bayesian hierarchical generalised linear mixed models and are expressed as a percent change of the abundance prior to disturbance. Colours represent management zone: blue denotes reefs open to fishing, and green denotes reefs inside no-take marine reserves. $P > 0$ is the posterior probability that the change in abundance is positive (i.e., abundance increasing after disturbance).

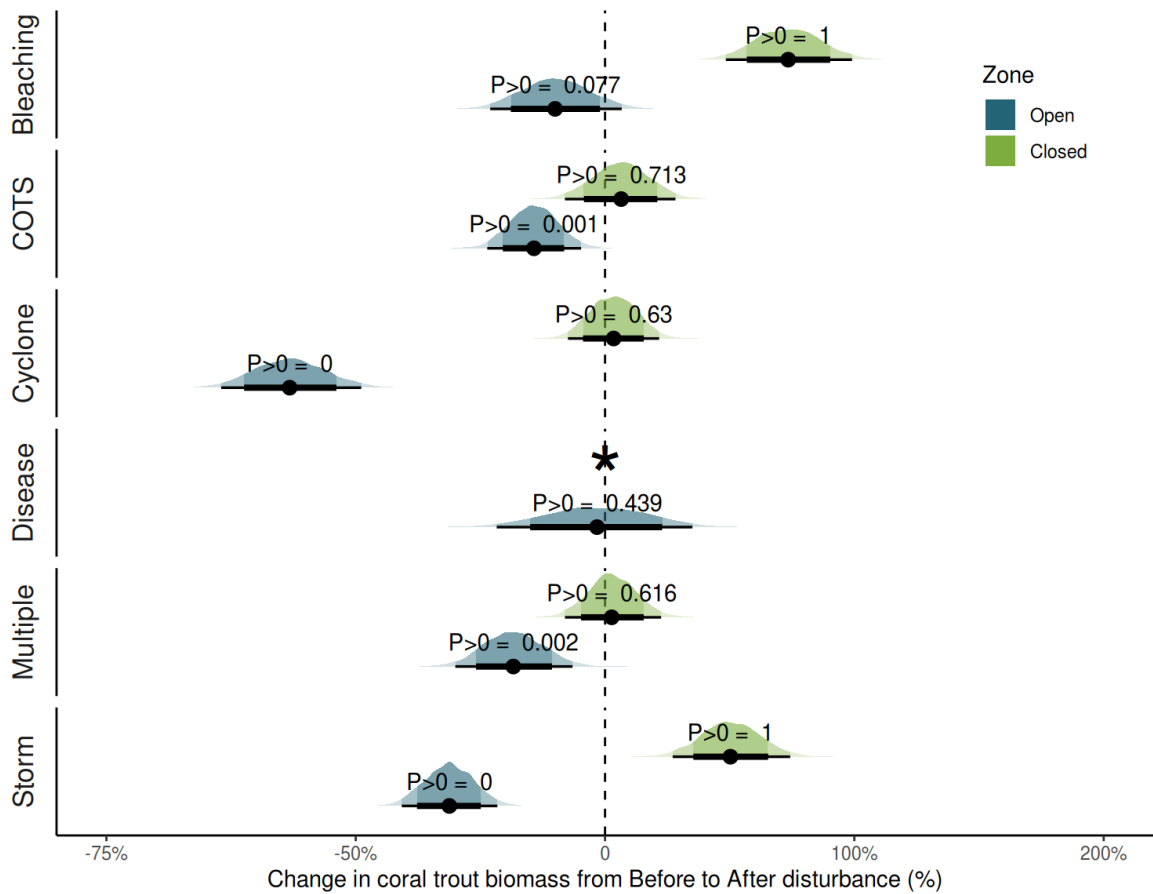


Figure 31. Change in Coral Trout biomass following acute disturbances on the Great Barrier Reef. Data are effect sizes from Bayesian hierarchical generalised linear mixed models and are expressed as a percent change of the biomass prior to disturbance. Colours represent management zone: blue = reefs open to fishing, green = reefs inside no-take marine reserves. P>0 is the posterior probability that the change in biomass is positive (i.e., biomass increasing after disturbance).

