Swim for it: effects of simulated fisheries capture on the post-release behaviour of four Great Barrier Reef fishes

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ABSTRACT

After being caught and released by a fishery, some animals may be sufficiently impaired so as to be vulnerable to predators. The duration and severity of post-release impairments have rarely been studied under natural conditions; the vitality of animals is usually assessed aboard a vessel, prior to release, while examinations of post-release behaviour are usually restricted to what is within view of a vessel. In this study, we quantified the post-release behavior of the common coral trout (*Plectropomus leopardus*), two species of emperor (*Lethrinus* spp.), and the Spanish flag snapper (*Lutjanus carponotatus*), each of which is actively fished throughout the Great Barrier Reef. SCUBA divers followed fish in the field and recorded their behavior with underwater video cameras after a simulated catch-and-release event. Relative to a low stress treatment (held in an aerated tank prior to release), fish exposed to forced exercise and 5 min of air exposure spent more time in vulnerable positions after release, including 5.8× more time immobile under the boat upon release, 1.6× more time to reach the reef floor, and 2.4× longer to reach the protection of the reef. The effects of the catch-and-release simulation on tailbeat frequency, ventilation rate, and the proportion of overall time spent immobile were not significant except in *L. carponotatus*, which spent significantly more time immobile when exposed to the high stress treatment. Indeed, there were some notable differences among species, with the magnitude of the behavioural impairments being lower and less variable in coral trout than in *Lethrinus* spp. or *L. carponotatus*. These findings provide support for the notion that minimizing air exposure time in hook-and-line fisheries should reduce post-release behavioural impairments and thus vulnerability to predators.

Key words: Lethrinidae, grouper, discards, bycatch, post-release predation

1. Introduction

Fisheries have long been recognized as a leading driver of contemporary changes to marine ecosystems (Halpern et al., 2007; Altieri et al., 2012). One of the strategies for reducing the ecosystem impacts of fisheries has been to improve selectivity via changes to gear (Graham et al., 2007), to fishing practices (Graham et al., 2007), and by releasing non-target animals (Davis, 2002). The latter practice frequently occurs simply because the catch has no value to the fisher/fishery (Hall, 1996; Arlinghaus et al., 2007). However, especially in the developed world, fish are often released as a conservation tactic; a tactic based on a presumption that the animal is likely to resume normal behaviour and survive (Cooke and Schramm, 2007). It is often visually obvious that fish lack vitality at the time of release from a fishery (Davis, 2010) – a result of the stress, exhaustion, and (sometimes significant) injury experienced by the animal. It is now widely known in fisheries science (reviewed in Davis, 2002) and by some fishers (e.g., Nguyen et al., 2013; Raby et al., 2014a) that fish can die after release as a result of the stress and/or injury caused by their encounter with the fishing gear.

There are hundreds of published studies (Donaldson et al., 2008; Patterson et al., 2017) about the effects of catch-and-release on fishes, but relatively few of these have focused on sub-lethal behavioural impairments or, relatedly, post-release predation (Raby et al., 2014b). Post-release predation (PRP), a consequence of physiological and behavioural impairments in the released animal, could conceivably make up all or most of the post-release mortality that occurs in locations where predator densities are high. PRP is sometimes directly observable from the surface. For example, marine mammals and seabirds are often seen following commercial fishing vessels to prey on discards (e.g., Evans et al., 1994; Broadhurst, 1998). However, most PRP likely occurs below the surface and thus out of human view, making it an inherently difficult problem for empirical study. Previous work on PRP has made use of telemetry tracking, direct underwater observation, and laboratory experiments to either quantify PRP directly or to measure proxies for predation risk (Raby et al., 2014b).

Australia's iconic Great Barrier Reef (GBR) supports recreational and commercial fisheries that target reef fishes (McLeay et al., 2002). Similar to other managed fisheries in the developed world, fish are routinely released (i.e., discarded, Welch et al., 2008) from these fisheries for diverse reasons (McLeay et al., 2002) including minimum or maximum size limits, catch limits (bag/trip limits, individual transferable quotas), mandatory release for protected species, or because of fisher attitudes or preferences (e.g., high-grading, species preferences, conservation ethic). Common coral trout (*Plectropomus leopardus*) are of particular value among the ~125 species harvested in the GBR's fisheries, making up ~50% of the commercial harvest in recent times – much of which is sold in the southeast Asia live fish trade at extremely lucrative prices (Welch et al., 2008). Release rates for coral trout in the commercial hand line fishery may have, in the recent past, been >50%, with release rates for non-preferred or non-target species likely to approach 100% (Welch et al., 2008). Fish are also released in large numbers by the recreational hook-and-line fishery for a variety of reasons (Sumpton et al., 2010). As a result, there is interest among GBR anglers (Sumpton et al., 2010) and fisheries managers (McLeay et al., 2002) in assessing the fate of discards. A previous study in the GBR found that simulated catch-and-release elicited evidence of physiological, locomotory, and cognitive short-term impairments in the Spanish flag snapper, *Lutjanus carponotatus* – but that study was confined to a small laboratory-based behavioural arena and thus emphasized the need to expand the research to the natural environment (Cooke et al., 2014).

Here, we report on a field-based experiment designed to assess post-release behaviour and vulnerability to predators of reef fishes after catch-and-release stressors of differing severity. Four species were used in the study, including the economically valuable common coral trout and members of the genera *Lethrinus* and *Lutjanus*, both of which are commonly targeted or encountered in tropical reef fisheries around the world. Fish were captured by hand line and transported to the laboratory for temporary captivity to ensure that pre-capture stressors were controlled for. Thereafter, the fish were released individually in a controlled manner at a single field site and followed by SCUBA divers, who recorded behaviour with underwater video cameras. The response variables we quantified were partly designed to be proxies for predation risk, like much of the previous literature that has relied on behavioural proxies because direct observations of predation can be rare (Raby et al., 2014b). Based on previous studies performed in the laboratory and in mesocosms (e.g., Brownscombe et al., 2014; Cooke et al., 2014) we predicted that longer durations of forced exercise and air exposure would affect post-release behaviour in ways indicative of increased predation risk, including increases in the time required for fish to locate, reach, and enter the protective shelter of the reef. By focusing on otherwise unobservable sub-lethal endpoints, the data here can be used to inform best handling practices for catch-and-release in reef fisheries.

