

1 Direct and indirect effects of heatwaves on a coral reef fishery

2 **Running title:** Effects of heatwaves on a coral reef fishery

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10 **Abstract**

11 Marine heatwaves are increasing in frequency and intensity, and indirectly impacting coral reef fisheries
12 through bleaching-induced degradation of live coral habitats. Marine heatwaves also affect fish metabolism
13 and catchability, but such direct effects of elevated temperatures on reef fisheries are largely unknown. We
14 investigated direct and indirect effects of the devastating 2016 marine heatwave on the largest reef fishery
15 operating along the Great Barrier Reef (GBR). We used a combination of fishery-independent underwater
16 census data on coral trout biomass (*Plectropomus* and *Variola* spp.) and catch-per-unit-effort (CPUE) data
17 from the commercial fishery to evaluate changes in the fishery resulting from the 2016 heatwave. The
18 heatwave caused widespread, yet locally patchy, declines in coral cover, but we observed little effect of
19 local coral loss on coral trout biomass. Instead, a pattern of decreasing biomass at northern sites and stable
20 or increasing biomass at southern sites suggested a direct response of populations to the heatwave.
21 Analysis of the fishery-independent data and CPUE found that in-water coral trout biomass estimates were
22 positively related to CPUE, and that coral trout catch rates increased with warmer temperatures.
23 Temperature effects on catch rates were consistent with the thermal affinities of the multiple species
24 contributing to this fishery. Scaling-up the effect of temperature on coral trout catch rates across the region
25 suggests that GBR-wide catches were 18% higher for a given level of effort during the heatwave year
26 relative to catch rates under the mean temperatures in the preceding 6 years. These results highlight a
27 potentially large effect of heatwaves on catch rates of reef fishes, independent of changes in reef habitats,
28 that can add substantial uncertainty to estimates of stock trends inferred from fishery-dependent (CPUE)
29 data. Overestimation of CPUE could initiate declines in reef fisheries that are currently fully exploited, and
30 threaten sustainable management of reef stocks.

31 **Key words:** Heatwave, coral reef fishery, coral trout, coral bleaching, catchability, Bayesian modelling,
32 climate change.

33 Introduction

34 Rapid changes in climate are an important driver of the exploitation status of fisheries (Brander, 2010; Free
35 et al., 2019), with extreme climate events implicated in both fisheries collapses and unexpected
36 productivity booms (Belhabib, Dridi, Padilla, Ang, & Le Billon, 2018). Marine heatwaves, in particular, are
37 increasing in frequency and intensity under climate change, impacting the habitats and ecosystems that
38 regulate the productivity of fisheries (Graham et al., 2007; Lefcheck, Wilcox, Murphy, Marion, & Orth, 2017;
39 Oliver et al., 2018; Robinson et al., 2019; Smale et al., 2019) and directly affecting the behaviour, ecological
40 interactions, spawning, survival and the distribution of fishery species (Auth, Daly, Brodeur, & Fisher, 2018;
41 Caputi et al., 2019). Heatwaves can impact fisheries productivity through the direct effects of temperature
42 on the physiology of target species and indirect effects that play out through impacts on their ecosystem,
43 but these are seldom distinguished.

44 Coral reef fisheries support millions of livelihoods globally (Burke, Reyta, Spalding, & Perry, 2011), but their
45 productivity may be jeopardized by effects of heatwaves on fish physiology and behaviour (Pratchett et al.,
46 2017), foodwebs (Hempson et al., 2017; Rogers, Blanchard, & Mumby, 2018), and through the loss of coral
47 habitats that are sensitive to heatwaves (Hughes et al., 2018; Stuart-Smith, Brown, Ceccarelli, & Edgar,
48 2018). Coral habitat loss is the most frequently observed cause of indirect heatwave impacts on reef
49 fisheries to date (Bell et al., 2013; Graham et al., 2007; Robinson et al., 2019). Coral death causes shifts in
50 benthic community composition (Darling et al., 2019; Hughes et al., 2018) and changes in structural
51 complexity (Ferrari et al., 2016), both of which are important for early life-stages of reef fishery species
52 (Graham & Nash, 2013; Wen, Pratchett, Almany, & Jones, 2013). The effects of warming on the physiology
53 and ecology of fishes may also impact reef fisheries, by directly changing survival, growth, activity patterns,
54 and therefore the availability of fish to the fishery (Pratchett et al., 2017), or indirectly by affecting habitat
55 and prey availability (Hempson et al., 2017). The direct effects of heatwaves on reef fishes are strongly
56 supported by experimental studies (Pratchett et al., 2017), but effects of contemporary heatwaves on reef
57 fisheries remain poorly understood.

58 The impacts of heatwaves on the growth and distribution of fish stocks are likely to be confounded with
59 other environmental changes, because these impacts will play out over multiple years. Short-term impacts
60 of heatwaves on fisheries species may be expected through sudden declines in survival and behavioural
61 change. In particular, behavioural responses of reef fishes to changes in temperature can be strong
62 (Pratchett et al., 2017). These behavioural responses to temperature change can affect the catchability of
63 fish by fisheries, where catchability is commonly defined as a scaling constant relating catch-per-unit-effort
64 (CPUE) to biomass (Patterson, Pitcher, & Stokes, 1993; Wilberg, Thorson, Linton, & Berkson, 2009).
65 Importantly, catchability can change over time and space, depending on a number of behavioural attributes
66 of the fishes, including changes in activity, feeding rates or escape responses – most of which are
67 temperature-dependent (e.g. Bacheler & Shertzer, 2020). If catchability increases go unnoticed, a fishery

68 may maintain catch-per-unit-effort even as biomass declines, potentially resulting in a sudden unexpected
69 collapse (e.g. Hamilton et al., 2016). For example, overfishing of the chub mackerel (*Scomber japonicus*)
70 fishery off Ecuador was associated with temperature-driven changes in catchability that caused increases in
71 fishing mortality, despite effort remaining consistent over years (Patterson et al., 1993). Temperature is
72 known to affect the catchability of some reef species (Bacheler & Shertzer, 2020), though it is not clear
73 whether heatwave events could induce changes in catchability. Such effects of temperature on catchability
74 might be expected for reef fishes, given their sensitivity to temperature change (Pratchett et al., 2008).

75 Here we analysed changes in the in-water biomass and catch rates of coral trout (*Plectropomus and Variola*
76 *spp.*), the major targets of the largest commercial reef fish fishery along Australia's Great Barrier Reef
77 (GBR). The GBR is a World Heritage area and is managed through an extensive marine park and a number of
78 fisheries regulations (Hopf, Jones, Williamson, & Connolly, 2016; Little et al., 2011). The major values of the
79 reef for biodiversity, tourism and fisheries are increasingly under threat from repeated marine heatwaves
80 that have caused mass bleaching events, and severe cyclones (GBRMPA, 2019; Mellin et al., 2019). The
81 2016 pan-tropical heatwave caused coral bleaching on 60% of the GBR's reefs, with widespread coral
82 mortality subsequently observed (Hughes et al., 2018; Stuart-Smith et al., 2018). Changes in fish community
83 structure were also evident along the entire GBR, much of which appeared to be in direct response to
84 warming rather than a result of coral mortality (Stuart-Smith et al., 2018), although coral mortality also had
85 clear impacts, particularly on small coral-dependent reef fishes (Richardson, Graham, Pratchett, Eurich, &
86 Hoey, 2018). It is not clear whether the heatwave also affected reef fisheries. The reef line fishery is the
87 largest fishery operating in the GBR marine park and the main targets are coral trout. Coral trout physiology
88 and behaviour are sensitive to changes in temperature (Pratchett et al., 2017), but they also respond to
89 changes in prey fish abundance (Hempson et al., 2017) and some species are dependent on coral habitats
90 for settlement (Wen et al., 2013). Like many other reef fishery targets, the multiple potential responses of
91 coral trout to elevated temperatures imply a high likelihood of impacts of the 2016 heatwave on the
92 fishery.

