# UNIVERSITY OF EXETER

# Ecological implications of motorboat noise on coral reef fish communities

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# Abstract

Anthropogenic noise is recognised as a major pollutant of international concern. Motorised vessels are the dominant source of anthropogenic noise in the marine environment. Small motorboats are widespread among coastal regions, exposing shallow marine ecosystems to noise disturbance. Short-term exposure to motorboat noise can have a profound impact on fish physiology and behaviour. However, it remains unclear how such impacts translate to wild fish assemblages. No study has yet investigated the community-wide implications of motorboat noise. The aim of this thesis is to review the current understanding of motorboat noise on fish ecology; provide the first assessment of chronic motorboat noise on a wild fish community; and consider future directions in research, management and mitigation. Using existing spatial variation in motorboat traffic across coral reefs in French Polynesia we carried out visual census techniques to investigate the effect of chronic motorboat noise on a coral reef fish community. In addition, we conducted a month-long motorboat manipulation of a coral reef with minimal disturbance history to test whether community responses can be experimentally induced. There was no difference in the overall fish abundance, species richness and diversity on coral reefs exposed to chronic motorboat noise. Yet, 5 species had significantly lower abundances, whilst 8 species had significantly greater abundances on reef exposed to chronic motorboat noise, resulting in a significant difference in the overall community composition. In addition, the month-long motorboat manipulation replicated the same response in two species as the previous study; though this was not enough to significantly alter the community composition. This study demonstrates that fish species respond differently to chronic motorboat noise, and community implications are more complex than previously predicted. Future studies should consider the diversity of functional traits, noise tolerance and interspecific interactions when investigating the ecological implications of motorboat noise on fishes.

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## Author's declaration

The data chapter of this thesis details my own contribution to a joint research project with Harry Harding (PhD student, University of Bristol) that is to be submitted for publication with both of us as joint first author. I certify that all material which is not my own has been identified and that any material that has been previously submitted and approved for the award of a degree by this or any other University has been acknowledged.

# Chapter 1: Literature review

# **Advances in the assessment of motorised vessel noise on fish ecology**

*1.01 Introduction*

The oceans, covering 71% of the Earth's surface and making up over 99% of the worlds habitable space, were once considered so vast that the human population could never tarnish them. Yet, the rapid rise of the human population after the onset of the industrial revolution, from less than a billion to the current 7.7 billion, has forced dramatic changes upon the World's natural terrestrial and marine environments. Human activity alone has triggered global climate change, destroyed natural habitats, polluted terrestrial and marine systems and driven extinction to 100–1000 times its normal rate (Zetterström 2010). These unprecedented global changes occurring in such a brief moment of Earth's living history is now defined by many scientists as the onset of a new epoch—the 'Anthropocene' (Steffen *et al.* 2007). Pollution is commonly perceived as the material by-products from human activity released into natural environments; such as plastic, pesticides, industrial chemicals and sewage. Yet, sound and light pollution are changing the immediate physical properties of these natural environments with potentially far reaching impacts on ecosystems. Anthropogenic noise is now recognised as one of the most hazardous forms of anthropogenically driven environmental change and as a major global pollutant of international concern (stated by the World Health Organization, US National Environment Policy Act, European Commission Marine Strategy Framework Directive, International Maritime Organization Marine Environmental Protection Committee). In the marine environment the most dominant and ubiquitous sources of anthropogenic noise is emitted unintentionally by motorised vessels, from giant cargo ships to recreational jet skis. There is now a growing body of literature exploring impacts of anthropogenic noise on aquatic life.

The purpose of this chapter is to review the advancement in scientific understanding of motorised vessel noise on fish ecology. This chapter is not intended as an extensive review of the effects of all forms of marine anthropogenic noise (e.g. pile driving, sonar and seismic surveying) across all marine and aquatic taxa. Rather, the focus of this review is to collate and examine the evidence for the implications of boat noise on the physiology, behaviour and ecology of fishes; highlight areas where knowledge is lacking; and, introduce my research aims in addressing the knowledge gaps identified in this chapter.

*1.02 Motorised vessel noise*

Human-generated noise is increasingly recognised as an environmental pollutant of global concern. Since the industrial revolution, the range, intensity and prevalence of anthropogenic noise has grown considerably, without indication of amelioration. Motorised vessels, ranging from giant cargo vessels to small recreational craft, are the most pervasive source of anthropogenic noise in the marine environment (Ross 1976; NRC 2000; Firestone & Jarvis 2007). In the past 60 years the number of ships has doubled, and their size and propulsion power has increased (Chapman & Price 2011). As a consequence, low frequency sound (10–100 Hz) in the oceans has elevated (Ross 1993; Andrew *et al.* 2002; McDonald *et al.* 2006; Chapman & Price 2011). The noise emitted by motorised vessels is generated unintentionally via mechanical vibration of engine hulls, water displacement and, most predominantly, propeller cavitation. A phenomenon whereby air pockets on the surface of spinning propeller blades form and collapse, discharging energy in the form of sound (Ross 1976).

When assessing the effect of 'motorised vessel' noise on marine ecosystems care must be taken to account for the acoustic and spatial disparity between ships and small motorboats. Large ships, depending on ship type, can emit broad frequency ranges from below 100 Hz to 30 kHz (Arveson & Vendittis 2002; Aguilar Soto *et al.* 2006). Propeller cavitation is responsible for the high frequency band, whereas the low frequency band (most dominant) is generated by engines and other machinery. Small vessels have a different noise signature, emitting higher peak frequencies between 2–10 kHz (Bittencourt *et al.* 2014) due

to the lack of low frequency vibrations from large engines. Large ships and small motorboats also contrast in their oceanic distribution. Large ships (typically cargo vessels, tankers, cruise ships and commercial fishing vessels) spend the majority of time at coastal ports where marine traffic is concentrated, and then crossing deep pelagic water, outputting their highest sound levels. Small motorised vessels (artisanal fishing boats, recreational motorboats, water taxis, etc.) emit less energy at low frequencies compared with large ships, however they operate in shallow coastal waters, within close proximity to marine organisms that exist in dense and diverse communities compared with the pelagic zone.