2. Materials and methods

2.1. Fish capture and captivity

From 25-08-2014 to 06-09-2014, study animals were caught within 3.5 km of Lizard Island Research Station (LIRS; 14°40’44.3” S, 145°26’52.5” E) using monofilament (24-kg test) hand-lines baited with pilchards (*Sardinops neopilchardus*) on 8/0 hooks. Fish were hooked adjacent to reef structures at depths of 5-20 m, landed in <30 s, de-hooked, and placed in seawater-filled plastic containers (80 L volume). Any individuals showing signs of barotrauma were vented with a 16-gauge needle. Catch rates were sufficiently high to warrant the inclusion of four species in the experiment: coral trout (*Plectropomus leopardus*, 38-61 cm total length, n = 42), Spanish flag snapper (*Lutjanus carponotatus*, 25-34 cm, n = 11), yellow-tailed emperor (*Lethrinus atkinsoni*, 27-34 cm, n = 17), and spangled emperor (*Lethrinus nebulosus*, 39-43 cm, n = 6). These species were retained in the water-filled containers, which were frequently replenished with fresh seawater, and transported back to LIRS within 4 h. Water temperature ranged from 23.6-24.0°C throughout the study (source: Australian Institute of Marine Science temperature monitoring station at 14°41'17.4" S, 145°26'33.0" E, 6.7 m depth; data publicly available at: http://data.aims.gov.au/aimsrtds/datatool.xhtml).

Once at LIRS, each fish was immersed in a freshwater bath for ~2 min (as an anti-parasite treatment) and tagged with a numbered T-bar anchor tag (Hallprint, Hindmarsh Valley, Australia). After tagging, fish were transferred to a 30,000 L round outdoor tank that was continuously flushed with fresh seawater and aerated with three large air stones, which ensured dissolved oxygen was maintained between 90-100% air saturation. Salinity was 34 ± 0.5 ppt, and water temperature in the tank was 23.3 ± 0.98 °C (mean ± standard deviation; temperature recorded every 10 min using an iButton thermal logger, Maxim Integrated Products Inc., Sunnyvale, CA, U.S.A.). None of the fish in this study died while in captivity. Several sections of large polyvinyl chloride pipe were added to the bottom of the tank to provide shelters within which fish readily hid, and a submersible pump was used to generate flow (~10 cm s^{-1} near the wall of the tank). Fish were fed *ad libitum* with chopped pilchards every 2-3 days while in captivity but were left unfed for a minimum of 16 h prior to use in experiments.

2.2. Behavioural experiment

From 30-08-2014 through 07-09-2014, experimental animals were gently netted from the holding tank and transported by boat to a release site for a simulated catch-and-release event and subsequent behavioural observations. Fish were transported in groups of 8-12 in two 80 L water-filled plastic containers, which were frequently flushed with fresh seawater. Using both a bow anchor and a stern anchor, the boat was fixed to the same location for each field release (14°41’17.6” S, 145°26’37.4” E). At the release site, the water was 5 m deep with a sandy bottom and small-to-large patch reefs 8-12 m away, similar in character to the sites where fish were initially caught. The patch reefs were only present to the south and south-east of the boat location; the west and north were large areas of sand-only habitat. The distance between the reef and the release site (the boat) was short enough to be visible to a snorkeler, but far enough that the fish needed to have the cognitive and locomotory capacity to identify and reach the reef.

Fish were randomly assigned to one of three groups for the catch-and-release simulation, which are referred to here as high, moderate, and low intensity stress treatments. Only the coral trout were exposed to the moderate stress treatment because of sample size limitations with the other species. The high stress treatment involved a fish being netted (with a soft-mesh landing net) from the holding container for transfer to a circular tank (1.5 m diameter) filled to a depth of 40 cm that was set up on the deck of the boat. Fork length (nearest cm) was measured and the T-bar anchor tag was clipped-off before the fish was manually chased around the circular tank for 1 min to elicit burst swimming and simulate the exercise that would occur during a typical hook-and-line capture event. Next, the fish was netted from the tank and exposed to air for 5 min, a duration chosen to mimic poor catch-and-release handling practices characterized by long hookremoval times and extensive pre-release photography. After the air exposure period, the fish was released over the stern of the boat. The moderate stress treatment was identical to the high stress treatment, except that the duration of the air exposure was reduced from 5 min to 1 min. The low stress treatment involved releasing the fish without any forced exercise or air exposure. Because of the transport and need to move fish via net, this group is referred to as low stress as opposed to control.

Prior to the release of each fish, two SCUBA divers positioned themselves near the boat, each with an already-recording underwater video camera (diver 1 = Nikon J3 with a Nikkor 10-30 lens in a Nikon WP-N2 underwater housing; diver 2 = Hero3, GoPro Inc., San Mateo, CA, USA) pointed towards the surface at the release point. Two divers were used for safety reasons and so that a backup camera angle was available. Videos from diver 1 were used for all but nine fish, for which the videos from diver 2 were used. Once a fish was released, the divers followed it with their video cameras, and aimed to record the fish on video for 3-4 min (mean duration = 3 min 22 s; maximum = 5 min 30 s). In some cases, fish swam away from the release point (and towards the reef) so quickly that the divers could not keep pace with it; in others, the fish was lost from the view of the divers within the confines of a reef structure (minimum video tracking duration = 29 s). While this is a relatively short time frame for post-release behavioural observations, it likely represents the period where the fish are most vulnerable to predators (Danylchuk et al., 2007). If the fish was still accessible after the 3-4 min monitoring period, one diver tapped the tail of the fish to check for a fleeing response (online video supplement available at: https://youtu.be/Rb9F6w_IhgQ).