93 We used underwater visual census (UVC) data from 65 reef sites on the GBR that were surveyed before and
94 after the 2016 heatwave along with CPUE data from the Queensland line fishery, enabling a concurrent
95 assessment of how the heatwave and associated habitat changes affected both coral trout populations and
96 the fishery. We first hypothesized that the heatwave decreased coral trout biomass on northern reefs,
97 where (1) temperatures exceeded those found at the warmest sites most of the coral trout species have
98 previously been recorded (Stuart-Smith, Edgar, & Bates, 2017; Wolanski, Andutta, Deleersnijder, Li, &
99 Thomas, 2017), and (2) loss of coral habitat was greatest (Stuart-Smith et al., 2018). Warming beyond
100 optimal temperatures of 25-31°C also affects multiple physiological and behavioural traits for *P. leopardus*,
101 which together would be expected to reduce survival rates (Johansen et al., 2015; Pratchett et al., 2017).
102 Therefore, we predicted that temperature rises above ~27°C would cause declines in biomass the year after

103 the heatwave. Second, we hypothesized that warming may increase the catchability of fish in the line
104 fishery. We base this hypothesis on experimental studies of coral trout thermal performance curves, which
105 indicate they eat more at warmer temperatures (Johansen et al., 2015), so they may be more likely to take
106 a lure or baited line. We then used the empirical analysis on the response of the fishery to the heat wave to
107 scale-up the data and estimate the effect of the heatwave on the annual catch of the fishery. We ultimately
108 aimed to determine how the direct and indirect effects of heatwaves on coral reef fisheries may help or
109 hinder the productivity and ongoing sustainable management of reef fish stocks.

110 **Methods**

111 Our analysis was divided into three stages. To address the first hypothesis, we used the fishery-
112 independent UVC data to model the association between coral trout biomass and environmental
113 covariates, including the heatwave anomaly and coral habitat. We then predicted coral trout biomass at the
114 scale of the entire GBR reef line fishery and analysed the association between predicted biomass and
115 fishery-dependent catch-per-unit-effort data. This analysis allowed us to test the hypothesis that warming
116 would increase catchability of coral trout. Finally, we estimated the effect of the heatwave on catches at
117 the scale of the entire GBR.

118 *Analysis of fishery-independent data on coral trout biomass from the underwater visual census*

119 Underwater visual censuses were conducted from 2010 to 2017, comprising 117 surveys before the 2016
120 heatwave and 124 surveys at the same sites between 6 months and 1 year after the heatwave (fig. 1a)
121 (Stuart-Smith et al., 2018). The UVC methodology followed the standardized Reef Life Survey protocol
122 (Edgar & Stuart-Smith, 2014), as detailed in an online methods manual (www.reeflifesurvey.com). The
123 methods consist of diver counts and size estimates of reef fishes observed along 50 m transect lines
124 ('surveys') in duplicate 5 m wide belts (total area per transect = 500 m²). Biomass was calculated from fish
125 length and counts using species-specific length-weight coefficients obtained from FishBase
126 (www.fishbase.org) and a correction factor for diver-bias in estimation of size, as used in previous studies
127 with these data (Edgar, Barrett, & Morton, 2004). Although UVC data distinguished seven species of coral
128 trout that are caught by fishers (dominated by *Plectropomus leopardus*, but also including four other
129 *Plectropomus* spp. and two *Variola* spp.), these are not distinguished in the fishery statistics. Therefore,
130 UVC data on coral trout species were aggregated for the main analyses to be consistent with the fisheries
131 data.

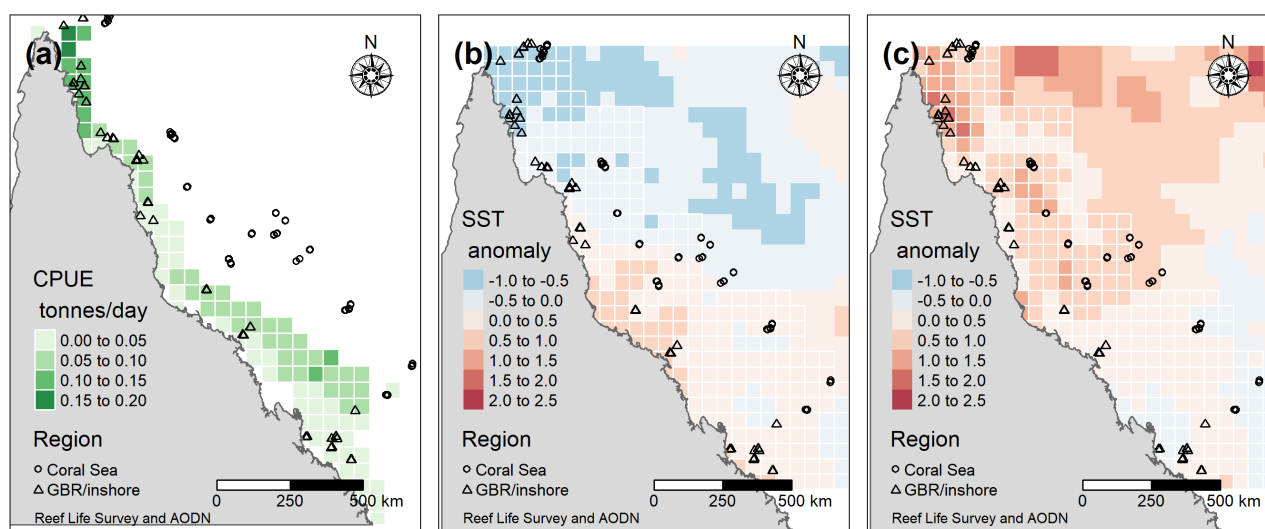


Figure 1 (A) Map of the mean annual catch-per-unit-effort in the line fishery (2007-2016) across the Great Barrier Reef and the locations of the UVC sites (note that sites outside of the GBR in the western Coral Sea shown were used for the supplemental analysis of species composition, but are outside of the limits of the fishery, so were not used for matching to the fisheries data), (B) SST anomaly for 2015 with sites surveyed before the heatwave, and (C) SST anomaly for 2016 with sites surveyed after the heatwave.

We modelled coral trout biomass from the UVC in response to the heatwave and other environmental covariates using a Bayesian generalized linear mixed effects model (GLMM). There was a high frequency of zero biomasses observed in the UVC, so we used a log-normal hurdle model. The hurdle model modelled presence-absence of coral trout on surveys using a Bernoulli GLMM with a logit link function, and then biomass of coral trout on surveys where they were present with a log-normal distribution. The mean expected biomass from the model for a given covariate combination is the product of predicted presence rate and biomass conditional on presence (e.g. Mellin, Russell, Connell, Brook, & Fordham, 2012).