Water is an excellent transmitter of sound due to its high molecular density. Waterborne sound propagates across greater distances, maintains higher amplitudes and travels five times faster than airborne sound (Slabbekoorn *et al.* 2010). In contrast, underwater light is attenuated rapidly, limiting visibility; and chemical cues are subject to displacement via directional currents. Therefore, most marine animals rely on sound as their primary directional distance sense to extract essential survival information from their environment for navigation, foraging, predator avoidance, reproduction and communication (see section '*1.03 Uses of sound in fish*'). However, the invasive noise emitted from motorised vessels overlaps the critical hearing frequency bandwidth of all fish species, typically 30–1000 Hz (Slabbekoorn *et al.* 2010). The ability of water to propagate high-amplitude invasive noise disrupting natural marine soundscapes, combined with the essential role of sound in the lives of aquatic animals, can arguably render anthropogenic noise a more potent pollutant in aquatic rather than terrestrial environments.

*1.03 Uses of sound in fish*

The realisation that sound plays a vital role in the lives of fish has only been established relatively recently. The notion that the underwater world is silent was conveyed in the ground-breaking 1956 marine documentary, "Le Monde Du Silence", when Jacques Cousteau and his team gave the world its first glance at the marine realm and its inhabitants. This notion remained generally unchallenged for many years due to the poor ability of the human ear to detect

sound underwater, reinforced by the regular stream of bubbles released from scuba equipment. Yet, almost a century before Cousteau's popular marine documentary there were reports of sounds that could be voluntarily produced in fishes (Dufossé 1874). Aware of this, Charles Darwin predicted that sound production in fish could play a role in sexual selection, as it does in insects (Pauly 2004; Lobel *et al.* 2010). The innovation of technologies such as the hydrophone in the 1960s, and later the accelerometer, to measure sound pressure and particle motion underwater made the world of aquatic sound finally accessible to scientists. Ever since, momentum has gathered in understanding the role of sound in fishes.

Fish use sound for many behavioural processes essential to their survival. In the early life stages of the majority of coral reef fishes, sound plays a major role in determining their future survival. Weeks of development spent in the pelagic ocean, from fertilised eggs to active swimming larvae (Stobutzki & Bellwood 1997), prepares young fishes to begin their greatest voyage to a coral reef, where they will settle and persist for the remainder of their lives. Visual and chemical cues are at the mercy of light attenuation and currents, yet as discussed previously, sound can travel many kilometres underwater with little influence from water movement and physical barriers. Larval fish use acoustic cues, produced by invertebrates and fishes inhabiting the reef, to orientate towards, select and settle on coral reefs (Simpson *et al.* 2005). If successfully settled, surviving the onslaught of predation throughout their early life thus far, fishes will begin to use sound for a host of new purposes as they enter adult life on the reef.

The majority of fishes that are able to produce sounds commonly do so during agonistic behaviours. These include aggressive, threatening, submissive, fleeing and distress tendencies in both intra- and interspecific interactions (Ladich 1997). Many site-attached species also use aggressive vocalisations to defend their territories. Members of the Holocentridae family, nocturnal coral reef fishes that include soldier- and squirrelfishes, emit grunts and staccato sounds to deter moray eels from invading their daytime refuge (Winn *et al.* 1964; Salmon 1967). Many members of the Pomacentridae family, coral reef damselfishes, vocalise against hetero- or conspecifics to defend broods, or, in the case of farming damselfish, maintain turfs of epilithic algae (Myrberg 1972; Tricas & Boyle 2014). Sound production is an essential element of these agonistic interactions as they

provide a clear warning to competitors or predators; without which, energy demanding physical disputes resulting in injury or death could result (Ladich & Myrberg 2006).

Sound production in fishes is also commonly utilised in reproductive behaviours. Indeed, it is during the breeding season that sound production is at its most intense in soniferous species (Bass & McKibben 2003). Sound levels produced by spawning haddock can be heard at such high amplitudes that they may be used as a means for fishermen to locate aggregations of these commercially valuable species (Casaretto *et al.* 2014). To date, members of 15 coral reef fish families have been confirmed to produce sounds associated with breeding (Boyle & Cox 2009; Lobel *et al.* 2010). During courtship displays it is commonly the males that vocalise, often in combination with elaborate visual displays, with the purpose of attracting females to their territories (Lobel *et al.* 2010). Thus, as predicted by Darwin, sound does play a key role in sexual selection in many fish species.

Coral reef fish communities have long been reported to generate choruses, whereby members of a species aggregate and vocalise *en masse* at a consistent period of the diel cycle, and often at a certain time of the year (McCauley 2012; McWilliam *et al.* 2017). The purpose of fish choruses is poorly understood, but choruses have been proposed as an aid to spawning in the breeding season, occurring only within a few months, or to maintain school structure and aid feeding at night, occurring year round (McCauley 2012; Parsons *et al.* 2017). However, the process in which choruses may aid feeding, and the species responsible, still mostly remains a mystery. McCauley has attributed recordings of night-time choruses around coral reefs of Northern Australia to feeding nocturnal planktivorous fish from the Holocentridae, Priacanthidae and Apogonidae families (McCauley 2012). Nonetheless, it is clear that fish choruses make up a vital component of coral reef soundscapes, and it might be possible that the composition of choruses may attract or deter particular species of settlement stage larval fishes, influencing the arrival and establishment of future generations.

The sounds emitted by fishes and invertebrates during acoustic spawning and agonistic interactions have the potential to be intercepted by predators. It has been hypothesised that predatory fish may eavesdrop on the sound generated

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by their prey to aid hunting (Holt & Johnston 2011). This hypothesis is supported by the case that some fish species silence their vocalisations having detected a nearby predator (Luczkovich *et al.* 2000; Remage-Healey *et al.* 2006; Luczkovich & Keusenkothen 2007). However, other species have, in contrast, been found to increase their acoustic activity to confront and deter a predator (Winn *et al.* 1964). The use of acoustic cues in hunting fishes has only once been empirically tested; whereby Holt and Johnston (2011) found that predatory river fishes orientate towards loudspeaker playback of rock shuffling noises that mimic the presence of invertebrates disturbing the rocky substrate. This is a compelling indicator that, at least in a freshwater river system, fishes may use acoustic cues to detect prey. This behaviour has yet to be explored on the naturally noisy coral reefs, to identify what extent predatory fish species eavesdrop on prey sounds as a hunting strategy, especially considering nocturnal species in limited visibility. A greater understanding of how predatory fishes use the biotic soundscape for hunting would be of great value when inferring the potential impact of acoustic interference from anthropogenic noise on fish community composition and ecosystem functioning.