2.3. Video analysis

Videos were manually scored using the computer software Observer® XT 10.5 (Noldus Information Technology, The Netherlands). All periods of time from when the fish was released from the boat until the divers stopped following it was categorized as time spent either swimming or immobile. While fish were immobile, they were further categorized as being i) in the water column under/next to the boat (Fig. 2A), ii) in the open (i.e., on a sandy bottom, away from reef structures; Fig. 2B), iii) in an exposed reef location (e.g., on or close to a reef structure but clearly visible; typically resting on sand at the reef's edge; Fig. 2C), or iv) in shelter (i.e., inside/under a reef structure so as to not be visible to a predator swimming overhead; Fig. 2D). While swimming, fish were categorized as i) swimming in the water column (> 1 m above the ocean floor or any reef structure), ii) swimming along the bottom in open sandy areas (< 1 m from ocean floor), or iii) swimming in/through/on reef structures. Because the software enabled us to mark timestamps for each of these status changes, we were able to quantify time elapsed (in seconds) from release until the fish a) reached the ocean floor, b) reached the reef, and c) entered sheltered reef structure (for those that did so). We also recorded the exact time (to 0.01 s) for each visible tailbeat during swimming (i.e., a full tailbeat cycle) and for each visible opercular beat; these data allowed us to calculate tailbeat frequency during swimming and ventilation rate during periods of immobility, respectively. Videos were played in slow motion (e.g., ½ speed) during analysis when needed to ensure tailbeats and opercular beats were correctly time-stamped. Video analysis was performed with the observer blinded to the stress treatment.

2.4. Statistical analyses

Behavioural data were analysed for the effect of stress treatment, species, and their interaction using generalized linear models (GLMs). Because coral trout were exposed to one of three stress treatments (low, moderate, high) while the other species were divided between two (low, high), for our primary analyses, coral trout in the 'moderate' treatment were excluded. The two Lethrinid species (*Lethrinus atkinsoni* and *Lethrinus nebulosus*) were grouped for statistical analyses because of insufficient sample sizes for each species individually, particularly for *L. nebulosus*. We also separately modelled the effect of treatment (3 levels) in coral trout alone, using separate GLMs. The response variables we modelled included: (1) time required (from release) to reach the ocean floor (in seconds; GLM using a negative binomial distribution), (2) time to reach the reef (in seconds, GLM using a negative binomial distribution and a variance structure to control for differences in variance among groups), (3) time to enter sheltered reef structure (in seconds, GLM using a negative binomial distribution), (4) the proportion of the behavioural trial the fish spent immobile (GLM using a quasibinomial distribution and a variance structure), (5) the time fish spent immobile under the boat upon release (in the water column, away from the ocean floor; in seconds – negative binomial GLM), (6) median tailbeat frequency (GLM using a Gaussian distribution), and (7) median ventilation rate (GLM using a Gaussian distribution).

Median tailbeat frequency and ventilation rate (one median value per individual) was only modelled for fish with ≥ 5 values (for tailbeats s^{-1} or opercular beats s^{-1}) from which to draw a median. Tailbeat frequency values for each fish were based on the time difference between successive tailbeats during the initial part of the behavioural trial when the fish was required to swim to the reef. If the fish then went into an immobile state and then later resumed swimming, these later tailbeats were not counted towards that fish's median tailbeat value, which, for these analyses, was meant to capture swimming effort within the first minute after release, while the fish was *en route* to the safety of the reef. Values for ventilation rate (opercular beats s^{-1}) were generated in a similar way (minimum of five raw values required for a median) for each fish except that all opercular beats from the entire trial were used. Ventilation rate data were confined to periods where the fish was immobile and visible in camera close-up shots such that opercular beats could be counted (i.e., using the optical zoom function on the camera used by diver 1). In some instances, fish spent time immobile in dark sheltered reef structures where they were not visible on camera. Because so few *L. carponotatus* spent time immobile in places that made them reachable by video camera (n = 4 across the two treatments), they were excluded from analyses of median ventilation rate. Ventilation rate data from the entire trial were included because we did not anticipate respiratory rate or oxygen requirements to change markedly during the 3-5 min behavioural trial (Cooke et al., 2014).

GLMs were checked for over/under-dispersion, independence, homogeneity, normality, and outliers (as applicable) following procedures described in Zuur *et al*. (2010) and Zuur and Ieno (2016). Residuals of models were compared against predicted (fitted) values of the model and against all covariates, including those not included in the final model. Because we tested effects of treatment and species on seven response variables, α was set to 0.007 (0.05 / 7 ~ 0.007). Significance of model terms were assessed using "drop1(model, test = "Chi")" in R (following Zuur et al., 2009), which uses an analysis of deviance test to compare model fit against nested models without the inclusion of each explanatory variable. Interactions were removed (and the model re-run) if not significant in initial models. All analyses were conducted using R (version 3.3.0 and the package MASS, Venables and Ripley, 2002).

3. Results

Upon release, fish spent a median of 3.6 s immobile under the boat in relatively open water before beginning to swim towards the reef. There was a significant positive effect (i.e., longer duration) of the high stress treatment ($P < 0.001$) on the time fish spent immobile under the boat before they began swimming (negative binomial GLM, overall model generalized $R^2 = 0.20$), and no effect of species (Table 1, Table 2). Fish then required a median of 12.7 s to reach the ocean floor; those in the high stress group took 59% longer, on average, to do so according to the model main effect term (treatment effect; Fig. 3B, Table 1). Additionally, there was an overall effect of species whereby Lethrinids took ~39% less time to reach the ocean than did coral trout (Table 1). The amount of time required for fish to reach the reef was more variable, particularly for Lethrinids and *L. carponotatus* in the high stress groups (Fig. 3C). Fish in the high stress treatment took 2.4× longer (model estimate; $P < 0.001$) to reach the reef than did those in the low stress group (Fig. 3C); with no significant effect of species and with the species × interaction term excluded from the final model (Table 1, Table 2). We also assessed how long fish took to enter a protective reef shelter (i.e., covered from an overhead view). There was a greater range in time to enter shelter for the high stress fish among *L. carponotatus* and especially for *Lethrinus* spp. (Fig. 3C). The overall effect of species was significant whereas treatment was not (Table 2).

Median tailbeat frequency during the initial period of swimming after release tended to be lower in the high stress group than in the low stress group but this effect did not reach significance ($P = 0.008$) nor did the interaction or the main effect of species (Fig. 4A; Table 1, Table 2). There were no significant effects of stress treatment on time spent immobile in coral trout or Lethrinids, but there was an interaction (Table 2) whereby stress treatment had a significant effect in *L. carponotatus* (for overall interaction term; Fig. 4B). Focusing only on coral trout and Lethrinids, there was no significant overall effect of treatment, and mean ventilation rate during periods of immobility was 0.3 beats s^{-1} higher in Lethrinids overall than in coral trout (Table 1). Separately analysing the behavioural data from coral trout alone with an intermediate (third) stress treatment level (i.e., 'moderate') revealed no significant overall effect of stress treatment in any of the seven variables (all $P > 0.007$; Fig. 5).