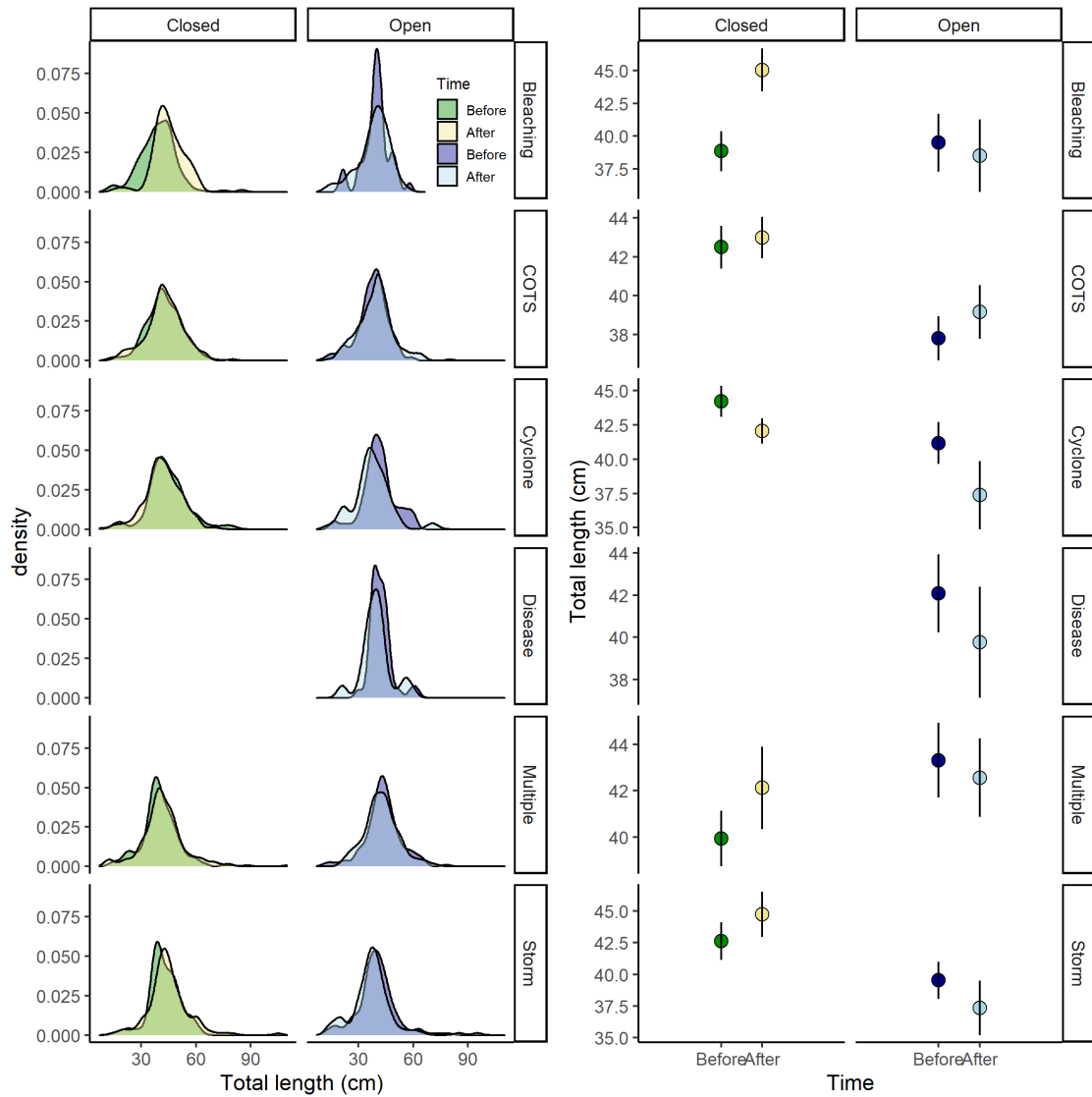


Figure 32. Change in Coral Trout length-frequency distribution (left panel) and average total length before and after disturbances in management zones closed to fishing (green) and open to fishing (blue). Data are density kernel estimates of Coral Trout total length, and the average total length (± 2 standard errors).

5. Discussion

5.1 Behavioural responses of Common Coral Trout (*P. leopardus*) subject to elevated temperatures

Understanding how increasing ocean temperatures and severe marine heatwaves affect large predatory and commercially important coral reef fishes is considered critically important, given potential declines in the individual performance and fitness of fishes that may undermine fisheries productivity and/or sustainability. Fishes exposed to increased temperature will have higher metabolic rates, which may be partially compensated for through increased food intake, but for predatory species increased food capture invariably requires increased movement, further exacerbating energetic demands. *In situ* observations of Coral Trout on the GBR have shown that periods of inactivity increase with temperature between 21 and 32°C (across latitudes and seasons), with activity becoming highly variable above 30°C, potentially indicative of thermal stress (Scott et al. 2017). Tank-based observations corroborate these findings, showing that Coral Trout spend more time resting at temperatures $\geq 30^\circ\text{C}$ (Johansen et al., 2014). This is likely to be an energy-conserving behaviour to compensate for increased metabolic rate (Clark et al., 2017; Messmer et al., 2017). Coral Trout are also less able to survive additional stressors, like exhaustive exercise, at temperatures $\geq 30^\circ\text{C}$ (Clark et al., 2017). Taken together, these data suggest that the thermal optima for Common Coral Trout (*P. leopardus*) on the GBR is $\sim 27^\circ\text{C}$, and this does not seem to vary significantly between populations sampled in the northern versus southern GBR (Pratchett et al. 2017). It is unknown however, whether the *P. leopardus* actually prefer temperatures close to the apparent thermal optima, and will preference behavioural thermoregulation over other potential demands (e.g., conserving energy).