Owing to the growth of research in fish acoustic behaviour and ecology, particularly spanning the last two decades, it has become evident that sound plays an essential role in the life histories and survival of fish. And so, the likely disruption of acoustic behaviours via the invasion of anthropogenic noise in the marine environment has the potential to cause a host of implications across a range of important processes in fish. The following sections introduce the modes that anthropogenic noise may interfere with fish and will review the studies that have uncovered the physical, physiological and behavioural impacts of anthropogenic noise.

*1.04 Modes of acoustic interference with fishes*

Ocean soundscapes have remained unchanged over millennia, until the last century when the introduction of motorised vessels, along with other anthropogenic noise sources, began to dominate many natural soundscapes. Underwater anthropogenic noise is, in relation to the natural history of the oceans,

extremely novel and unfamiliar to the animals inhabiting marine environments. This high amplitude pervasive noise, spread over broad frequency bands and great stretches of ocean, directly competes with the natural soundscapes that fishes depend on. It has the potential to mask important acoustic cues and distract, stress and potentially even harm fishes.

One of the most apparent forms of acoustic interference with marine communities is through auditory masking; whereby biologically relevant acoustic signals are harder to perceive in the presence of biologically irrelevant noise (Slabbekoorn *et al.* 2010). The noise emitted by motorboats overlaps the peak frequencies of the majority of fish vocalisations at <1000 Hz (Tricas & Boyle 2014; Neenan *et al.* 2016), potentially reducing the communication space between individuals of a population (Putland *et al.* 2018) and inhibiting acoustic behaviours discussed previously. In a few cases there is evidence that fishes may compensate for auditory masking by elevating the amplitude of their vocalisations in the presence of increased background noise, so as to maintain the signal-to-noise ratio and communication space (Holt & Johnston 2014; Luczkovich *et al.* 2017). This phenomenon, known as the 'Lombard effect' (Lombard 1911), has been documented across many other soniferous members of the animal kingdom including birds (Brumm & Todt 2002; Brumm 2004), cetaceans (Lesage *et al.* 1999; Scheifele *et al.* 2005; Holt *et al.* 2009), amphibians (Parris *et al.* 2009), monkeys (Brumm *et al.* 2004) and humans (Lane & Tranel 1971). Animals may also raise their chances of being heard against a noisy background by altering the peak frequency (Parris *et al.* 2009) and timings (Brumm 2003) of their calls. In some species the Lombard effect may provide an effective coping strategy against rising ocean anthropogenic noise. However, this requires that a species possesses the capacity to alter their vocalisations, which may incur high metabolic costs (Jensen *et al.* 2009) and sonic muscle fatigue (Mitchell *et al.* 2008).

Not only does anthropogenic noise physically alter the immediate acoustic environment, it can also interfere directly with cognitive processes, distracting animals from natural baseline behaviours and inducing stress. Acoustic distraction is the process of shifting an individual's attention away from primary tasks, such as predator vigilance, mating and foraging (Chan *et al.* 2010). Thus, in contrast to the masking effects of noise, distraction can lead to implications

beyond communication in soniferous species. Distraction may explain the behavioural changes in fishes brought on by motorboat noise that have been uncovered in recent years (see *'1.06 Effects of boat noise on fish behaviour'*). However, distraction is extremely difficult to quantify; and so, scientists have had to assess changes in behaviours that may rely on cognition as an assay for acoustic distraction (Chan *et al.* 2010; Rosa & Koper 2018). Yet, stress is another direct means for noise to interfere with fish that is easier to quantifiably test for via measurements of physiological indicators, such as elevated metabolic rate, heart rate and cortisol levels (Remage-Healey *et al.* 2006; Wysocki *et al.* 2006; Simpson *et al.* 2016b; Jain-Schlaepfer *et al.* 2018; Fakan & McCormick 2019). I consider the effects of boat noise on fish physiology below.

*1.05 Effects of boat noise on fish physiology*

Studies over the last decade have established that motorboat noise can incur physiological changes in fishes. Recently, Simpson and colleagues (2016) identified that the Ambon damselfish (*Pomacentrus amboinesis*), a common Pomacentrid of the Great Barrier Reef, increased their oxygen-consumption rate by more than a third when exposed to motorboat noise; indicating higher metabolic rate—a physiological sign of stress. Noise induced stress may well have caused a reduced ability for the Ambon damselfish to detect approaching predators, leading to elevated mortality by predation when exposed *in situ* to motorboat noise (Simpson *et al.* 2016). Elevated oxygen-consumption rates were also found in juvenile European eels exposed to ship noise playback in tanks (Simpson *et al.* 2015) and in cichlids exposed *in situ* to motorboat noise in Lake Malawi (Harding *et al.* 2018).

Cardiac output has been monitored as another useful indicator for stress in fishes. Adult freshwater largemouth bass (*Micropterus salmoides*) had a significantly elevated heart rate when exposed to the playback of motorboat noise (Graham & Cooke 2008). The same response was also found in embryos of three coral reef damselfishes, the staghorn damselfish (*Amblyglyphidodon curacao*), spiny chromis (*Acanthochromis polyacanthus*) and cinnamon clownfish (*Amphiprion melanopus*) (Jain-Schlaepfer *et al.* 2018; Fakan & McCormick

2019). In most cases, an adult fish heart rate is difficult to measure without an invasive procedure, such as the surgical insertion of a flow probe, as used by Graham and Crooke (2008). The undeveloped transparent tissues in fish embryos allow for non-invasive visual heart rate monitoring (Jain-Schlaepfer *et al.* 2018; Fakan & McCormick 2019). However, this limits the use of cardiac monitoring to one stage in a fish life cycle. Today, developing technology is opening the possibility of heart rate monitoring using implantable bio-loggers. These still require surgical implantation, causing initial invasive stress to the animal, but they are becoming increasingly smaller and allow for studies on free roaming animals that are no longer required to be confined to the lab (Brijs *et al.* 2019).