4. Discussion

In this study, we followed fish below the surface with video cameras and in doing so, found evidence to support our prediction that air exposure and forced exercise lead to an amplification of post-release behavioural impairments. Animal vitality and behavioural impairment have frequently been assessed in previous research and found to be responsive to increasing stressor severity. However, nearly all of these previous studies used on-board (pre-release) vitality assessments (Davis, 2010) or assessed post-release behaviour to the extent that it was observable from the vessel (e.g., Campbell et al., 2010). The use of underwater video is therefore relatively novel in research on catch-and-release fishing, but reflects the widespread availability, low cost, and rapidly growing popularity of waterproof "action cameras" (Struthers et al., 2015). We expect the use of video evidence to continue to proliferate in research on fishes, which will lead to new insights into animal behaviour while also promoting scientific transparency (Clark, 2017).

Hundreds of tonnes of fish captured by hook-and-line on the Great Barrier Reef are released every year (Welch et al., 2008; Sumpton et al., 2010), yet little is known about their fate. Fish in this study exposed to the 'high stress' treatment spent more time immobile under the boat upon release, and required more time to reach the ocean floor and the reef structure. These differences, while only a short duration (Fig. 3), could conceivably translate to differences in predation risk in predator-rich waters. We presume that no fish were observed being attacked by predators in this study partly because of two differences from a true fishing scenario: a) two divers were present and close to the focal fish at all times, and b) sharks and other predators were not attracted to the area by the struggling of fish during angling or by the release of blood from a hooking wound (because the fish were exposed to simulated angling on board the boat). Nevertheless, control (low stress) fish tended to immediately swim towards the reef upon release, sometimes quite rapidly (e.g., part 1 in video - https://youtu.be/Rb9F6w_IhgQ). High stress fish, on the other hand, consistently took a greater median time to orient themselves, while in a vulnerable position under the boat (e.g., video supplement part 4 - https://youtu.be/Rb9F6w_IhgQ?t=517), before beginning to swim towards the ocean floor or towards the reef structure.

There was remarkable variability in the magnitude of the behavioural impairments caused by the high stress treatment, both within and among species. The magnitude of the impairments caused by the high stress treatment was lower and less variable for coral trout than in Lethrinids or *L. carponotatus*, particularly for the time they required to reach the reef and the proportion of the trial they spent immobile. On the whole, however, the behavioural impairments we observed tended to be smaller than what might be expected based on previous studies, possibly due to the fact that this experiment was conducted in winter with water temperatures of ~23.5°C (5-7°C less than the peak summer water temperatures at Lizard Island). Indeed, summer temperatures can result in more severe impairments for a given stressor (Gale et al., 2013; Clark et al., 2017). In this context, Cooke et al. (2014) exposed *L. carponotatus* to a forced exercise + 5 min air exposure stress at 28°C (in laboratory trials at LIRS) and found that fish took ~1000-2000 s to enter an artificial shelter that was ~2 m away from their release point in a 51-cm deep behavioural arena. In the present study, nearly all fish were recorded reaching the reef in under

200 s, which was ~5 m below the surface and ~10 m laterally from the release point. In addition to immediate impairments, temperature can affect survival, as shown in a laboratory study of coral trout in which a stress of 3 min exercise + 1 min air exposure was enough to cause significant post-release mortality once acclimation temperatures reached 30°C (mortality within 3-13 d) and 33°C (mortality within 1.8-14.9 h) (Clark et al., 2017). Thus, if the experiments conducted here were to be repeated in summer we would envision more severe behavioural impairments, clearer separation between stress treatments, and possibly delayed mortalities.

Behavioural impairments caused by fishing-induced exhaustion likely represent some combination of cognitive and locomotory impairments. Previous experiments have found evidence that some behavioural impairments after catch-and-release may be cognitive rather than locomotory in origin. For example, *L. carponotatus* approached and "inspected" a shelter shortly after release (in a laboratory behavioural arena), but took far longer after the initial 'inspection' to enter the shelter if they had been exposed to an exercise + air exposure stressor (Cooke et al., 2014). Similarly, great barracuda exposed to fishing-related stress and released into a mesocosm spent less time swimming and made more directional changes than did control fish and consequently took more time to enter protective mangrove habitat (Brownscombe et al., 2014); evidence that the fish were disoriented but not lacking the physical capacity to swim. In our study we observed similar patterns. The few fish that spent their entire post-release behavioural trial immobile in a vulnerable position on an open and sandy ocean floor habitat swam away rapidly when stimulated by a diver tapping their caudal fin after the end of the behavioural trial (e.g., video part 8 - https://youtu.be/Rb9F6w_IhgQ?t=1539). Such a reaction suggests that the fish were in a state that might speculatively be described as a 'daze'; remaining motionless in an extremely vulnerable position despite apparently already having regained the locomotory capacity to swim to protective reef shelter that was only meters away.

The species differences observed in this study may have arisen due to natural differences in behavioural or physiological traits. The most extreme behavioural reactions to our treatments occurred in *Lethrinus* spp. and *L. carponotatus*. Fish in the 'low stress' treatment for both groups typically began swimming away from the boat immediately and rapidly (e.g., video part 7 - https://youtu.be/Rb9F6w_IhgQ?t=1311). The only individuals that burst-swam away from the boat so rapidly as to be impossible for the SCUBA divers to follow for a full three minutes were *Lethrinus* spp. Likewise, 'high stress' fish of these species were the only fish we observed effectively "sinking" to the bottom and remaining immobile on open sand below the boat for an extended period (e.g., https://youtu.be/Rb9F6w_IhgQ?t=1539). In contrast, coral trout were minimally affected by our treatments (Fig. 4), with substantial overlap in behavioural variables among treatments and no individuals in the 'high stress' treatment exhibiting the extreme levels of impairment that occurred in some Lethrinids and *L. carponotatus*. These trends support the notion that guidelines for minimizing the impacts of catch-and-release may, in some cases, need to be species-specific (Cooke and Suski, 2005). It may be more necessary, for instance, to consider providing some individuals or species with a safe revival environment for a short period of time before release (Brownscombe et al., 2013; Cooke et al., 2014), especially in predator-rich waters (although relative predation risk may not be obvious from the surface). However, the way in which the species comparison data could be useful to fishery management is as a form of triage; pointing towards species or genera that may be more vulnerable to catch-and-release fishing. More detailed laboratory or field experiments with physiological endpoints could be used to confirm the consistency of the among-species differences and to identify potential causes. For example, there may be differences in reactivity to stress (Davis, 2010; Cook et al., 2014), the magnitude of metabolic and cardiovascular responses (e.g., changes in lactate, arterial pO_2), or the level of exertion exhibited by fish during forced exercise or hook-and-line capture (Clark et al., 2017).