We modelled both occurrence (i.e. a binary variable for presence/absence), and biomass if present, as functions of three nested random effects and multiple environmental covariates including the long-term mean temperature for a location, the temperature anomaly for that location in the year of the survey, marine protected (MPA) area zone status, percent cover of live hard corals, wave exposure, depth and commercial fishing pressure. The random effects were included to model the spatial hierarchy of sampling and included: surveys (transect scale) within sites, and sites within the fishery logbook reporting grids (0.5 degree grid cells, fig. 1). The MPA zone status was either fished (including restricted fishing 'yellow zones') or no-take ('green zones'). Wave exposure was scored on a three-point scale with 1 = sheltered from winds in the prevailing direction; 2 = exposure to wind from the prevailing direction; and 3 = exposed to ocean swells. Depth was binned into three categories of <4 metres, 4-10 metres, >10 metres. Commercial fishing pressure was quantified as the sum of all days of fishing since 2007 in each survey's logbook grid.

157 Sea surface temperature data was measured by AVHRR instrument on the NOAA-19 satellites (Integrated
 158 Marine Observing System, 2014). We obtained composite (IMOS - SRS - SST - L3C) sea surface temperatures
 159 at a daily resolution from night-time passes at a 0.02 by 0.02 degree resolution (L3S dataset, cylindrical
 160 equidistant projection) for 2010-2016. We chose this time period to be consistent with the time-period of
 161 the UVC data. Validation against ocean buoy data suggests that bias is usually $<0.05^{\circ}\text{C}$ (Integrated Marine
 162 Observing System, 2014). We then aggregated the daily data to monthly values by taking the maximum at
 163 any given grid cell in each month of each year. Monthly maximums were then resampled to unprojected
 164 coordinates, using a bilinear interpolation, and finally aggregated to the scale of the logbook reporting grids
 165 again by taking the maximum value. All analyses were performed in the R programming language (3.6.2
 166 Team, 2019) using the packages 'raster' (Hijmans, 2020) and 'sf' (Pebesma, 2018).

167 The temperature data were pre-analysed to create two covariates representing the mean temperature for
 168 each logbook reporting grid (averaging over all days from 2010-2016) and the annual temperature anomaly
 169 for the year of the UVC survey. Years were taken as Australian financial years (1st July-30th June) that span
 170 summer and are consistent with the reporting of fish catch in Queensland. The anomaly was calculated per
 171 grid as the grid's annual mean temperature minus its 2010-2016 mean (fig. 1b & c). Both temperature
 172 covariates were calculated at the scale of the logbook reporting grids to be consistent with the fishery data.

173 The mean temperature was included to capture spatial gradients of biomass that relate to temperature,
 174 the anomaly was included to capture year-to-year responses of biomass to temperature. We also included
 175 a term for the interaction between the mean temperature (reflecting latitudinal gradients) and the
 176 anomaly. The interaction allowed for our hypothesis that in the year after the heatwave biomass would
 177 decrease at northern sites and show little response at southern sites.

178 The model of biomass did not allow for different performance curves for different coral trout species.
 179 However, it is likely that *Plectropomus* species have similar thermal performance curves. The range mid-
 180 point for all five *Plectropomus* species investigated occurs at average annual temperatures of 22-29°C and
 181 all three have similar latitudinal extents (Waldock, Stuart-Smith, Edgar, Bird, & Bates, 2019). *Variola* spp.
 182 tend to occur in warmer waters than *Plectropomus* spp. (and often a little deeper), but were more rarely
 183 observed in the UVC data and are a minor portion of the catch in the commercial fishery (Leigh, Campbell,
 184 Lunow, & O'Neill, 2014).

185 Seasonal extremes of temperature may have a greater influence on fish range limits than annual means
 186 (Stuart-Smith et al 2017), so we compared models that used three different sea temperature metrics. The
 187 first metric was the annual mean and annual anomaly, as described above. We also ran models using either
 188 March maximum or July minimum sea temperatures to calculate the spatial gradient and anomalies.
 189 Comparisons of models fit with the three different temperature measures were made by comparing the
 190 models for their leave-one-out cross-validation scores (LOO). The LOO was computed using the efficient

approximate algorithm (Bürkner, 2018; Vehtari, Gelman, & Gabry, 2017). Some observations were a poor fit to the approximation, for these we calculated exact cross-validation scores (Bürkner, 2018). Model fits were verified by checking the spread of the Dunn-Smyth residuals of both the occurrence and biomass stages. We also confirmed there was no spatial auto-correlation present in the Dunn-Smyth residuals.

We then sought to estimate how reliably we could extrapolate the biomass predictions to regions with no UVC surveys. After choosing the most parsimonious temperature covariate, we made one more comparison of the full model to a reduced model. The reduced model included only those covariates that were available across the entire GBR (i.e. fixed effects of SST covariates, MPA zone, commercial fishing pressure, and the random effects). The comparison of the full and reduced models was made with the LOO as above.

All models were fitted with the “Bayesian Regression Models using Stan” (*brms*) R package (Bürkner, 2018), with four chains, where each chain had a warm-up of 1000 iterations and then 2000 samples. We confirmed algorithm convergence with visual checks and the Rhat statistic. We chose conservative priors that promoted shrinkage of effects towards zero, including a $N(0, 10)$ prior for fixed effects and $Exp(1)$ priors for the random effect standard deviations (McElreath, 2020).

We present results as predicted change in expected biomass across the temperature gradients and anomalies. This facilitates interpretation of interactive terms. Other effects were plotted with marginal uncertainty intervals, and we calculated the 2-tailed probability of whether the estimate was different to zero.

Analysis of catch-per-unit effort data

Fisheries catch data for coral trout were provided by the Queensland Government (State of Queensland Department of Agriculture Fisheries and Forestry, 2020), obtained from mandatory logbooks filled out by commercially licensed fisheries operating in Queensland waters and the Great Barrier Reef Marine Park. Species-specific data for coral trout from the fishery are not considered accurate, but the fishery catch is primarily composed of *P. leopardus* (Leigh et al., 2014). Catch and effort (days of fishing) are available on an annual basis (financial years 1st July – 30th June) since 1990 for the fisheries reporting grids (fig. 1). The fishery generally operates in depths <30 metres. Grid/year combinations with less than five boats fishing are not available due to data privacy rules.

We next estimated how catchability varied with temperature. We defined catchability as slope of the relationship between biomass and CPUE:

$$CPUE_{i,t} = e^{q_0} e^{q_1 T_{i,t}} B_{i,t} e^{\epsilon_{i,t}}; \quad \text{Equation 1}$$

Where the term $e^{q_0} e^{q_1 T_{i,t}}$ reflected the ‘catchability coefficient’ with intercept q_0 and a slope of q_1 on $T_{i,t}$, the annual mean sea surface temperature in a grid, i , in a year t . $B_{i,t}$ was the unobserved biomass in a grid

223 and there are log-normally distributed errors $\epsilon_{i,t}$ on CPUE. If we log this equation, then we have a log-linear
224 model that can be fit using Bayesian regression and a normal distribution on $\ln(\text{CPUE})$.