Cortisol is a hormone that is widely accepted as an indicator for stress in animals, including fish (Barton 2006). Exposure to motorised vessel noise has been found to elevate cortisol secretion in freshwater (Wysocki *et al.* 2006) and marine fishes (Nichols *et al.* 2015; Celi *et al.* 2016). If chronically exposed to motorboat noise, long-term elevated cortisol could lead to further problems such as increased infection susceptibility (Anderson *et al.* 2011) and slower growth rates in fishes (McCormick *et al.* 1998). The diversity of fish families, from a variety of aquatic systems, exhibiting stress responses indicates that vessel noise may induce stress across a range of fish groups, rather than just a few noise sensitive species, which may lead to repercussions in vital behavioural processes.

Adverse physiological implications from vessel noise are important to unearth, as they could indicate reduced physical fitness. However, the ecological ramifications of altered physiology are impossible to gauge without proper analysis of resultant behaviours. Although many fishes studied to date have shown similar stress responses to vessel noise, the knock-on behavioural effects may vary significantly depending on life histories, trophic levels, functional traits, interspecific interactions and ecological niches. Furthermore, fishes may exhibit behavioural responses to vessel noise, with no detectable physiological harm: such as reduced vigilance to predation resulting from diverted attention; or lower reproductive success as a consequence of masked courtship vocalisations. A key issue surrounding the above physiological measures is that they are difficult to carry-out *in situ*, meaning many experiments are conducted in tanks. While the

controlled environment of tanks brings many advantages, there is a danger that captivity itself could cause high levels of stress, with the potential to elevate heart rate and oxygen consumption towards its maximum capacity before introducing a stressor, such as noise. If the field of underwater physiology in fishes were to progress it would require technological innovations to allow for field-based monitoring. For these reasons much of the recent literature has focussed on exploring the behavioural responses of wild fish to boat noise.

*1.06 Effects of boat noise on fish behaviour*

Motorboat noise is particularly pervasive in populated coastal regions due to transport, fishing and tourism (Davenport & Davenport 2006). However, the shallow regions along the continental shelves are also home to the world's coral reefs. Coral reefs are naturally noisy places, making them easy to detect from kilometres out in the pelagic ocean. Yet, as the growing human population continues to expand along coastlines and the noise emitted from waterborne transportation increases, the detectability of biologically relevant acoustic cues on coral reefs will wane amidst the noise; making coral reefs one of the most vulnerable ecosystems to anthropogenic noise. Discussed earlier was the importance of sound in the early life history stages of fish as a settlement cue to coral reefs. Holles and her team (now Nedelec; 2013) found that this natural settlement instinct was hampered in the presence of motorboat noise. Fewer larval cardinal fishes (Apogonidae) swam towards playbacks of reef noise when combined with motorboat noise. In addition, a significant proportion of larvae swam away from motorboat noise. A second study by the same research team broadcast a combination of reef and boat noise playbacks from underwater speakers near experimental patch reefs to study the effect of boat noise on wild fish recruitment (Simpson *et al.* 2016a). Their findings provided further evidence of reduced recruitment of settlement stage reef fish in the presence of motorboat noise. These findings pose a worrying concern that coral reefs, which are regularly visited by motorboats or situated near permanent boat channels, could receive a reduced influx of larval fishes during each recruitment cycle. This would result in significant alterations to the community composition and functioning of a coral reef.

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Most coral reef fishes reproduce by releasing fertilised eggs into the open ocean and the offspring develop through their embryonic and larval phases out in the pelagic zone. However, some site attached species rear their offspring on the reef within their territories. One such species is the Mediterranean chromis (*Chromis chromis*), common to subtropical Mediterranean and Atlantic coral reefs. When wild adults were exposed to motorboat noise playback the males spent less time than usual tending their nests, i.e. ventilating eggs and nest cleaning (Picciulin *et al.* 2010). The Indo-Pacific spiny chromis (*Acanthochromis polyacanthus*) exhibits the rarer bi-parental care of eggs *and* juveniles in their territories. When adults were exposed to motorboat noise they made twice as many defensive acts to protect their offspring (Nedelec *et al.* 2017b). Initially seeming as increased vigilance, this elevated defensive behaviour coincided with reduced feeding in adults and a significantly greater proportion of broods suffering complete mortality. Thus, the responsibility of a parent may require a fine balance in the time and energy allocated towards multiple tasks, and if this balance is tipped the survival of their offspring may be at stake. Parental care is energetically expensive and so broadcast spawning species that do not exhibit parental care, releasing fertilised eggs out to sea, may have more energy available to cope with the stress and distraction of motorboat noise without jeopardising their offspring.

The impact of motorboat noise on post-reproductive behaviour has been addressed, but the influence of motorboat noise on the behaviours that result in reproduction, such as courting and spawning, has so far been overlooked. Breeding behaviour is energetically expensive and is, as discussed previously (see *1.03 Uses of sound in fish*), one of the most dominant behaviours to utilise sound production in fishes. Thus, there is a high potential for acoustic masking from motorboats to reduce spawning efficiency. An older study by Boussard (1981) reported that spawning activities of roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) were interrupted by a fast moving power-boat. Therefore, there is great value in future research exploring this further, as it would provide a strong basis on a management level for the restriction of boating activity during important breeding months, to allow reproductive success to return to previous levels.

Motorised vessel noise has been identified to cause detrimental impacts on the foraging efficiency of freshwater and marine planktivorous fishes. All

planktivorous species studied so far have exhibited significantly reduced zooplankton consumption when exposed to motorboat noise playbacks (Bracciali *et al.* 2012; Voellmy *et al.* 2014a). The three-spined stickleback (*Gasterosteus aculeatus*) made more foraging errors (unsuccessful strikes or strikes against non-food items), whereas the European minnow (*Phoxinus phoxinus*) and *C. chromis* exhibited reduced foraging effort (reduced pecking rates). The freshwater minnow and sticklebacks had not likely been pre-exposed to motorised vessel noise, as they were sourced from a pond; so, it is difficult to determine whether these species could habituate to the long-term presence of motorboat noise. On the other hand, the foraging efficiency of the subtropical marine *C. chromis* was filmed *in situ* and compared between areas of historically high boat traffic levels and an area off-limits to boat traffic. This suggests that some species may not have the capacity to habituate or adapt their foraging strategy when subjected to long-term, repetitive exposures of motorboat noise.