In summary, the present study provides field-based evidence that confirms coral reef fishes experience post-release behavioural impairments when exposed to forced exercise and air exposure; an experience that would be characterized as poor handling practices in a catch-and-release context (Cook et al., 2015; Brownscombe et al., 2017). These sub-lethal impairments, which were generally mild given the low water temperatures at the time of the study, could presumably lead to cryptic instances of predation on predator-rich reefs. Importantly, although there were some notable among-species differences, the direction of the effects of the capture simulation was the same in all cases, which supports the generalizability of the need for anglers to minimize air exposure (Cook et al., 2015). In cases where fish are visibly lethargic/exhausted, the one obvious solution is to employ the use of a well-aerated live well or revival bag before releasing the fish (Brownscombe et al., 2014, 2013). Further field-based trials in predator-rich waters could be used to validate the utility of revival approaches among GBR fishes.

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FIGURE CAPTIONS

Fig. 1. Photos of the four species included in the study.

Fig. 2. Still photos taken from the videos recorded by SCUBA divers for this experiment showing four behavioural categories into which fish were placed for analyses while immobile: A) under/next to the boat, B) on the bottom in the open, C) in an exposed location, and D) resting in shelter within reef structure.

Fig. 3. A comparison among species and between the two treatment groups in A) the amount of time fish spent immobile in the water column under/near the boat upon release (e.g., Fig. 1A), B) time elapsed between when fish were released from the boat and when they reached the ocean floor, C) time elapsed between when fish were released from the boat and when they reached the reef structure, and D) time elapsed until the fish entered protected reef shelter (e.g., Fig. 1D). The horizontal line within each boxplot corresponds to the median, the lower and upper ends of the box are the 1st and 3rd quartiles, the upper and lower whiskers are 1.5× the interquartile range or the most extreme value (whichever is closer to the median). Sample sizes are given below each box. Statistical outputs for corresponding models are given in Table 1.

Fig. 4. A comparison among species and between the two treatment groups in A) median tailbeat frequency (one value per fish), B) the proportion of time fish spent immobile during the entire post-release observation period, and C) median ventilation rate for the two groups of fish (coral trout and Lethrinids) for which we had sufficient data. The horizontal line within each boxplot corresponds to the median, the lower and upper ends of the box are the 1st and 3rd quartiles, and

the upper and lower whiskers are 1.5× the interquartile range or the most extreme value (whichever is closer to the median). Sample sizes are given below each box. Statistical outputs for corresponding models are given in Table 1.

Fig. 5. Visualization of the data for all seven behavioural response variables as a function of the three stress treatment levels to which coral trout (*Plectropomus leopardus*) were exposed. The horizontal line within each boxplot corresponds to the median, the lower and upper ends of the box are the 1st and 3rd quartiles, and the upper and lower whiskers are 1.5× the interquartile range or the most extreme value (whichever is closer to the median).

Tables

Table 1. The effects of catch-and-release stress treatment (low and high) and species (coral trout *Plectropomus leopardus*, Spanish flag snapper, *Lutjanus carponotatus*, yellow-tailed emperor *Lethrinus atkinsoni*, spangled emperor *Lethrinus nebulosus*) and their interaction on the seven behavioural responses. Parameter estimates, model fit (generalized R^2), and P-values for generalized linear models. Only 'final' models are shown. Note that main effects of species group and treatment were left in place regardless of whether they were significant. Corresponding sample sizes are provided in Fig. 3 and 4. The significance of explanatory variables for model fit are shown in Table 2.

Response variable	Model type, R^2	Model parameter (parameter level)	Parameter estimate ± standard error	P value
Time immobile under boat (s) N = 62	Negative binomial GLM (log link), $R^2 = 0.20$	Intercept	0.95 ± 0.41	
		Treatment (high)	1.76 ± 0.43	**< 0.001**
		Species (*Lethrinus* spp.)	0.09 ± 0.47	0.855
		Species (*L. carponotatus*)	-0.90 ± 0.62	0.145
Time to reach oceanfloor (s) N = 62	Negative binomial GLM (log link), $R^2 = 0.33$	Intercept	2.55 ± 0.11	
		Treatment (high)	0.46 ± 0.12	**< 0.001**
		Species (*Lethrinus* spp.)	-0.49 ± 0.14	**< 0.001**
		Species (*L. carponotatus*)	-0.05 ± 0.17	0.765
Time to reach the reef (s) N = 58	Negative binomial GLM (log link) with variance structure, $R^2 = 0.28$	Intercept	2.88 ± 0.20	
		Treatment (high)	0.86 ± 0.24	**< 0.001**
		Species (*Lethrinus* spp.)	0.16 ± 0.30	0.592
		Species (*L. carponotatus*)	0.14 ± 0.33	0.672
Time to enter covered reef shelter (s) N = 41	Negative binomial GLM (log link), $R^2 = 0.31$	Intercept	3.02 ± 0.23	
		Treatment (high)	0.61 ± 0.26	0.021
		Species (*Lethrinus* spp.)	0.60 ± 0.31	0.051
		Species (*L. carponotatus*)	1.24 ± 0.36	**< 0.001**
Tailbeat frequency (beats s^{-1}) N = 38	Gaussian GLM, $R^2 = 0.28$	Intercept	1.96 ± 0.18	
		Treatment (high)	-0.47 ± 0.18	0.013
		Species (*Lethrinus* spp.)	0.10 ± 0.21	0.638
		Species (*L. carponotatus*)	0.46 ± 0.22	0.047

Proportion of time spent immobile (across the entire trial) N = 61	Quasibinomial GLM with variance structure, $R^2 = 0.73$	Intercept	1.72 ± 0.29	
		Treatment (high)	-0.11 ± 0.37	0.77
		Species (*Lethrinus* spp.)	-0.003 ± 0.41	0.99
		Species (*L. carponotatus*)	-5.52 ± 1.13	**< 0.001**
		Interaction (*Lethrinus* spp. × 'high stress' treatment)	0.36 ± 0.57	0.53
		Interaction (*L. carponotatus* × 'high stress' treatment)	4.61 ± 1.20	**< 0.001**
Ventilation rate (opercular beats s^{-1}) N = 35	Gaussian GLM, $R^2 = 0.64$	Intercept	0.67 ± 0.03	
		Treatment (high)	-0.09 ± 0.04	0.04
		Species (*Lethrinus* spp.)	0.30 ± 0.04	**< 0.001**