Given that temperature plays such a pervasive role in regulating the physiological processes of aquatic ectotherms, highly mobile fishes such as Coral Trout would be expected to exploit inherent variability in thermal conditions (e.g., among micro-habitats or with depth) to buffer exposure to temperatures that are significantly lower (sub-optimal) or higher (supra-optimal) than 27°C , and thereby maintain their body temperature at close to their thermal optima. We tested this in a static experimental arena where fish were intentionally exposed to ambient temperatures ($17.5\text{--}20.5^\circ\text{C}$) that were substantially lower than their presumed thermal optima ($\sim 27^\circ\text{C}$). While fish readily used the hides provided, they rarely used the hides that were heated, and therefore, did avail themselves of the opportunity to substantially increase their body temperature. These results add to a growing body of literature suggesting that behavioural thermoregulation is a relatively low priority for many fishes, at least under controlled conditions (e.g., Myrick et al. 2004; Gräns et al. 2010), and Coral Trout may be quite impartial to the water temperatures they encounter in their natural habitat, so long as temperatures remain within the historical (pre-industrial) range (estimated at $\sim 18\text{--}30^\circ\text{C}$; Rayner et al. 2003). This behaviour may also reflect the limited opportunities for behavioural thermoregulation in reef environments (e.g., Figure 8), such that reef fishes are resigned to fluctuations in their body temperature with diurnal and seasonal changes in ambient conditions (*sensu* Nay et al. 2021).

While shallow tropical marine habitats (e.g., reef crests) may be relatively homogeneous with regard to temperature (e.g., Nay et al. 2021), there is widespread and increasing emphasis given to deeper coral reef environments as potential refuges (e.g., Currey et al. 2015; Sih et al. 2017; Rocha et al. 2018). This is because disturbances such as coral bleaching and storm damage attenuate relatively quickly with increasing depth (e.g., Bridge et al. 2014). Deeper habitats may, therefore, offer a refuge from both environmental and habitat disturbances, especially during severe marine heatwaves. Currey et al. (2015) showed that Redthroat Emperor, *Lethrinus miniatus* actively moved to deeper water during periods of elevated temperature, presumably, therefore, exploiting cooler deep-water environments. Similar research conducted on *P. leopardus* using passive acoustic arrays to document space use, failed to show any seasonal shifts in the vertical habitat (i.e. depth) use of tagged fishes. We also failed to detect seasonal shifts in the depth by *P. leopardus* or any other fishery-targeted species using the intensive deployment of BRUVs at Linden Bank. Findings from these field-based studies complement the findings from the experimental test of behavioural thermoregulation (Section 4a), suggesting that *P. leopardus*, perhaps unlike some other fishes (e.g., *L. miniatus*), do not necessarily prioritise movement to deeper habitats to

mediate exposure to sub- or supra-optimal temperatures (see also Scott et al. 2019). Rather, *P. leopardus* appear more likely to reduce movement and activity patterns, and thereby conserve energy, when subject to supra-optimal temperatures (Johansen et al. 2014, 2015). Accordingly, we found that home ranges of *P. leopardus* declined with increasing temperature, especially when temperatures exceeded 27°C (Section 4.1c). Moreover, spatiotemporal contrasts of bioenergetics for *P. leopardus* revealed striking differences in diurnal patterns of activity, which suggested that individuals from the low-latitude location are compensating for an increase in energy use during the day, by largely resting throughout the night.

Data from this study adds to the increasing weight of evidence showing that *P. leopardus* moderate their feeding and activity to withstand short-term exposure to elevated temperatures, and may not therefore necessarily seek out preferred temperatures. It is acknowledged, however, that our test of depth re-distribution using intensive BRUV deployments was conducted in only a single year and at only one location. Further sampling may well reveal expected seasonal shifts in the depth distribution of *Plectropomus* spp. In particular, the limited variation in temperature recorded with increasing depth (up to 50m) in February 2017, and corresponding limitations in the availability or accessibility of temperature refugia, may be an anomaly associated with the sustained high temperatures that occurred in 2016-2017. There was every intention to undertake complementary sampling at another shoal located in the southern GBR, but the planned field work in summer 2019 had to be cancelled (due to COVID-19). Moreover, the benefit of undertaking complementary sampling at a higher latitude location was considered very marginal, because any seasonal differences in depth use by fishes were expected to be most apparent at low latitudes. It must also be emphasised that, as with all fish census techniques, there are a number of biases associated with BRUVs, including the potential inflation of density estimates due to fish being drawn from outside visible sampling areas, unknown areas of attraction as a by-product of variable bait plume dispersion, alteration of fish behaviours, competitive exclusion, and/or preferential sampling of predator and scavenger populations with corresponding reductions to other functional groups (Harvey et al. 2007; Dorman et al. 2012). However, comparisons between baited and unbaited camera stations have shown that while carnivore and scavenger abundances tend to increase in the presence of bait, no commensurate changes are detected in herbivore or omnivore abundances (Harvey et al. 2007). Furthermore, by using BRUVs 'diver effects' are substantially reduced when compared to other fish census techniques. There is also often greater opportunity to confirm the identity of different species from video recordings rather than *in situ* sightings and surveys.