*1.07 Effects of boat noise on interspecific interactions*

Despite the growing body of literature on the effects of motorised vessel noise on fishes, our understanding is largely limited to the responses of single species. These previous intraspecific studies have been valuable in advancing our knowledge on the implications of motorised vessel noise on physiology and behaviour of fishes. However, the information that can be drawn from species-specific experimentation is limited, restricting our ability to predict the larger ecological-scale impacts. In order for this field to progress to a level where we can predict and model the impact of boat noise on aquatic ecosystems, we must consider important interactions between species of an ecosystem, including predator–prey dynamics, competitors for resources and symbiotic relationships.

A particularly common finding in the literature is that motorboat noise hampers risk assessment and predator avoidance efficiency in fishes (Voellmy *et al.* 2014b; Nedelec *et al.* 2016b; Simpson *et al.* 2016b; Holmes *et al.* 2017; McCormick *et al.* 2018a,b). Here, I discuss the two most comprehensive studies to date that have provided compelling evidence for the interference of motorboat noise in fish predator prey–dynamics. The first study, conducted by Simpson and

colleagues (2016) found that Ambon damselfish (*Pomacentrus amboinensis*) were less able to startle (an anti-predator strategy) to simulated predatory strikes when exposed to motorboat noise. The same study went further to test the impact of noise on the interactions between the prey species and their natural predator, the dusky dottyback (*Pseudochromis fuscus*). They found that the strike success rate of the predator was significantly greater under noisy conditions. Furthermore, during *in situ* trials *P. amboinensis* suffered significantly higher mortality due to predation from *P. fuscus*. This comprehensive study provided compelling evidence that a damselfish is less able to avoid predation when disturbed by motorboat noise; and Simpson *et al.* suggested that this response was a likely consequence of noise-induced stress, as determined from metabolic rates within the same study.

The same predator–prey relationship between *P. amboinensis* and *P. fuscus* was later studied for the impact of motorboat noise on cognition and predator learning. Ferrari and colleagues (2018) found that juvenile *P. amboinensis* presented with the odour of *P. fuscus* in a predatory context while exposed to boat noise playbacks failed to subsequently respond appropriately to the predator. This contrasted with individuals trained to recognise a predator under ambient reef noise playback, which did respond appropriately. Despite learning of a predation cue, individuals exposed to motorboat noise behaved similarly to untrained, predator-naïve individuals. Therefore, this study indicates that, in addition to stress, motorboat noise can also induce cognitive impairment in learning. While stress is an immediate physiological response to noise, reduced cognition is much harder to diagnose and has latent effects that may only be detectable later in life. Thus, this study is the first to uncover the detrimental influence of motorboat noise on fish cognition, and highlights the requirement for further investigations on the long-term effects of motorboat noise on fish.

The long-term consequences of altered predator–prey dynamics in response to motorboat noise has the potential to incur trophic cascades within marine ecosystems. Yet some species play a vital role in the health of large fish assemblages and will interact with almost every member of the community. Cleaner wrasse provide a service to clean and remove parasites from fish clients on coral reefs, an interspecific symbiosis that is commonplace in the marine

environment. Nedelec *et al.* (2017a) assessed the effect of motorboat noise on the interactions between bluestreak cleaner wrasse (*Labroides dimidiatus*) and their fish clients. In the presence of short-term motorboat disturbance, Nedelec identified delayed and less cooperative cleaning interactions of *L. dimidiatus* and their clients. Cleaner–client interactions play an essential function globally in reducing the spread of parasites and associated diseases among fish communities (Grutter 1999), and the absence of such a cleaning service can cause a marked decline in the abundance and diversity of fishes within a reef community (Grutter *et al.* 2003). Therefore, stressors with detrimental impacts on cleaner interactions could have marked ecological consequences.

*1.08 Fish bio-acoustic diversity*

Fishes have evolved the largest variety of sound generating mechanisms for acoustic communication of any vertebrate group (Ladich 2000). Teleost fishes generate low frequency sounds (~100 Hz) through muscular vibrations of the swimbladder or the pectoral girdle (Ladich & Fine 1994); whereas the rubbing of specialised pectoral spines, plucking of fin tendons (Ladich & Bass 1998) and grinding of pharyngeal teeth (Lanzing 1974) typically generate higher frequency stridulatory sounds above 1 kHz. Perhaps the most abnormal mechanism for sound generation exists in the Atlantic herring whereby the release of gas from the swim-bladder via the anal duct produces frequencies from 1.7 to at least 22 kHz (Wilson *et al.* 2004). However, caution should be applied in using sound production as an indicator of sound detection ability, as it has often been shown across many taxa that vocal activity does not predict hearing performance (Barber *et al.* 2010), especially considering for many fish species there is no account of sound production (Tricas & Boyle 2014).

Not only do fishes possess a wide diversity of sound generating mechanisms, they also vary considerably in their hearing capabilities, perhaps more so than any other vertebrate group (Popper & Fay 2011). This is due to the significant variety of anatomical structures associated with sound detection in fishes. Compared with most other vertebrates, that use solely the hearing organs of the inner ear to detect sound, fishes may use additional peripheral structures

along their bodies to detect sound. Because fish are a similar density as the medium surrounding them, in comparison to terrestrial animals, the movement of particles from a sound wave continues through them, which enables all fish to detect the particle motion domain of sound (Hawkins 2011). All fishes share the same basic ear structures, including three otolithic organs, the saccule, lagena and utricle, along with semi-circular canals and their sensory cristae (Retzius 1881), and each of these structures contain sensory hair cells that detect particle motion up to hundreds or even thousands of Hz (depending on species) (Slabbekoorn *et al.* 2010). Sensory hair cells also run along the lateral line, the main purpose of which is to detect water movement generated by conspecifics or prey. Yet, the lateral line has the added ability to detect low-frequency sound below 100 Hz (Slabbekoorn *et al.* 2010).