225 Biomass ($B_{i,t}$) at the scale of the logbook grids was unknown, so we predicted it from the reduced model of
226 coral trout biomass in UVC surveys. This meant we matched UVC collected at the scale of 500 m² surveys to
227 the fishery grid cells (~2900 km², fig. 1a). The disparity in scale meant it was important to account for
228 uncertainty when scaling-up biomass predictions. So the unknown logbook scale biomass was modelled
229 with a measurement error model:

$$230 \quad \ln(B_{i,t}) = \ln(\overline{B_{i,t}}) + z_{i,t}; \quad \text{Equation 2}$$

231 Where $\overline{B_{i,t}}$ was the predicted mean grid level biomass, $z_{i,t}$ was an error term taken as the standard error of
232 the posterior predictive estimate of $\overline{B_{i,t}}$ from the biomass model. Predictions for coral trout kg/ha were
233 conditional on the grid level random effects, disregarding site level variation. For each grid we then
234 obtained posterior distributions for grid-level biomass by multiplying posterior distributions for kg/ha by
235 the grid's area.

236 The scale matching model had CPUE data from 25 grid/year combinations from 17 logbook grids and
237 spanned an area of 1.22 million ha of reef and 21% of annual mean catch over 2010-2016. The model was
238 fitted with the 'brms' R package using the measurement error model specification and 18000 samples from
239 4 chains to achieve convergence. Priors and model verification were as above for the biomass model.

240 Our hypothesis that temperature directly affects catchability may be invalidated if there were shifts in
241 species composition before and after the heatwave, since different coral trout species may have different
242 catchability. To confirm the dominance of *P. leopardus*, we examined the proportional composition of the
243 biomass of the coral trout taxa observed in the UVC data by species before versus after the heatwave. We
244 plotted composition for two regional covariates: inshore Great Barrier Reef, offshore Great Barrier Reef or
245 Coral Sea, and southern (> 20.5°S), mid (20.5°S – 15.3°S) and northern regions (< 15.3°S). Regions were
246 chosen to ensure a relatively even spread of sites among the different regions and capture known regional
247 variation in species composition. We included an additional 121 Coral Sea sites from (Stuart-Smith et al.,
248 2018) in this analysis, but note these were not included in the model of coral trout biomass because paired
249 CPUE data were lacking.

250 *Analysis of all CPUE data using reef area as a proxy of biomass*

251 We verified the relationship between CPUE and UVC data by conducting a further analysis on all annual
252 CPUE data from 2011 onwards, giving us a sample size of 461 grid/years (compared to 25 grid/ year
253 combinations in the UVC analysis). We chose to use data from 2011 because this recent period has had
254 reasonably stable management regulations (Leigh et al., 2014). For this verification, we included reef area
255 per grid cell as a proxy of coral trout biomass. We also included covariates for cumulative fishing effort

(days of fishing) over the past five years, as proxies for coral trout biomass. UVC biomass was highly variable across survey sites, and at the scale of the fisheries grids, variation in biomass was primarily driven by the area of reefs (fig S1). Fishing effort is also likely an important driver of spatial patterns in coral trout biomass. The larger sample of data allowed us to consider additional covariates that are known to affect catchability (Leigh et al., 2014). These were number of High-wind Days per year (number of days with mean wind speed over 20 knots) and number of cyclones per year (Bureau of Meteorology, 2020). Wind and cyclones were included because coral trout are believed to move deeper than the typical fishing depths after high-wind events (Leigh et al., 2014). We also used historical fishing effort (summed over the past 5 years), area of reef in the grid cell, and a smoother on financial year. High wind days was estimated using the Cross-Calibrated Multi-Platform gridded surface vector winds product, which is an interpolated global wind product that uses a combination of remote and in-situ data (Wentz et al., 2015). We fit this model as a generalized additive mixed model (GAMM, (Wood, 2017)), estimating the effect of each covariate with thin plate smoothing splines. The GAMM framework allowed us to include spatio-temporal random effects, which would capture other spatial gradients in CPUE not related to the covariates. These were individual grid cell level random intercepts and a Gaussian process smooth for grid cell location, with the smooth varying by years (Wood, 2017). The model was fitted using restricted maximum likelihood optimisation and Bayesian credible intervals were estimated as per Wood (2017). We performed stepwise simplification on the full model using the AIC criteria (steps given in Table S1), choosing the model with the lowest AIC for analysis of effect sizes.

Scaling up the impact of the heatwave on fishery catches

We aimed to estimate the impact of the heatwave on fishery catches during the heatwave year. We first evaluated errors in the prediction of CPUE. We calculated the root-mean-square error by comparing model predictions for $\ln(\text{CPUE})$ to observed $\ln(\text{CPUE})$ for all grid/year combinations with no UVC survey over 2010-2016. $\ln(\text{CPUE})$ was normalized against the range of $\ln(\text{CPUE})$. As a further comparison we compared predicted catch, based on the 2015-2016 effort distribution to observed catch. These estimates of error are important when interpreting the strength of results of the scaling-up.

To estimate the effect of the heatwave on the total catch of the fishery, we predicted CPUE across all grid cells in the 2015-2016 financial year using temperature conditions from that year. We then multiplied by effort to get the predicted catch distribution for that year. We compare the predicted catch distribution in 2015-2016 against catch predicted for the average (2010-2016) temperature distribution.

286

Results

Response of coral trout biomass to the heatwave and other environmental covariates

Model selection did not discriminate among the three models with annual and seasonal temperature metrics, the LOO was 1622 (± 81.2 S.E.), 1621 (± 81 S.E.), 1622 (± 81.5 S.E.) for the annual average, March maximum and July minimum temperatures respectively. We therefore proceeded with models based on the March maximum, because this matched the season when the heatwave was most severe.

The biomass model had a predictive R^2 of 0.30 (0.17-0.40, 95% CIs), and the occurrence model had an in-sample AUC of 0.69 (0.62-0.75, 95% CIs). Model verification indicated normality assumptions were satisfied (fig. S1), and that there was no detectable spatial autocorrelation in Dunn-Smyth residuals.