5.2 Effects of recent severe marine heatwaves (2016-2017) and corresponding coral loss on Common Coral Trout (*Plectropomus leopardus*)

Mass bleaching of corals, which is unequivocally linked to thermal anomalies (Hoegh-Guldberg 1999; Hughes et al. 2017), has occurred at fairly regular intervals on the GBR since 1980 (Pratchett et al. 2021). The extent and severity of mass bleaching has increased since 1980, but the most severe episode of mass-bleaching (and the highest recorded thermal anomalies) on the GBR occurred in 2016 (Hughes et al. 2017, Pratchett et al. 2021). Extensive coral loss and marked shifts in coral composition were documented across many reefs that experienced extreme levels of mass bleaching in 2016 (Hughes et al. 2018b) mostly due to disproportionate declines in abundance of branching *Acropora* spp. and Pocilloporidae corals. These corals are, however, also capable of rapid growth (Linares et al. 2011; Johns et al. 2014; McWilliam et al. 2020), and have contributed to relatively rapid recovery in the aftermath of the 2016-2017 mass bleaching on at least some reefs in the northern GBR. This study considered reefs in varying condition, whereby coral cover ranged from 3.00-48.33% (Figure 14). Coral cover was generally lower on reefs in the northern GBR, which is at least partly attributable to the 2016-2017 mass bleaching, though there are many other factors that are causing coral mortality and contributing to coral loss across the GBR (Ortiz et al. 2018; Mellin et al. 2019). In particular, there were some reefs in the southern (Swains) sector that had very low coral cover, mainly attributable to localised infestations of CoTS.

Densities and biomass of *P. leopardus* recorded in the aftermath of the recent mass bleaching of corals was found to vary within and among reefs, mostly with respect to depth. There was not, however, significant or consistent variation in the densities or abundance of *P. leopardus* with respect to local coral cover at

specific survey sites. Indeed, highest biomass of Common Coral Trout was recorded on reefs in the southern-most section of the Swains (Conspicuous and Sandshoe Reefs) that had the lowest hard coral cover. For the most part, densities and biomass of *P. leopardus* was insensitive to variation in coral cover, especially when local coral cover was >20%.

Despite limited variation in the density or biomass across reefs with very different levels of contemporary coral cover recorded in the 4-5 years after significant mass bleaching, there were apparent differences in the diet and condition of *P. leopardus* that might be related to habitat structure and condition. In terms of overall diet, $\delta^{13}\text{C}$ signatures decreased and $\delta^{15}\text{N}$ signatures increased with average coral cover. While changes in stable isotope signature reflected in these meso-predators may relate to fundamental changes in the isotopic signatures of basal trophic components that are linked to habitat degradation, which was not tested, there is strong evidence that *P. leopardus* exploit different sources of prey on reefs with high versus low coral cover (see also Hempson et al. 2017). This reflects the high dietary versatility of Coral Trout (e.g., Kingsford 1992) and likely, contributes to increased resilience to changes in habitat structure and associated prey communities. Shifts in the composition of prey species and corresponding diet may, nonetheless, have significant impacts on the physiological condition and longer-term population viability of predatory fishes (Graham et al. 2007; Hempson et al. 2017).

In this study, the physiological condition of *P. leopardus* and especially HV, which is expected to vary in response to changes in prey quality and quantity (Pratchett et al. 2004), varied with the size of fish, and among reefs, mostly with respect to latitude. Variation in the physiological condition of *P. leopardus* was also apparent based on BIA, which may provide a useful method for measuring overall condition of Coral Trouts in future studies (especially, given it may be recorded for live fishes; Cox and Hartman, 2005). However, neither HV or BIA of *P. leopardus* consistently varied in relation to the local coral cover where individual fish were captured. This is not to say that physiological condition does not vary with habitat structure and reef condition, but there are many other factors (e.g., size of fishes) that also influence condition and may obscure this relationship. Changes in the individual condition of fishes is also important given it may have a direct bearing on reproductive fitness (e.g., Donelson et al. 2008), which may have long-term consequences for population viability and fisheries sustainability.

5.3 Spatiotemporal variation in wild stocks of Coral Trout relative to large-scale disturbances and associated changes in habitat condition on the Great Barrier Reef

Long-term trends in coral cover on the GBR vary greatly among reefs and regions (Cheal et al. 2008; Wilson et al. 2009) and regions (Osborne et al. 2011), mostly in accordance with spatiotemporal patterns in the occurrence of major disturbances. Distinct episodes of coral loss may occur due to mass coral bleaching (Hughes et al. 2018), but also storm damage, and especially very intense cyclonic storms ('cyclones'), population irruptions of CoTS (e.g., De'ath et al. 2012), and also outbreaks of coral disease (Osborne et al. 2011). There has been particularly high incidence of intense (category 4-5) cyclones crossing the GBR since 2009 (Puotinen et al. 2016; Cheal et al. 2017), which collectively affected much of the GBR. Severe cyclones have dramatic effects on the structure and function of coral reef ecosystems (Cheal et al. 2017; Wilson et al. 2006), not only causing extensive coral loss, but greatly altering physical habitat structure (e.g., Madin et al. 2018). By comparison, outbreaks of CoTS result in much more protracted coral mortality (Pratchett et al. 2014), but also leave dead coral colonies structurally intact (Wilson et al. 2006). Similarly, coral bleaching and coral disease may kill corals but leave the skeleton intact, at least until inevitable decomposition and erosion lead to the collapse of erect and fragile coral skeletons (Pratchett et al. 2008).