A classification of fishes, known as Otophysans, are especially adapted to detect sound pressure. They possess specialised hearing structures called Weberian ossicles, which are fluid filled canals that intimately connect the swim bladder to the ear (Popper & Fay 2011). This mechanical connection allows for the ear to detect sound pressure that vibrates the swim bladder. Some species do not possess this otophysic connection, yet their swim bladder is positioned close enough to the ear, or has extensions/horns extending the swim bladder towards the ears, which is suggested to still allow for some detection of sound pressure (Popper & Fay 2011; Ladich & Fay 2013). At the bottom end of the hearing spectrum are teleosts adapted for a demersal or deep sea existence which may possess swim bladders that are greatly reduced in size, and are positioned away from the ear; and elasmobranchs that lack a swim bladder entirely. These species are considered to have the lowest hearing sensitivities of all fishes, detecting only particle motion and lacking the ability to detect sound pressure.

Although we are able to quantify sound production in fishes, we are far less able to measure sound detection. Fish hearing measurements have been attempted via behavioural and electrophysical techniques. The behavioural method requires conditioning a fish, often using an electric shock, to exhibit a behavioural response when it detects a sound. Problems with this method include that is that it is restricted only to individuals who can be trained, eliminating larvae, the training process itself is likely to incur high levels of stress, and issues can arise

when individuals display a behavioural response in the absence of sound (Kenyon *et al.* 1998). The electrophysical technique records the auditory brainstem response (ABR), which is the electrical potential generated in response to sound in the brainstem auditory nuclei and eighth cranial nerve (Kenyon *et al.* 1998). The ABR technique produces hearing thresholds for fishes that are generally higher than the behavioural technique which could suggest that as a method it is less sensitive to detect a fish's perception of sound (Ladich & Fay 2013). Nonetheless, it has been proposed as the most consistent and reliable technique for measuring fish hearing. Due to the high diversity in fish bio-acoustic mechanisms we should expect fishes of different families and functional groups within a community to vary substantially in their responses to anthropogenic noise.

*1.09 Community-level responses to boat-noise*

Despite compelling evidence that motorboat noise has detrimental fitness impacts on fish at a species-level, there has been no empirical study to assess how these implications translate at a community-level. As is the case with many aquatic studies, the research into the effect of anthropogenic noise on marine communities is lagging behind terrestrial studies. In terrestrial systems traffic noise has reduced the abundance, species richness and composition of birds near highways (Reijnen & Foppen 1995; Kuitunen *et al.* 1998; Francis *et al.* 2009; Herrera-Montes & Aide 2011). Yet, there is greater complexity behind the initial observations of altered avian communities: Francis *et al.* (2009) identified that due to the greater impact of noise on a common avian egg predator, there was a higher hatching success rate in the resulting bird community closer to highways. It is therefore probable that the varied responses of species within a community to noise may be changing bird community compositions by means of altered predator–prey dynamics, resulting in trophic cascades. This highlights that any initial observations of motorboat noise on fish communities should carefully consider species interactions.

It has been suggested that free-swimming species may leave unfavourable noisy environments resulting in a drop in overall abundance and

diversity of a community (Peng *et al.* 2015); yet, so far, no study has set out to measure this in fishes. If we were to extrapolate from findings of the effects of motorboat noise on the independent species behaviours and interspecific interactions studied so far we may be able to guess potential changes to fish communities. The detrimental effect of motorboat noise on fish recruitment (Holles *et al.* 2013) may lead to a reduced influx of young fishes to coral reefs situated near high levels of motorboat activity. However, due to the diverse life-histories and hearing abilities of fishes, the response of a single species assessed by Holles *et al.* (2013) may not extend across all coral reef fishes. Thus, by means of recruitment interference there may be either a drop in the total abundance of fishes and/or a reduction in the diversity and a change in the species composition of the resultant fish community. The detrimental effect of motorboat noise identified on the parental vigilance of brooding damselfish (Nedelec *et al.* 2017b) may also indicate a potential loss in brooding species in noisy regions.

The reduced foraging efficiency of planktivorous fishes resulting from motorboat noise (Bracciali *et al.* 2012; Voellmy *et al.* 2014a) may result in malnutrition and reduced fitness, which could result in higher chances of predation and disease. If this response to motorboat noise is a widespread issue across this trophic level, it would lead to an imbalance in natural food webs. Furthermore, the reduced predator avoidance efficiency of the Ambon damselfish (Simpson *et al.* 2016; Ferrari *et al.* 2018), another planktivorous species on the reef (which also feeds on algae), may mean that this trophic level is highly vulnerable to the combined impacts of malnutrition and increased predation. However, this is extreme speculation which can only be explored via community assessments and further in-depth assessments of noise on trophic interactions.

There have been two very recent studies that have started to hint that motorised vessels may be altering wild fish assemblages. The first, carried out by Lanham *et al.* (2018), used underwater video census to measure the influence of boat moorings on the nearby fish community in Port Jackson Estuary, Sydney. They discovered that fish abundance was lower near boat moorings, in combination with slight alterations in community composition. However, as the census was recorded at varying distances from 0–25 m to the nearest mooring, any surveys taken at <10 m to the mooring would be influenced by visual stimuli

or the physical disturbance of moored boats. Thus, in this study noise cannot be singled out as the leading factor causing alterations in fish communities.

The second study by González Correa *et al.* (2019) implemented passive acoustics to measure the impact of vessel noise on the "biophony" of the area – the biotic component of a soundscape. They found that the frequency and complexity of fish calls was reduced in areas exposed to high levels of motorboat noise. It may be possible that this difference in the biophony is a symptom of a decline in vocally active species. Yet this is highly speculative, as there are many other explanations for these findings. Rather than simply moving away from an invasive noise, species may have adjusted their acoustic behaviour in order to endure vessel noise, calling less frequently or shifting their vocalisations in frequency and timing (see 'Lombard effect' in '*1.04 Modes of acoustic interference in fishes*'). The use of passive acoustics to survey fish assemblages is most valuable when supported with an information library of fish species vocalisations, which in this study was lacking.