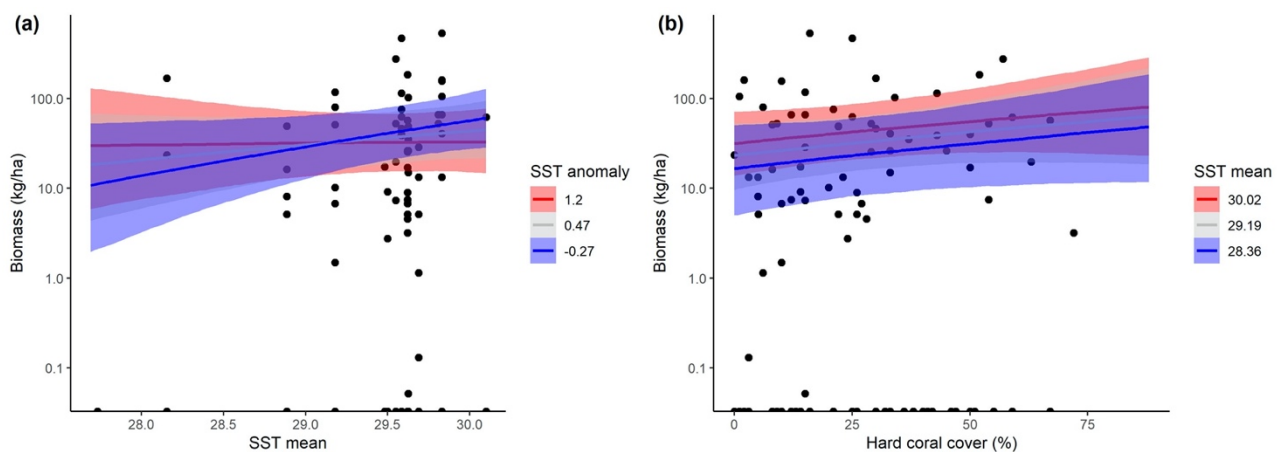
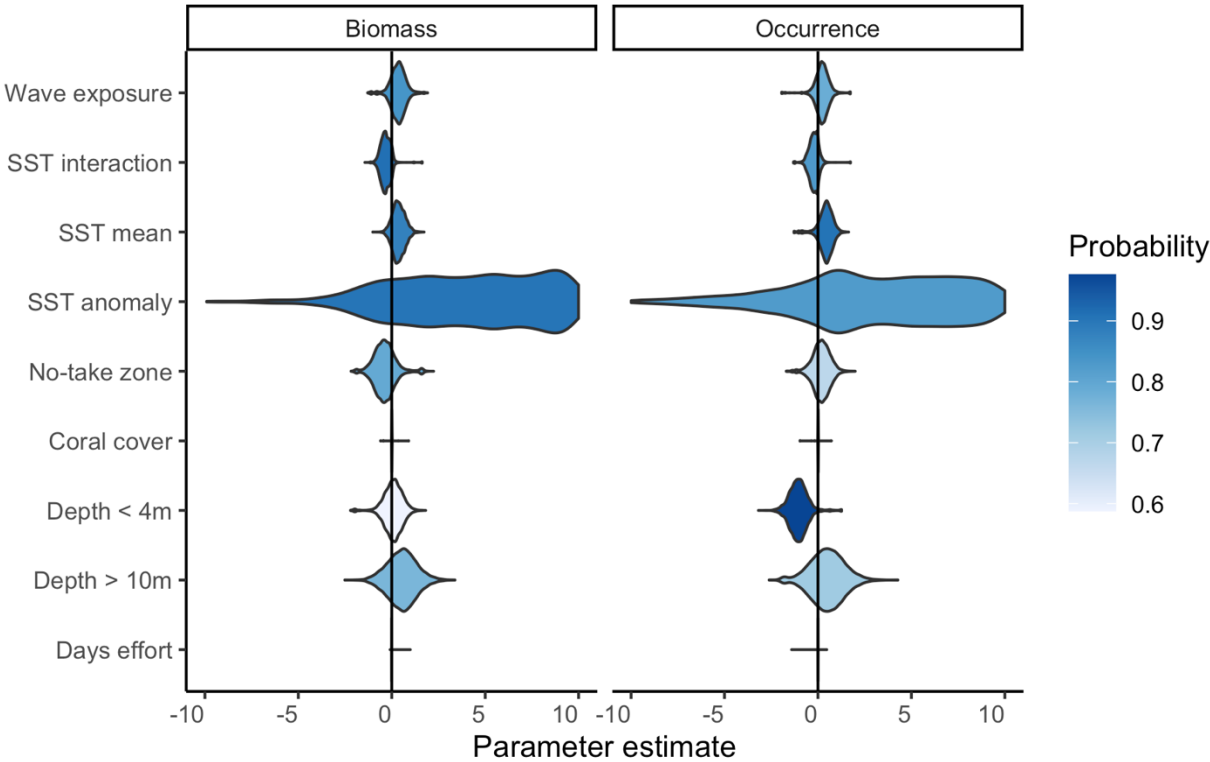


Figure 2 Expected biomass of coral trout on UVC surveys for mean SST and SST anomalies (a) and different levels of coral cover crossed with different mean SST (b).

The expected biomass of coral trout was higher in regions with higher long-term averaged SST, but overall there was high unexplained variation in the biomass trend, so the effect of SST was weak (fig. 2). During the heatwave, the warmer than average SST flattened the gradient of biomass, such that warmer sites were predicted to have slightly lower biomass and cooler sites predicted to have slightly higher biomass (fig. 2). This flattening was indicated by high probability that mean SST and the SST anomaly interacted to affect biomass (probability the effect was $< 0 = 0.94$, fig. 3). There was slightly less evidence for an interactive effect on the occurrence rate (probability the effect was $> 0 = 0.91$, fig. 3). For example, the average temperature anomaly at sampling sites before the heatwave was -0.1° , whereas during the heatwave it was $+1.0^\circ$. Given these anomalies, the models suggested with high probability that coral trout biomass showed regional increases after the heatwave in the coolest fishery grid cells (average SST 27.7°C ; probability = 0.94) and decreased in the warmest grid cells (mean SST 30.1°C ; probability = 0.98). The broad uncertainty intervals indicate that this effect was weak relative to other sources of variation (fig. 2).

None of the other environmental covariates, including coral cover, had a strong effect on coral trout biomass, and only depth affected coral trout occurrence (fig. 3). Coral trout were predicted to occur less frequently in shallower water (< 4 metres deep; fig. 3, prob $>0 = 0.99$).

314 The reduced model that included only variables available across the GBR had a slightly poorer fit (fig. S1)
 315 than the models with the small-scale covariates, however the fit was within the error bounds of the full
 316 model LOO estimates (LOO = 1672, ± 81.5 S.E.). The estimates for the effect of the temperature anomaly in
 317 the reduced model were similar to the full model (fig. S2).



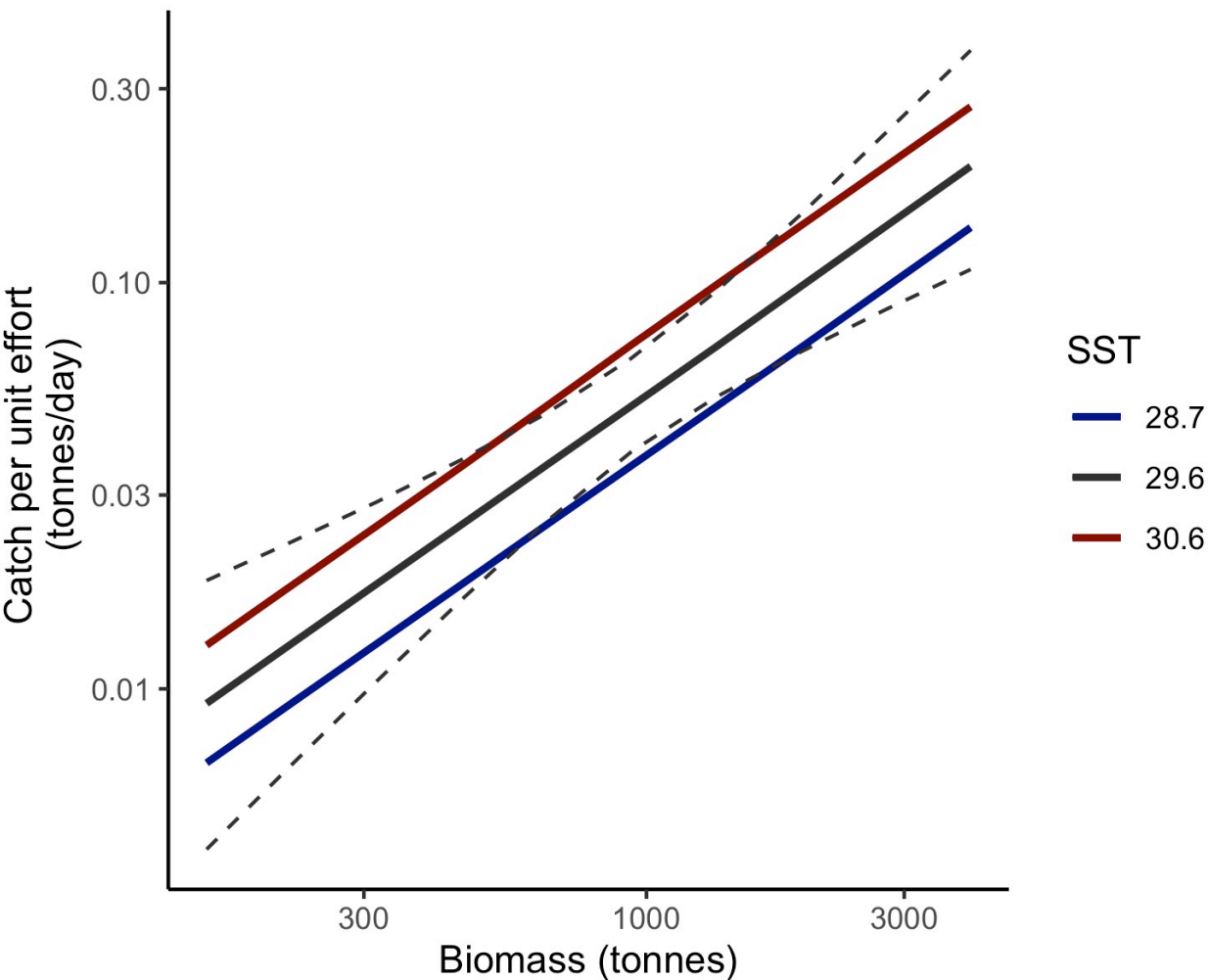
318
 319 **Figure 3** Distributions of the marginal parameter estimates from the environmental model of coral trout
 320 biomass (A) and occurrence (B). Colours indicate two tailed probabilities of $x > 0$ or $x < 0$, where darker
 321 colours indicate a higher probability the parameter estimate is different from zero. Note the x-axis is
 322 truncated at +10, the SST anomaly parameter estimates had long positive tails.