When comparing among major disturbances on the GBR, the largest changes (declines) in abundance and biomass of Coral Trouts were recorded in the aftermath of cyclones, and also other tropical storms (Figure 24 and 25). These effects were much more apparent in fished areas than in unfished areas. These differences were not attributable to variation in coral loss, which was most pronounced in the aftermath of CoTS and also multiple disturbances (Figure 23: see also Osborne et al. 2011; De'ath et al. 2012). Similarly, spatiotemporal variation in catch rates of Coral Trouts, like abundance, are often influenced by severe cyclones (Section 4.3a: see also Tobin et al. 2010), but do not clear or consistent responses to other major

disturbances, even when there is very extensive coral loss. It is possible, therefore, that Coral Trouts (*Plectropomus* spp.) are more sensitive to declines in the structural complexity of coral reef habitats rather than loss of live coral. This would explain, why disturbances such as coral bleaching and CoTS outbreaks (which have little effect on habitat complexity; Wilson et al. 2006), have limited discernible effects on Coral Trout densities or biomass, whereas cyclones and tropical storms (which can rapidly and greatly reduce habitat complexity) disproportionately impact Coral Trout populations. For Coral Trouts, declines in structural complexity of reef habitats may reduce availability of shelter, leading to reduced foraging efficiency and/or prey availability (Leigh et al. 2014). These effects may be further compounded by metabolic suppression due to reduced water temperatures in the aftermath of severe tropical cyclones (Tobin et al. 2010), which particularly effects the propensity to feed and ability to catch Coral Trouts.

6. Conclusions and Implications

This study reinforces that Common Coral Trout (*Plectropomus leopardus*) are sensitive to changes in temperature (see Pratchett et al. 2013; Johansen et al. 2014; Sun et al. 2015; Messmer et al. 2017), whereby temperature has a direct bearing on activity patterns and space use. However, Common Coral Trout can withstand a wide range of temperatures and do not necessarily behaviourally thermoregulate, or move among thermal gradients to regulate their temperature. Most notably, *P. leopardus* occur over a very wide depth range, but individual fish are generally site-attached; while *P. leopardus* living in shallow reef environments are more likely to be exposed to supra-optimal temperatures, unlike other fish species (e.g., Richards et al. 2012; Currey et al. 2015) Common Coral Trout do not appear move to deeper environments even if this provides refuge from seemingly adverse thermal conditions. Rather than exploiting natural thermal gradients, *P. leopardus* appear more likely to modify aspects of their behaviour to compensate for increases in environmental temperature. Specifically, increased temperatures have been linked to decreased movement and activity in *P. leopardus*, resulting in smaller home ranges, reduced feeding and increased time spent resting (Johansen et al. 2014, Scott et al. 2019). Given limited evidence that Common Coral Trout can or will moderate their exposure to changing environmental conditions, they will be directly affected by increasing ocean temperatures and severe marine heatwaves.

While Common Coral Trout can withstand short-term exposure to elevated (and like supra-optimal) temperatures (see also Johansen et al. 2014, 2015; Messmer et al. 2017), effects of increasing ocean temperatures on wild stocks of Common Coral Trout will likely be greatest at low latitudes, where summer-time temperatures already exceed the estimated thermal optima (27-30°C; Pratchett et al. 2013, 2017; Johansen et al. 2014), and can have significant deleterious effects on individual survival (Clark et al. 2017). Clark et al. (2017) showed that *P. leopardus* exposed to temperatures $\geq 30^{\circ}\text{C}$ exhibit reduced survivorship, especially following vigorous activity. Prior research also found limited evidence of acclimation to local temperature regimes for Common Coral Trout (e.g., Johansen et al. 2014), whereby individuals from different latitudes (and thereby thermal regimes) exhibited equivalent thermal sensitivity.