*1.10 Research aims*

Compelling evidence from the synthesis of two decades of research has established that motorboat noise is causing detrimental impacts on fish fitness and behaviour across freshwater and marine systems. Despite this there has been no community assessment of the ever-growing presence of motorboat noise on fish assemblages. Many review papers have now highlighted the value in understanding the ecological implications of anthropogenic noise on marine life, and have advocated for studies to assess community-level responses to noise (Williams *et al.* 2015; Kunc *et al.* 2016; Popper & Hawkins 2019).

**Chapter 2** provides the first comprehensive assessment, to my knowledge, of the impact of anthropogenic noise on a marine community, carried out by myself and Harry Harding, a PhD student at the University of Bristol. We addressed this major knowledge gap by conducting an extensive visual census of wild coral reef fish communities that have been chronically exposed to high levels of motorboat noise in French Polynesia. We compared community assessments of reef with high levels of motorboat noise disturbance with areas

of very low levels of motorboat noise. From these comparisons we assessed for differences in 1) total fish abundance, 2) species richness and diversity, and 3) species distributions. It was hypothesised that the high-disturbance regions would have a lower total fish abundance, species richness and diversity than the low-disturbance areas; and the high-disturbance communities would be dominated by tolerant fish species and lack the more vulnerable species.

We took this study further by exploring whether the findings from the community assessment could be recreated in a long-term motorboat manipulation experiment. Here we exposed a regions of coral reef, that had very low previous levels of motorboat disturbance, to a month-long motorboat manipulation regime. We compared community assessments of manipulated reef with undisturbed reef to see if, after a month, the introduction of motorboat noise changed the composition of a fish community on a coral reef.

# Chronic motorboat noise generates winners and losers in coral reef fish communities

## 2.1 Introduction

Anthropogenic noise is recognised as a pollutant of global concern in both terrestrial and aquatic environments (Hildebrand 2005; Buxton *et al.* 2017). Many noise-generating activities occur in coastal regions (Davenport & Davenport 2006), with human population growth, infrastructure development, increased transportation, fishing and tourism leading to ever-greater levels of motorboat traffic (Whitfield & Becker 2014). Coral reefs form a small yet essential component of tropical coastal waters: despite making up less than 1.2% of the worlds continental shelf area, they are home to 25% of the world's marine fishes (Spalding *et al.* 2001). Motorboat traffic, therefore, often comes into close proximity with reef fishes and recent research has demonstrated that noise from this source can have a range of physiological, developmental and behavioural impacts on individual fish species (Slabbekoorn *et al.* 2010; Kunc *et al.* 2016; Cox *et al.* 2018). For instance, damselfish exhibited elevated oxygen consumption and embryonic heart-rates (Simpson *et al.*, 2016; Jain-Schlaepfer *et al.* 2018), as well as reduced growth rates and changes in relative egg and hatchling size (Fakan & McCormick 2019). Across multiple species motorboat noise has caused changes in juvenile and adult behaviours, including predator avoidance (Simpson *et al.* 2015; Holmes *et al.* 2017; McCormick *et al.* 2018a, b), foraging efficiency (Bracciali *et al.* 2012; Voellmy *et al.* 2014a), territorial defence, brood protection (Sebastianutto *et al.* 2011; Nedelec *et al.* 2017b) and settlement (Holles *et al.* 2013; Simpson *et al.* 2016a). However, the majority of studies have only assessed the short-term effects of motorboats on a single species. Wild fish are subject to long-term, repeated exposures to motorboats and species are likely to differ in how they are affected, so chronic impacts on multispecies communities need experimental consideration.

Interspecific variation in responses to noise is expected in fishes as they have evolved an extremely high genetic and functional diversity, constituting over half of all extant vertebrates and occupying niches in almost every conceivable aquatic habitat type (Venkatesh 2003; Nelson 2006). Moreover, they possess a greater variety of sound-production and detection mechanisms than any other vertebrate group (Ladich 2000; Popper & Fay 2011). As such, differences in sonifereous activity, hearing sensitivities, and functional traits could influence the likely winners and losers in a multispecies community exposed to anthropogenic noise. There is some evidence from captive multispecies studies that different fishes vary in their response to the same boat noise treatments (Voellmy *et al.* 2014a, b; Shafiei Sabet *et al.* 2016; Fakan & McCormick 2019). In addition, studies on wild fishes have identified impacts to interspecific interactions showing alterations in predator–prey dynamics and mutualistic relationships when exposed to boat noise (Simpson *et al.* 2016b; Nedelec *et al.* 2017a; Ferrari *et al.* 2018). Understanding potential changes in such interactions, is important for determining how ecological processes are affected, but is not sufficient to predict impacts on entire communities.

While there have been some assessments of community-wide impacts of anthropogenic noise in terrestrial systems (see Francis *et al.* 2009; Herrera-Montes & Aide 2011), we know of only one related study in marine systems: Correa *et al.* (2019) used passive acoustics to show that there was reduced complexity of fish calls in the existing presence of motorboat disturbance. However, more comprehensive assessments of wild fish assemblages exposed to existing and experimentally manipulated motorboat disturbance are needed to better understand the influence of underwater anthropogenic noise on wild fish communities. Determining how communities will be affected in an increasingly noisy world is vital in order to predict how ecosystem function and stability may change in the future.

The current study aimed to investigate, for the first time, the ecological implications of anthropogenic noise on a fish community. We first used existing spatial variation in motorboat traffic across coral reefs to determine whether fish assemblages differ in relation to disturbance levels. This observational portion of the study explored whether long-term motorboat disturbance alters 1) overall fish abundance, 2) species richness, 3) diversity and 4) the distribution of individual

species in a coral reef fish community. In addition to this, we conducted a month-long experimental motorboat manipulation of natural sites with minimal previous disturbance history to test whether the community responses found in the historically disturbed sites of the previous study could be experimentally replicated following chronic experimental disturbance. This allowed us to isolate motorboat disturbance as a principal driver of any change in fish communities.