323
 324 *Catchability in relation to underwater biomass data and SST*

325 The estimates of UVC biomass for whole CPUE grid cells had a positive relationship with reef area, which
 326 flattened for reef areas $> 500 \text{ km}^2$ (fig. S3). Across all grid cells with coral-trout catch, CPUE was positively
 327 related to reef area (fig. S4).

328 CPUE was positively related to the estimates of mean in-water biomass (fig. 4; slope of 0.93, 0.57 to 1.34,
 329 95% CIs, fit to data shown in fig. S5). Deviations in the relationship between CPUE and in-water biomass
 330 were consistent with a positive effect of temperature on catchability (fig. 4, fit to data in fig. S6), with an
 331 average increase in CPUE of 1.4 times per 1 S.D. increase in temperature (1.08 to 1.78, 95% CIs) and a
 332 probability of 0.999 that the SST effect increased CPUE. For instance, at a biomass of 500 tonnes (per grid
 333 cell) there was a 0.003 probability that CPUE was > 0.03 tonnes/day at average temperatures but 0.89

334 probability that CPUE >0.03 for a temperature 1 S.D. (=0.98°C) above average. The increase in catchability
 335 under warming meant that more catch can be taken with an equal amount of effort in warmer years, or the
 336 same amount of catch can be taken with less effort (fig. 4).



337
 338 **Figure 4** Predicted relationship between grid-level expected biomass predictions and CPUE under different
 339 temperatures. Colours represent SST values (mean \pm 1 S.D.), 95% CIs, are given as dashed lines for just the
 340 mean SST for clarity of presentation.

341 We confirmed that the catchability change could not be explained by shifts in species composition.
 342 *Plectropomus leopardus* was the dominant coral trout species on underwater censuses across most of the
 343 Great Barrier Reef region (fig. S7), while *Plectropomus laevis* dominated at Coral Sea sites and *Plectropomus*
 344 *maculatus* dominated at inshore southern sites. There was no significant change in the dominant species
 345 before versus after the heatwave for any region, although *P. laevis* became slightly more common as *P.*
 346 *leopardus* declined at northern offshore Great Barrier Reef and northern Coral Sea sites (which do not
 347 overlap with the fishery data).

348 *Analysis of all CPUE data using reef area as a proxy of biomass*

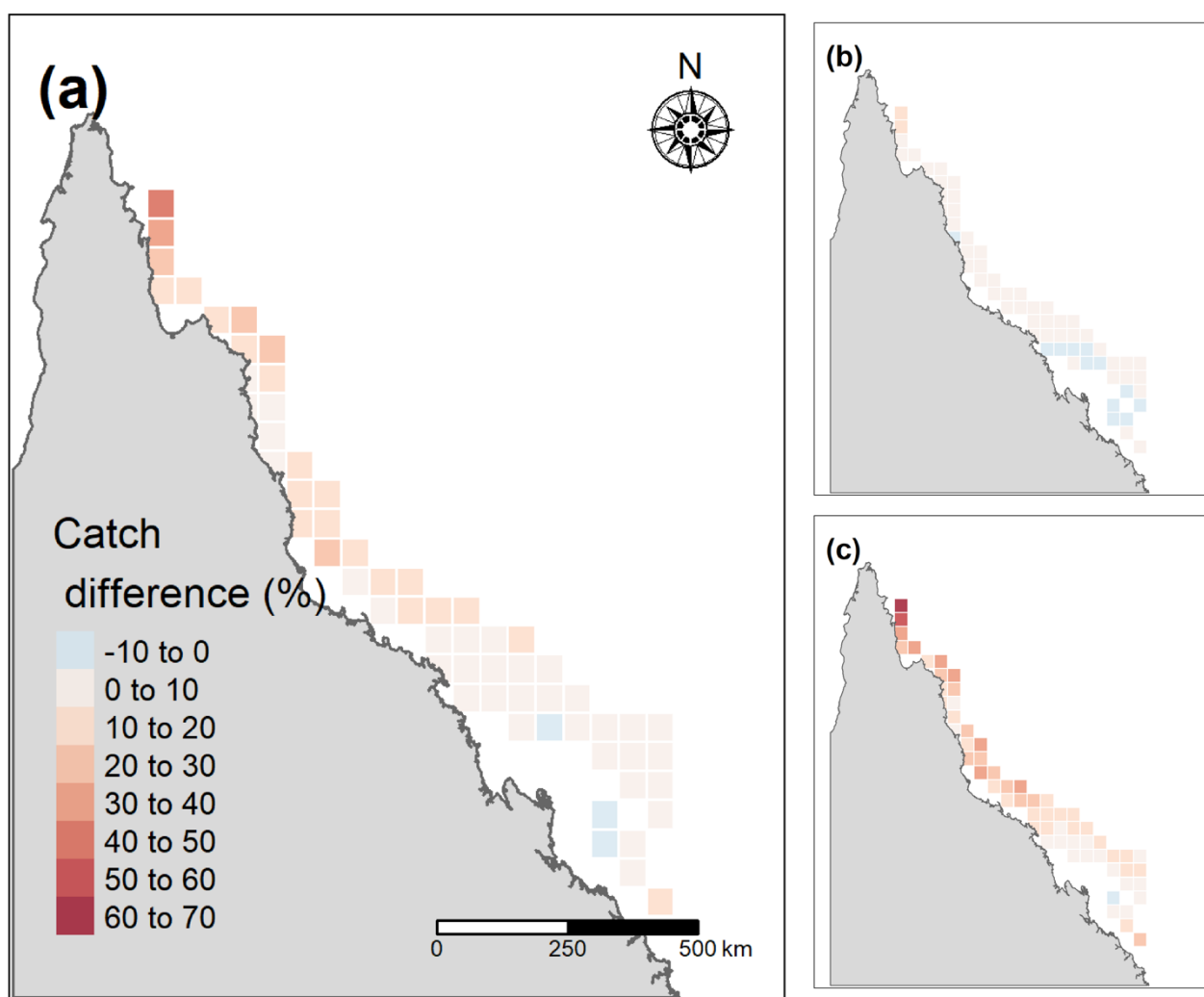
349 The analysis relating all available CPUE data back to 2011 to reef area (a proxy of biomass) and other
350 environmental covariates indicated that a model with a non-linear effect of reef area, linear effect of SST,
351 non-linear effect of year, and a spatial smooth that varied by years was optimal (Table S1). Wind and
352 cyclones were not important predictors of annual CPUE. The effect of area indicated increasing catch rates
353 up to a maximum at a reef area of 400 km² (fig. S4). Increases in SST in a grid in a year also increased CPUE
354 by a multiple that was of similar magnitude to that estimated by the UVC model: 1.32 times (fig. S7, 1.1 to
355 1.63, 95% CIs). The probability SST was associated with increased CPUE was also > 0.999.