Table 2. Significance of explanatory variables for model fit for each of the seven response variables (models) from an analysis of deviance test, which compares the full model deviance against that of nested models without the inclusion of each explanatory variable. Carried out using drop1(model, test = “Chi”) in R, following Zuur et al. (2009). Note that main (non-interaction) terms cannot be individually dropped where interactions are significant, as is the case for proportion of time spent immobile. In all other cases, models were re-run without interactions because this procedure showed that the interaction term did not significantly ($\alpha = 0.007$) improve model fit. Table 1 shows sample sizes, parameter estimates, and their significance for each final model.

Response variable	Dropped variable	Deviance	*P*
Time immobile under boat	(none)	64.83	
	Treatment	78.48	<0.001
	Species	67.19	0.308
Time to reach ocean floor	(none)	59.30	
	Treatment	73.78	<0.001
	Species	73.05	0.001
Time to reach the reef	(none)	35.04	
	Treatment	48.71	<0.001
	Species	35.44	0.818
Time to enter covered reef shelter	(none)	46.24	
	Treatment	51.16	0.027
	Species	60.45	<0.001
Tailbeat frequency	(none)	10.03	
	Treatment	12.05	0.008

	Species	11.34	0.097
Proportion of time spent immobile	(none) Treatment × Species	5.84 10.07	 <0.001
Ventilation rate	(none) Treatment Species	0.42 0.49 1.44	 0.025 <0.001

Fig1

Plectropomus leopardus
Lethrinus nebulosus
Lutjanus carponotatus
Lethrinus atkinsoni