Direct effects of increasing temperature on Coral Trout (e.g., Sun et al. 2015; Clark et al. 2017; Messmer et al. 2017), will likely be compounded by climate-induced shifts in the structure of coral reef habitats (Pratchett et al. 2017). Most notably, declines in habitat complexity (which invariably follow extensive coral loss; Pratchett et al. 2008) may lead to marked declines in abundance of Common Coral Trout. However, coral loss may also have other independent effects on Common Coral Trout (see Williamson et al. 2014), possibly effecting the availability or composition of prey species. These effects are likely to become more pronounced with ongoing environmental change, and increased frequency, severity and diversity of disturbances that cause coral loss (Wilson et al. 2006). The effects of habitat degradation and coral loss on Coral Trout do however, appear to vary spatially and taxonomically. In particular, the effects of habitat degradation and coral loss appear much more pronounced for the Barcheek Coral Trout (*Plectropomus maculatus*) compared to *P. leopardus* (Williamson et al. 2014). Effects of coral loss on coral trouts are also significantly moderated in areas that are closed to fishing (e.g., Williamson et al. 2014; Emslie et al. 2015). As such, ongoing habitat degradation may undermine fisheries sustainability, even if wild stocks are otherwise resilient to environmental change. Critically, it appears that other disturbances (e.g., storms and outbreaks of CoTS) pose a greater threat to Coral Trout than climate-induced coral bleaching. This may be explained by the timing and location of disturbances, rather than the specific nature of different disturbances; it is difficult to explain why storms (especially cyclones) and outbreaks of CoTS would cause deleterious changes in habitat structure and condition, but not mass coral bleaching (see Pratchett et al. 2014).

Given limited recorded changes in the abundance or biomass of Common Coral Trout in the aftermath of marine heatwaves and corresponding episodes of mass coral bleaching, it appears that this species is somewhat resilient to changing environmental and habitat condition, at least at the scale and extent of changes recorded thus far. This does not necessarily mean that Common Coral Trout will be unaffected by ongoing climate change. Increases in ocean temperature, and corresponding increases in metabolic rates of predatory fishes, will almost certainly necessitate increased foraging (Scott et al. 2017). At very high

temperatures (>30 °C) the energetic cost and prolonged metabolic debt of vigorous activity (Clark et al. 2017) may impose significant constraints on the capacity of *P. leopardus* to obtain sufficient prey resources (Scott et al. 2017). Reduced feeding (even if associated with conserving energy) will further limit the physiological condition and energetic reserves, potentially leading to reduced reproductive fitness and population viability. Recent marine heatwaves and acute episodes of coral loss may have also affected other life-history stages and processes (e.g., reproduction and recruitment), which were not considered in this study, and may only become apparent based on long-term changes in the abundance and stock status of Common Coral Trout (Graham et al. 2007, Brown et al. 2020).

Even if climate change and habitat degradation do not significantly affect the stock size and structure of Coral Trout, changes in catchability may have significant effects on the viability and sustainability of fisheries (e.g., Brown et al. 2020). It is uncertain how catchability may change over time, which is not only mediated by physiological responses of the fisheries target species to changing temperatures, but also foraging efficiency, prey availability and prey turnover (Brown et al. 2020), all of which may be affected by changing environmental and habitat conditions. Brown et al. (2020) reported that CPUE for Coral Trouts was higher than expected during the 2016 marine heatwave, based on fishery-independent estimates of fish abundance and biomass. If so, this might explain the apparent disconnect between catch rates and habitat condition recorded across the 11 distinct regions of the GBR, but also has ramifications for current stock-assessment models, which are largely reliant on catch data (assumed to reflect changes in stock status). If environmental change does increase catchability (even if only in the short term), this will need to be carefully managed to avoid undermining existing management arrangements intended to rebuild wild stocks of Coral Trouts (Brown et al. 2020).

8. Recommendations

Results of this project build upon extensive experimental, laboratory-based studies on the potential responses of Coral Trout (especially Common Coral Trout, *Plectropomus leopardus*) to changing environmental conditions (Pratchett et al. 2013; Johansen et al. 2014; Sun et al. 2015; Messmer et al. 2017). Notably previous experimental studies have shown that Common Coral Trout are sensitive to elevated temperatures (especially $\geq 30^{\circ}\text{C}$), and this study has shown that these species will be directly exposed to elevated temperatures, especially during severe marine heatwaves. Critically, wild stocks of Coral Trout in the northern Great Barrier Reef are already regularly exposed to summertime temperatures $>29^{\circ}\text{C}$ (Pratchett et al. 2017) and up to to 32°C . This is important given that *P. leopardus* are currently the foremost component of the commercial Reef Line Fishery on the GBR (e.g., Fox et al. 2022), and climate change is rapidly emerging as the foremost threat to coral reef species and systems (e.g., Hughes et al. 2018). To account for differential climate impacts, distinct stock assessment models and corresponding quota allocations may be necessary for different geographical regions (e.g., northern versus southern GBR). Fishing effort and catches of *P. leopardus* are already much higher in the southern GBR compared to the northern GBR (Leigh et al. 2014), largely reflecting differences in the size, condition and abundance of fish from different regions (Leigh et al. 2014). Such differences are likely to be further magnified with ocean warming and global climate change, but need to be explicitly managed both to ensure that fish stocks in the northern GBR are sufficient to maintain the ecological integrity of these systems, as well as preventing further concentration of effort and potential overfishing either in regions with highest abundance of fisheries target species, or regions that are most vulnerable to changing environmental and habitat conditions.