356 *Scaling-up catch estimates for 2016*

357 Total catch in the grid cells with data for the 2015-2016 financial year was reported to be 850 tonnes.
358 Transforming the predicted CPUE in all grid cells and using the 2015-2016 effort distribution gave an
359 expected catch of 798 tonnes (368-1934 tonnes, 95% CIs). This estimate accounted for uncertainty in the
360 grid level biomass estimates. The root mean square error for predictions of ln(CPUE) in grid squares that
361 did not have a UVC survey was 1.41, or error that was 30% of the range of ln(CPUE) values (20-54%, 95%
362 CIs). The error was high because of uncertainty in biomass and the estimated catchability coefficient.

363 When predictions were made conditional on the mean UVC biomass, the CPUE model predicted a catch of
364 805 tonnes in 2015-2016 (544-1224 tonnes, 95% CIs). The catch estimate was reduced to 680 tonnes (464-
365 1018 tonnes, 95% CIs) when predictions were made using average March temperatures over 2010-2016.
366 Thus, the model predicted catches during the heatwave year were 18% higher than under average
367 temperatures for the same amount of fishing effort. The greatest predicted effect of the heatwave on catch
368 was in the Northern and mid-GBR (fig. 5), where the temperature anomaly was the greatest (fig. 1). In the
369 north there was a high certainty of a positive effect of the heatwave on catches (95% CIs >0, fig. 5),
370 whereas in the south there was lower certainty as to the direction of the effect of the heatwave on catches
371 (95% CIs close to zero, fig. 5).

372 The effect of the heatwave was not evident in the overall spatial pattern of catch in 2015-2016, which were
373 largely consistent with earlier years (fig. S9). This suggests increases in catchability were compensated for
374 by reduced fishing effort.



375

376 **Figure 5** Expected difference in catch (%) during the heatwave year (2016) from mean temperature
 377 conditions. A, B, C show median and lower and upper 95% probability quantiles. Predictions were made
 378 assuming coral trout biomass was fixed at its mean for each fishery grid.

379 Discussion

380 The most significant effect of the heatwave on coral trout that we observed was a higher catch per unit
 381 effort where biomass had declined following the heatwave, caused by an increase in catchability. The
 382 increase in catchability could have many causes, but is consistent with experimental studies that have
 383 tested the physiological tolerance of coral trout to warming. Warming affects multiple physiological and
 384 behavioural traits that we hypothesize are related to catchability. Warming increases metabolic needs of
 385 individual fish, who respond by increasing their feeding rates (Johansen et al., 2015). Higher feeding rates in
 386 warmer seas may explain the increase in catchability: the reef line fishery uses bait or lures to catch fish
 387 (Leigh et al., 2014), so fish may be more likely to take the line if they are feeding at a higher rate. Warming
 388 to the extent that occurred in the heatwave reduces spontaneous swimming speed (Johansen, Messmer,
 389 Coker, Hoey, & Pratchett, 2014), and warmer climates and seasons are also associated with smaller home
 390 ranges (Scott, Heupel, Simpfendorfer, Matley, & Pratchett, 2019). Swimming speed and home range size

391 may both affect the likelihood that coral trout take bait or lures. Further work is needed to test how
392 changes in these behavioural traits affect fish preferences for bait versus wild prey, which may be harder to
393 catch.

394 Three alternate hypotheses for the causes of these changes in catchability include foraging efficiency, prey
395 availability and species turnover, all of which we consider less likely than physiologically mediated impacts
396 on catchability. First, loss of coral habitats may impact feeding success by coral trout (Hempson et al.,
397 2017), which could presumably affect their catchability in the fishery. It has been proposed that the
398 likelihood of coral trout taking bait or lures is lower after loss of structurally complex corals because it is
399 easier for coral trout to catch their prey (Brown, Taylor, Wabnitz, & Connolly, 2020; Leigh et al., 2014).
400 However, this hypothesis predicts declines in catchability following coral loss, the opposite pattern to what
401 we observed.

402 Second, declines in structurally complex coral may also see a reduction in prey fishes, increasing the
403 likelihood that coral trout take bait or lures. This process is most likely to affect coral trout over longer
404 time-scales than our study, because it requires erosion of reef structure to impact prey fishes. It is also
405 unlikely to impact such flexible predators as coral trout. Populations of *P. maculatus* can switch to feeding
406 through entirely different trophic pathways following coral degradation (Hempson et al., 2017). No
407 widespread changes in potential prey items (small fishes) were observed in the UVC data as a result of the
408 heatwave (although a subset of highly coral-dependent species suffered on the worst hit reefs)(Stuart-
409 Smith et al., 2018), and it is unlikely trout would be found at sites where they were food limited. Longer-
410 term degradation of coral will cause changes in food webs that may impact coral trout populations
411 (Hempson et al., 2017; Rogers et al., 2018) but we suggest that the major impact on fisheries would be
412 noticed through changes in occurrence and biomass rather than changes in catchability.

413 A third hypothesis we can exclude is that changes in the relative proportions of the different coral trout
414 species to the catch could also affect the overall catchability for the fishery. Our models predicted the
415 greatest increase in catchability on northern reefs, which remained dominated in the UVC data by *P.*
416 *leopardus* both before and after the heatwave (Fig. S8). Inshore northern reefs saw a decline in the biomass
417 of *P. maculatus* relative to other coral trout species and it is possible this change in species composition
418 may have contributed to changes in catchability if this species was harder to catch than the others. We are
419 not aware of any evidence documenting that coral trout species vary in their catchability in line fisheries,
420 but fish catch data resolved to the species level could help future studies to address this knowledge gap.