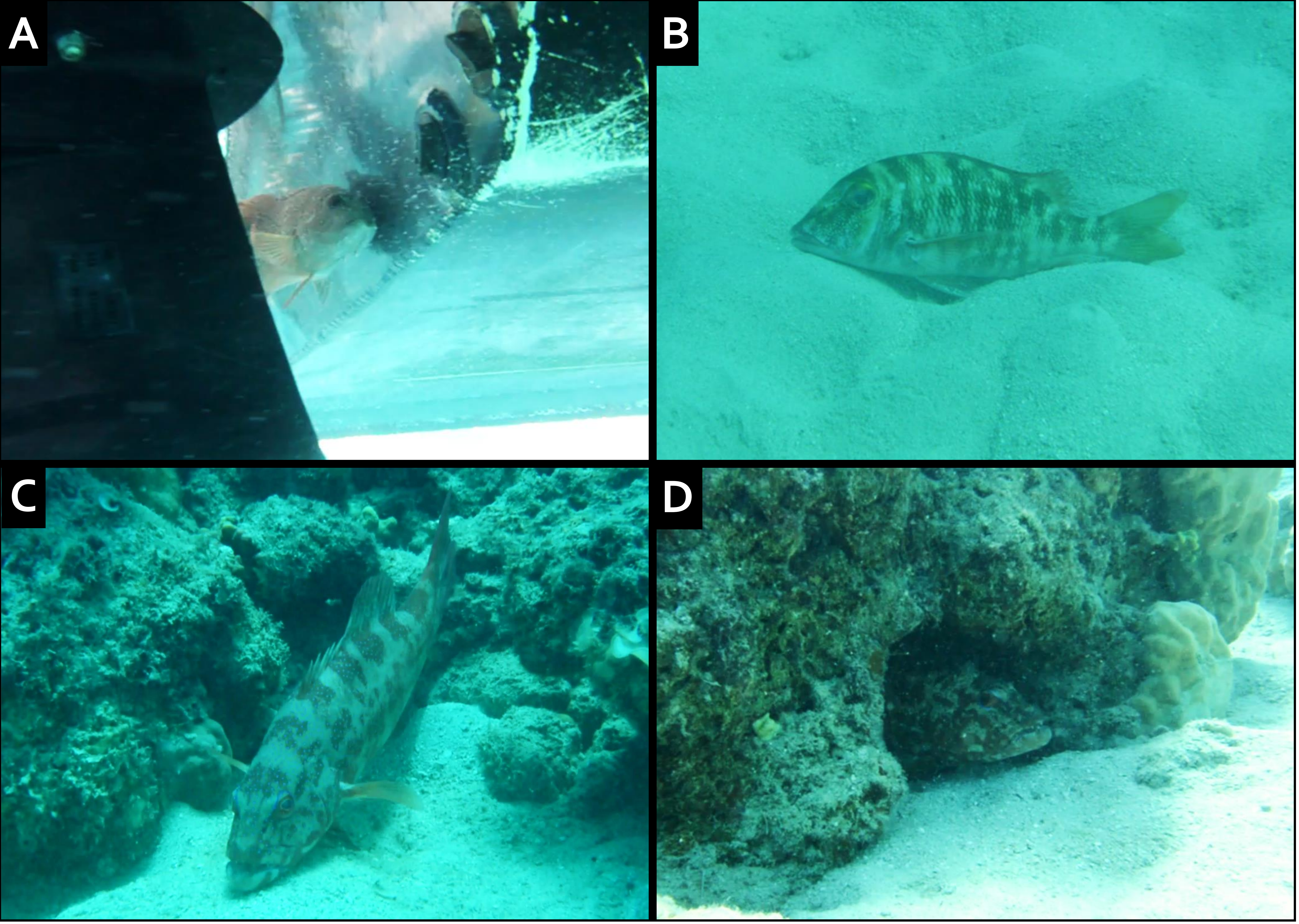

A
B
C
D

Fig3

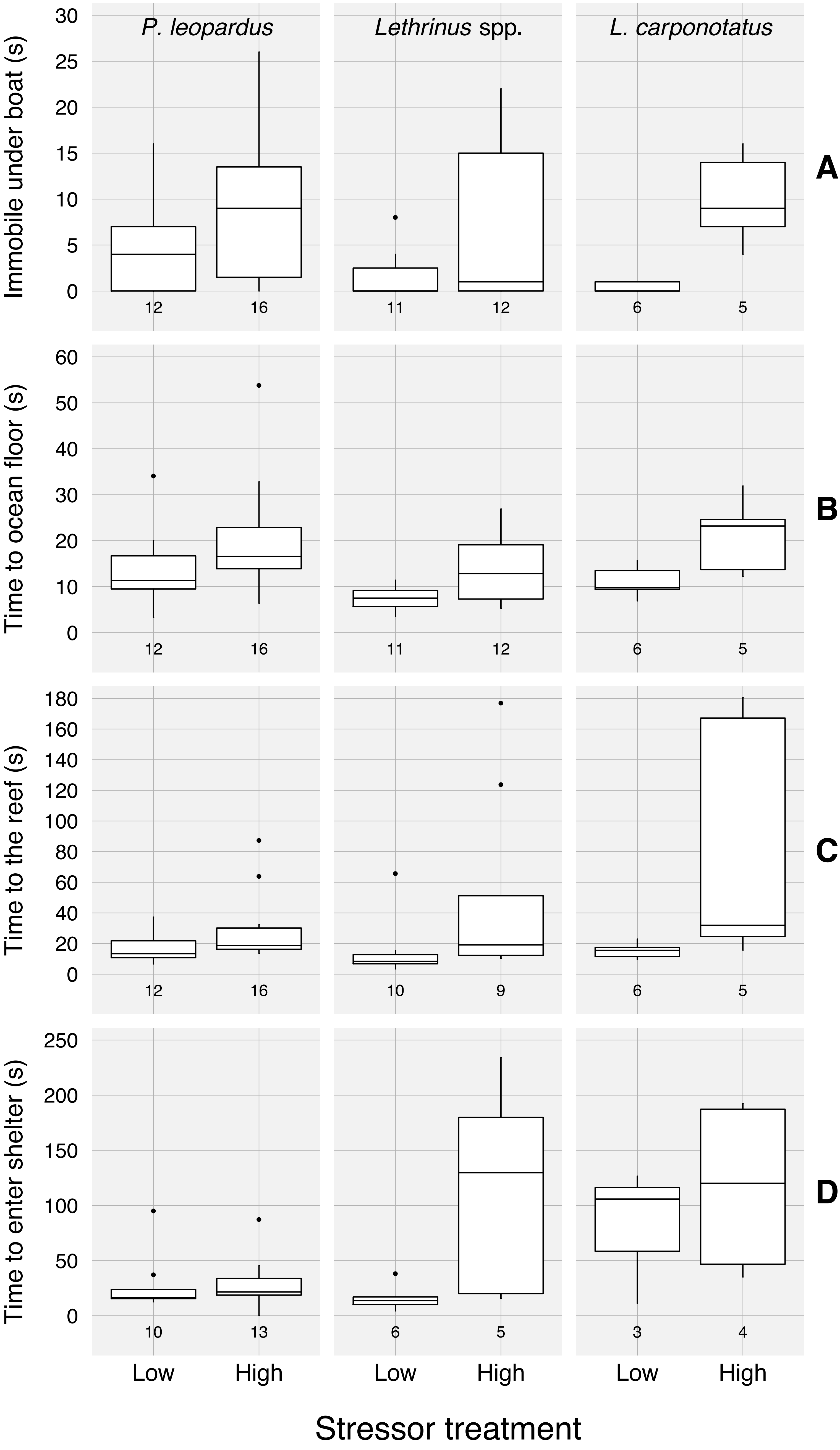
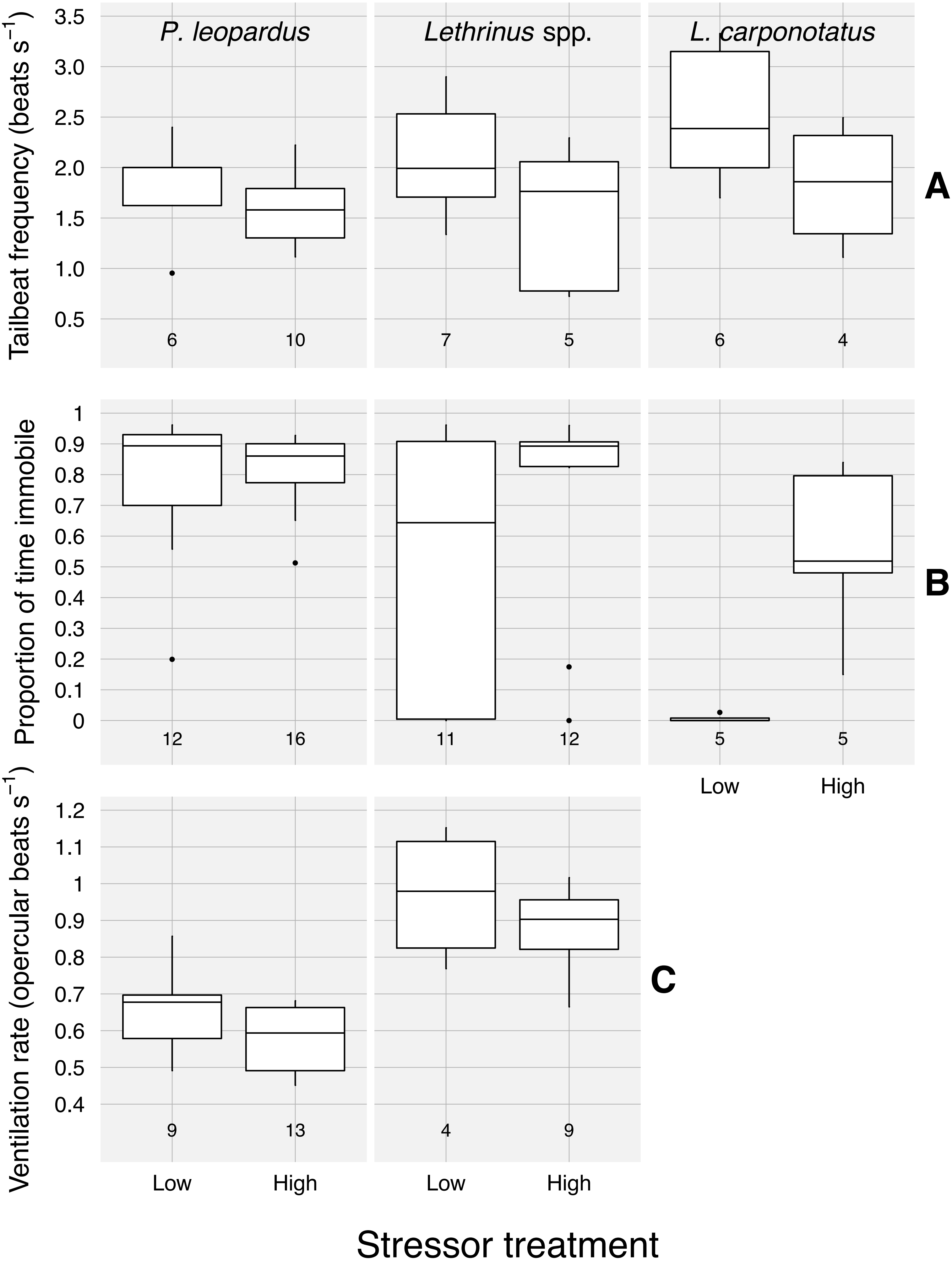
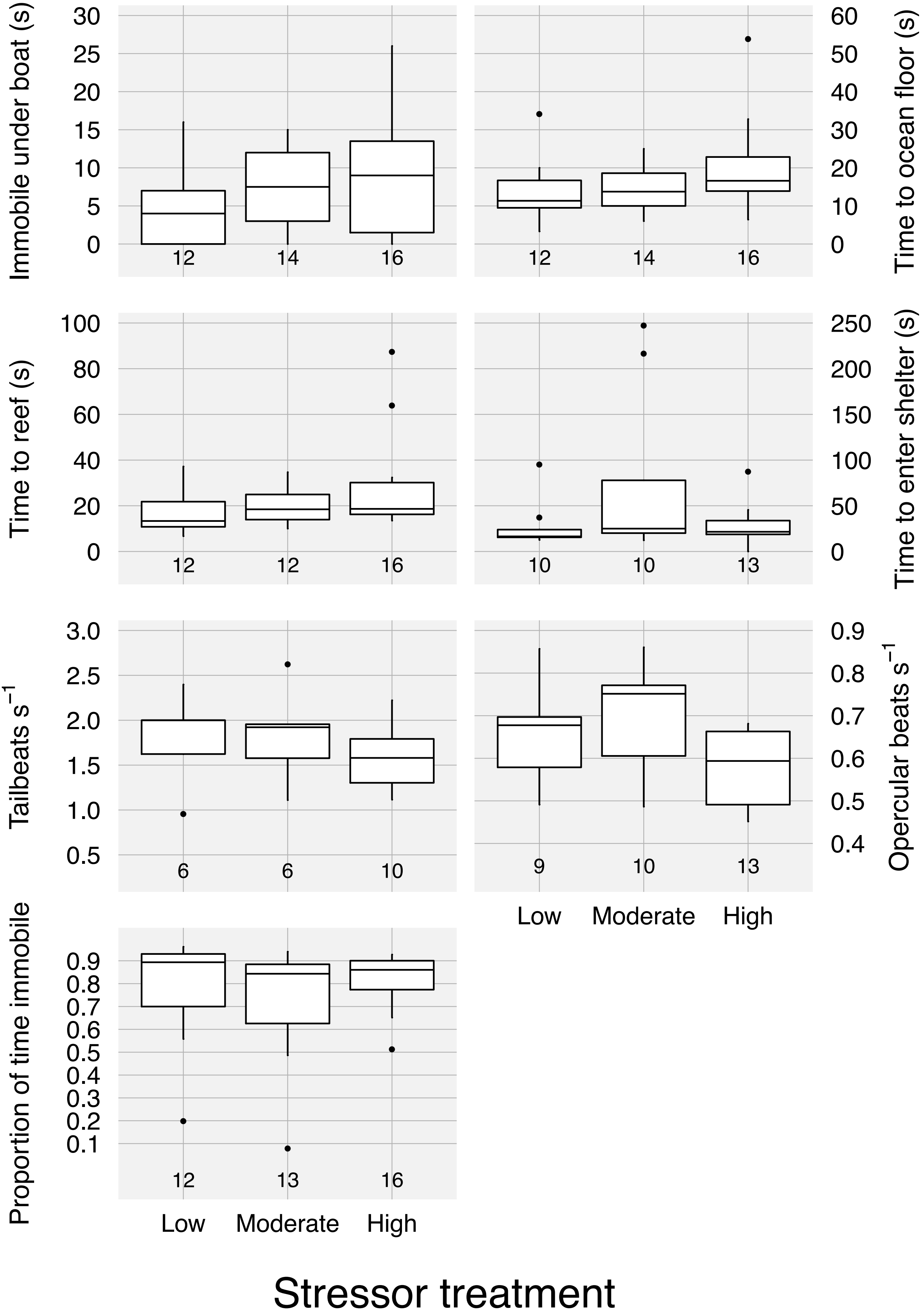