At present, the specific effects of changing environmental and habitat conditions on wild stocks of Coral Trout on the GBR are unclear. This is not to say that climate induced changes in environmental and habitat conditions, as well as increasing effects of other major disturbances and anthropogenic pressures, do not or will not have substantive effects on Coral Trout (let alone other major fisheries target species), but it is difficult to account for the specific effects with existing data and methods, thereby adding to uncertainty in stock assessment models and corresponding harvest limits (Fox et al. 2022). There is therefore, a critical need to carefully monitor both standardised catch rates and stock status and trends going forward, and specifically test for changes that may occur due to progressive shifts in environmental and habitat conditions. This will also provide the opportunity to reconcile independent changes in standardised catch rates versus the abundance or biomass of Coral Trout, which is important for assessing how catchability (and thereby fisheries viability) might change due climate change and/ or habitat degradation (e.g., Brown et al. 2020).

While there were limited apparent effects of recent marine heatwaves and corresponding mass coral bleaching and mortality on Common Coral Trout, consideration of the broadscale impacts of different large-scale disturbances have revealed contrasting effects of different disturbances (see Figure 31). Such differences suggest that Coral Trout (and predominately, *P. leopardus*) are not simply responding to changes in cover of hard corals. Important, effects of coral loss may be compounded by changes in habitat diversity and topographic complexity (Pratchett et al. 2014), but even the combination of these two factors do not readily account for disparate effects of Cyclones versus outbreaks of CoTS versus climate-induced coral bleaching. This suggests that further research is needed to understand the fundamental biology and ecology of Common Coral Trout, as well as many other fisheries target species, to better understand the resource requirement and specific vulnerability to changes in environmental and habitat conditions. This study also reinforces the broadscale benefits of no-take marine reserves to enhance stock status and resilience of fisheries target species (see also Williamson et al. 2014; Emslie et al. 2015), but again the mechanistic basis of these effects needs more research.

8.1 Further development

While adult stocks of Common Coral Trout appear to be somewhat resilient to changing environmental and habitat conditions, at least in the short term, further research is needed to test whether inevitable shifts in

coral reef environments and habitats will have long-term or progressive effects on wild stocks. It is possible, for example, that limited changes in the abundance, biomass or standardised catches of adult Coral Trout on the GBR in the aftermath of recent heatwaves and mass coral bleaching, may belie reductions in reproductive output and recruitment (Graham et al. 2007). If so, there may be protracted declines in the abundance of Coral Trout, not only linked to marine heatwaves and mass bleaching, but also cyclones and outbreaks of crown-of-thorns starfish. Limitations in reproduction and recruitment will be particularly critical in areas subject to fishing, potentially undermining fisheries sustainability.

Given the critical influence of cyclones (and other severe tropical storms) on the abundance and catches of Coral Trout (e.g., Tobin et al. 2010), there is a definite need for development of a better model of the effects of tropical cyclones on the GBR is desirable. Such a model should incorporate the “barrier” reefs of the outer GBR which provide protection from most directions. The existing model of Puotinen et al. (2016) estimates the probability that wave heights will exceed particular threshold value, but does not effectively account for the particular arrangement of reefs. Similarly, analyses by Leigh et al. (2014) calculates a cyclone’s wind energy density at different locations, but doesn’t consider either barrier reefs or the fetch lengths necessary to generate large waves.

9. Extension and Adoption

9.1 Extension and communication

Research undertaken as part of this project has resulted in 2 peer-reviewed journal articles publications, thus far (relating to projects 1a, and 1b, respectively):

1. Clark, T. D., Scheuffele, H., Pratchett, M. S. & Skeeles, M. R. (2022) Behavioural temperature regulation is a low priority in a coral reef fish (*Plectropomus leopardus*): insights from a novel behavioural thermoregulation system. *Journal of Experimental Biology*. 225 (18): 244212.

<https://journals.biologists.com/jeb/article/225/18/jeb244212/276686/Behavioural-temperature-regulation-is-a-low>

2. Scott, M. E., Tebbett, S. B., Whitman, K. L., Thompson, C. A., Mancini, F. B., Heupel, M. R., & Pratchett, M. S. (2022). Variation in abundance, diversity and composition of coral reef fishes with increasing depth at a submerged shoal in the northern Great Barrier Reef. *Reviews in Fish Biology and Fisheries* 32:941-962. <https://link.springer.com/article/10.1007/s11160-022-09716-9>

There is significant interest in the potential effects of climate change on wild stocks of fishery target species, which is particularly evident based on the recognised need to effectively account for climate impacts within management frameworks and decisions (e.g., in the annual allocation of commercial quota; Fox et al. 2022) as part of Queensland's Sustainable Fisheries Strategy 2017-2027. As such, this project was developed in consultation with a large number of stakeholders, including FRDC (QLD RAC), QDAF, GBRMPA, WWF, and numerous representatives of commercial and recreational fishing sectors. There was also a dedicated steering committee initially established to provide ongoing advice on the conduct of this project. This group was particularly important in revising and refining research priorities in the aftermath of COVID disruptions. However, COVID prohibited effective ongoing engagement with many initial members of the steering committee, which was compounded by the fact that many members experienced changes in their personal or professional circumstances and could not commit to meetings (even online) in the later stages of this project.