421 We also observed that coral trout biomass was reduced after the heatwave in warmer low latitude reefs,
422 but was stable or slightly increasing on cooler high latitude reefs. The model suggested that the decline in
423 biomass was attributed to the temperature anomaly, rather than fishing pressure, but the high variability in
424 predictions suggests further data are needed to confirm the effects of temperature on coral trout biomass

on the GBR. Further, it is unclear from this data if biomass changes were caused by migration or increased mortality. Coral trout population productivity may be sensitive to climate warming, and vulnerable to decline in low latitude locations that are already close to coral trout upper thermal limits (Stuart-Smith et al., 2017). Effects of high temperatures observed for coral trout species include reduced aerobic scope, swimming speeds and survival at temperatures from 27-30°C (Pratchett et al., 2017). These observations from laboratory studies are consistent with our finding that declining biomass may have occurred at the northern most edge of the range, where mean summer temperatures are close to 30°C and the heatwave raised temperatures by ~1°C (Wolanski et al., 2017). At higher latitudes, where typical temperatures are below the thermal optimal for coral trout, heatwaves may enhance coral trout survival and contribute to higher recruitment of early life-stage individuals (Bornt et al., 2015).

A caveat to our finding of reduced biomass is that behavioural change may also affect UVC estimates of biomass. Some fishes may respond to warming by migrating to deeper, cooler water (Dulvy et al., 2008), and coral trout are believed to migrate deeper in response to other extreme weather events, like cyclones (Leigh et al., 2014). However, it is unlikely that the reduction in biomass observed is indicative of coral trout migrating to reefs beyond the span of the UVC surveys, because coral trout are most common down to depths of 20 m (Leigh et al., 2014) and the UVC surveys included surveys to 17 m (Stuart-Smith et al., 2018). Home range size also changes in response to temperature (Scott et al., 2019), and home-range size may affect the likelihood of detecting fish on UVC surveys, though it is not clear in what direction. Electronic tagging studies (e.g. Scott et al., 2019) and paired catch-UVC studies (Bacheler & Shertzer, 2020) would help identify the mechanism for reduced biomass at warm sites.

Some coral trout species make use of live coral habitat for settlement (Wen et al., 2013) and feed on prey that use coral habitat (John, Russ, Brown, & Squire, 2001), so coral loss could cause declines in coral trout biomass over longer timespans than the duration of this study. Temperature may also impact spawning behaviour and affect fertilization and therefore numbers of settlers (Pratchett et al., 2017). Settling *P. maculatus* rely on structured corals for shelter, with enhanced recruitment in areas with higher live coral cover (Wen et al., 2013). Given the age at first breeding for coral trout is 2-3 years and that adult biomass is dominated by older age-classes, the impacts of reduced coral cover on adult biomass are unlikely to manifest for >5 years (Brown et al., 2020). The dependency of coral trout on coral may expose the productivity of the fishery to the multiple stressors, including poor water quality and climate warming, that are currently causing coral declines and hindering coral recovery (Mellin et al., 2019; Wolff, Mumby, Devlin, & Anthony, 2018). Continuing monitoring is needed to understand the magnitude of coral habitat loss effects on coral trout over longer timescales than were studied here.

Global warming could potentially affect sustainability of the coral trout fishery if heatwave-induced spikes in catchability are not accounted for in stock assessments. Currently, heatwave events of the magnitude observed in 2016 are predicted to occur every 3 years; with 1.5 degrees of global warming, 2016-like events

460 may occur more often than every 2 years on average (King, Karoly, & Henley, 2017). Since 2016, the GBR
461 has experienced successive heatwaves in 2017 and 2020. The management regime of the reef line fishery is
462 likely robust to infrequent changes in catchability of the magnitude we observed because catches are well
463 below the maximum sustainable yield (Campbell, Leigh, Bessel-Browne, & Lovett, 2019). The existing
464 management regime that mixes marine parks and catch quotas is also robust to regional variation in
465 ecological dynamics (Bode, Sanchirico, & Armsworth, 2016), overfishing (Hopf et al., 2016; Little et al.,
466 2011) and climatic change (Hopf, Jones, Williamson, & Connolly, 2019). A stock assessment conducted in
467 2014, which utilized UVC and CPUE data, did not find any effects of coral bleaching events on stock
468 productivity, and environmental change was found to have limited impact on the fishery (Leigh et al.,
469 2014). Regardless, this may not be the case in future. If contemporary 3-yearly spikes in catchability are
470 combined with productivity declines due to loss of recruitment habitat (Brown et al., 2020), the stock may
471 become susceptible to overfishing. Continued monitoring of coral trout biomass is needed to assess the
472 impacts recurrent heatwaves on catchability, so we can quantify the cumulative effects of multiple
473 heatwave events, which may be non-linear. The recreational catch of coral trout adds further uncertainty
474 (see below), and future increases in recreational effort could also take stocks to the point where
475 catchability changes induced by warmer seas could be critical. The latest stock assessment identified that
476 accounting for environmental change, including heatwaves, is a priority for future stock assessments
477 (Campbell et al., 2019).

478 Stock assessments, including stock parameter estimates, need updating more frequently in fisheries subject
479 to rapid environmental change, regardless of the ecological causes of population responses to
480 environmental change (Brown, Fulton, Possingham, & Richardson, 2012). For instance, the total current
481 allowable catch in the reef line fishery is set on the basis of the ratio between current CPUE and a target
482 CPUE (The State of Queensland, 2017), but this ratio assumes a constant linear relationship between CPUE
483 and biomass. More generally than Australia, coral trout are caught in many tropical reef fisheries, but those
484 fisheries are typically poorly regulated and often overfished (Frisch et al., 2016), and increasing catchability
485 would only be expected to worsen overfishing. Our results indicate that this assumption is only reasonable
486 in the absence of changing environmental temperatures, and highlights the critical importance of fishery
487 independent data for informing stock assessments.

488 An important caveat to our analysis is that we did not consider the impact of the recreational fishery on
489 biomass or the effects of heatwaves on catchability in the recreational fishery. Overall, recreational fishing
490 made up a minority of the catch in the 2017-2018 financial year (estimated at 17% of total catch (Campbell
491 et al., 2019)), but its effects may be locally intense. The recreational fishery targets coral trout with line
492 fishing and spearfishing. Line fishing is likely to be subject to similar increases in catchability during
493 heatwaves as we observed here, whereas it is unclear how high temperatures would affect catchability by
494 spear fishers. Data from the recreational fishery are only collected intermittently and are not spatially

495 resolved for detailed use in analyses such as those undertaken here (Webley, McInnes, Teixeira, Lawson, &
496 Quinn, 2015). Future research would usefully directly involve recreational fishers to better understand
497 factors affecting catchability.

498 Globally, fisheries are highly susceptible to climate change, potentially negatively affecting food security
499 and livelihoods of hundreds of millions of people (Cheung et al., 2010). While the predominant research
500 focus has been on impacts of habitat loss on coral reef fish assemblage composition and productivity (e.g.
501 Hopf et al., 2019; Robinson et al., 2019), our study adds to the evidence that temperature-driven changes
502 in catchability are important to consider in reef fishery management (Bacheler & Shertzer, 2020). We
503 suggested here that changes in catchability are heavily influenced by mechanisms stemming from
504 physiological responses to warming, but we recommend further experimental studies to explore ecological
505 mechanisms that may independently involve changes in prey or habitat. Increases in catchability during
506 heatwaves similar to that found for coral trout may also be widespread globally, given the prevalence of
507 line and trap capture methods amongst coral reef fisheries. To avoid collapses induced by environmental
508 change, fisheries management should use data on stock biomass that are independent of fishery catches.
509 Our work highlights the importance of fisheries-independent data, which unfortunately are not collected
510 for most reef fisheries (Pauly & Zeller, 2016), and precautionary management that is adaptive to climate
511 change to sustain reef fisheries into the future.

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