P. leopardus
Lethrinus spp.
L. carponotatus
Immobile under boat (s)
0
5
10
15
20
25
30
12
16
11
12
6
5
A
Time to ocean floor (s)
0
10
20
30
40
50
60
12
16
11
12
6
5
B
Time to the reef (s)
0
20
40
60
80
100
120
140
160
180
12
16
10
9
6
5
C
Time to enter shelter (s)
0
50
100
150
200
250
10
13
6
5
3
4
D
Low
High
Low
High
Low
High
Stressor treatment

Fig4



P. leopardus
Lethrinus spp.
L. carponotatus
Tailbeat frequency (beats s−1)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
6
10
7
5
6
4
A
Proportion of time immobile
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
12
16
11
12
5
5
B
Low
High
Ventilation rate (opercular beats s−1)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
9
13
4
9
C
Low
High
Low
High
Stressor treatment

Fig5


Immobile under boat (s)
30
25
20
15
10
5
0
12
14
16
Time to ocean floor (s)
60
50
40
30
20
10
0
12
14
16
Time to reef (s)
100
80
60
40
20
0
12
12
16
Time to enter shelter (s)
250
200
150
100
50
0
10
10
13
Tailbeats s^{-1}
3.0
2.5
2.0
1.5
1.0
0.5
6
6
10
Opercular beats s^{-1}
0.9
0.8
0.7
0.6
0.5
0.4
9
10
13
Low
Moderate
High
Proportion of time immobile
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
12
13
16
Low
Moderate
High
Stressor treatment