Alternative steering committee members were identified as required, mostly through connections made on the QDAF working group for the Reef Line Fishery. Moreover, the RLF working group (which includes representatives for commercial, charter and recreational fishing sectors, as well as key management agencies and non-government organisations) expressed considerable interest in receiving periodic updates on the progress of this report, along with any other relevant research on the effects of climate change on fisheries target species. As such, formative discussions regarding the progress, outcomes and ramifications of this project have occurred via the bi-annual RLF working group meetings, especially the in-person meeting held in Cairns (22-23 April 2021), but also subsequent virtual meetings (18 March 2022, and 13 July 2022). To further extend and communicate key outcomes of this project to a broad cross-section of stakeholders, including representatives of the commercial, charter and recreational fishing sectors, as well as manager and researchers, all members of the RLF working group were invited, to a one day meeting held in Brisbane (August 25th, 2022) and partly facilitated by Queensland Department of Agriculture and Fisheries.

COVID-19 has also led to postponement (and or cancellation) of scientific meetings and conferences during the formative stages of this project. Most critically, key outcomes of this research were to be presented at World Fisheries Congress (Adelaide, September 2020), but researchers were unable to commit to the revised dates for the virtual event (20-24 September 2021).

9.1 Adoption

The Queensland Sustainable Fisheries Strategy (2017-2027) commits to providing decision-making processes that are more responsive to changing conditions, while also ensuring that wild stocks are more resilient to climate change and habitat degradation. However, the harvest strategy and stock assessment

models that underpin contemporary management of the Coral Trouts and other reef fishes targeted by the RLF, are yet to explicitly or specifically account for apparent effects of environmental and habitat change on *P. leopardus* (Fox et al. 2022). This has occurred partly because there is insufficient information and certainty to explicitly key parameters used in the stock assessment model (e.g., natural mortality, or length at age) to relevant measures of changing environmental or habitat conditions (e.g., coral cover), for which there is effective and ongoing monitoring to provide updated information. The adoption of existing information, and also setting of future research priorities, will therefore necessitate, much better alignment between the biological responses being measured and the most influential parameters in existing stock-assessment models.

Without necessary information on the relationship between existing model parameters and relevant measures of changing environmental or habitat conditions, the most effective way to account for climate impacts on *P. leopardus* is to further discount the recommended biological harvest levels to account for increased uncertainty. However, model uncertainty could also be reduced through improved monitoring and catch data (Fox et al. 2022).

Some outcomes of this project can be perceived as good news in that there is little evidence that Coral Trout abundance is affected by coral bleaching, and hence fishery management and stock assessment do not require drastic change. In particular, the findings of the project do not support the originally intended goal of adjusting the regional carrying capacity based on current measures of habitat condition. The effects on Common Coral Trout abundance that were found, predominantly due to outbreaks of CoTS and tropical cyclones, were not consistent or persistent. Common Coral Trout abundance appears to be affected by local and regional changes in habitat structure and general reef health, potentially related to changes related to local productivity and abundance of potential prey species. The key drivers of such effects, together with the time scales and time lags on which they operate, are currently unclear.

This study also shows that effects of habitat degradation on Coral Trout are significantly moderated in areas that are closed to fishing (see also Williamson et al. 2014; Emslie et al. 2015), which provides increased impetus for increasing the effectiveness, if not the extent, of no-take marine reserves on the GBR. This can be achieved through new and renewed approaches to minimise non-compliance, *sensu* Bergseth et al. (2017).

10. Appendices

10.1 Additional contributors

Name	Affiliation	Contribution(s)
Hanna Scheuffele	Deakin University	Experimental setup (1a)
Michael Skeeles	Deakin University	Data collection (1a)
Teish Prescott	JCU	Data collection (1b)
Cassandra Thompson	JCU	Data collection (1b)
Deborah Burn	JCU	Data collection (2a)
Eva McClure	JCU	Analyses (2a)
Sam Mc Cormack	JCU	Analyses (2a and 2b)
Ciemon Caballes	JCU	Analyses (2a and 2b)
Brock Bergseth	JCU	Sample collection (2b)
Joey DiBattista	Australian Museum	Sample collection (2b)
Peter Waldie	The Nature Conservancy	Sample collection (2b)
Brett Taylor	University of Guam	Otolith processing (2b)
Michael O'Neill	DAF	Input to project proposal
Sian Breen	DAF	Review and recommendations
Chad Lunow	DAF	Review and recommendations
Jeffrey Ikin	DAF	Review and recommendations
Darren Cameron	GBRMPA	Review and recommendations
Chris Brown	Griffith University	Review and recommendations

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