## 2.2 Methods

*Study system and sites*

All observational and experimental work was conducted during October–November 2017 in the lagoon surrounding the Pacific Island of Mo'orea, French Polynesia. Observational data were collected on fish communities on the north fringing reef of Mo'orea along two boat channels that have been active for over 30 years (Fig. 1a–b). The Matautia (mean ± SE width: 17 ± 3 m; length: 1.23 km) and Vaipahu (width: 17 ± 1 m; length: 1.61 km) boat channels allow the safe passage for tourism vessels, pleasure craft and artisanal fishing boats through continuous sections of reef habitat in the lagoon. As a result, the channels receive regular motorboat traffic (Matautia: 17.7 ± 1.9 (mean ± SE) boats per hour, 10 h of observation across 4 days; Vaipahu: 5.7 ± 0.9 boats per hour, 15.5 h of observation across 9 days). Community assemblages were considered at two distances perpendicular to the boat channels (see below), allowing a comparison of high- and low-disturbance sites (Fig. 1a–b).

Sites for experimental manipulation of motorboat disturbance were situated on the north-western side of the island, 170–340 m away from the nearest boating channel, (5.5 ± 0.9 boats per hour were seen operating in the distant channel, 77 h of observation across 25 days; with 1.5% of boat passes seen closer to the study sites than the distant channel; Fig. 1c).The spatial separation of individual coral bommies (isolated sections of reef) facilitated experimental motorboat driving.
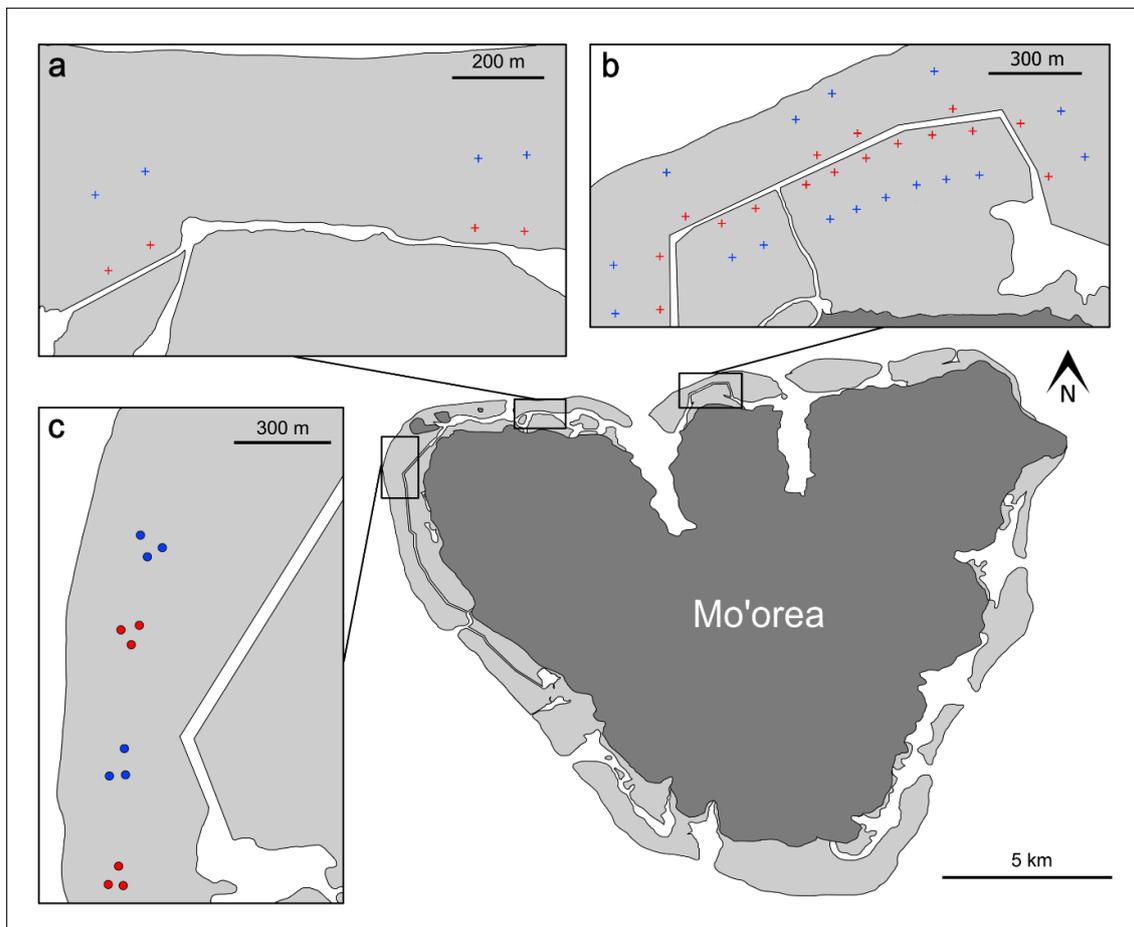
**Figure 1**. Map of Mo'orea (dark grey), its surrounding reef (light grey) and boat channels (white). The observational fish-community study sites, denoted with red (high disturbance) and blue (low disturbance) crosses within sampling pairs, were situated at the northern **a**) Matautia and **b**) Vaipahu boat channels. Experimental-manipulation study sites, denoted with red (chronic motorboat disturbance) and blue (chronic ambient) circles, were situated on the **c**) north-western reef away from any boat channels.

*Fish community differences in relation to existing variation in motorboat disturbance*

Reef sites within 20–40 m of the boat channels were characterised as 'high disturbance'; the minimum distance of 20 m from the channel reduced the potential influence of other channel-associated factors on fish assemblages, including edge effects (Sambrook *et al.* 2016) and the wake and visual stimulus of passing boats. Reef sites between 100 and 140 m from the boat channels were

characterised as 'low disturbance'. High- and low-disturbance sites were coupled in 'sampling pairs', which extended perpendicular from the channel, to account for potential larger-scale variation in fish assemblages along the >1 km boat channels. At each high- and low-disturbance site, 50 m survey transects were sampled parallel to the boat channel; transects at neighbouring sampling pairs were separated by a minimum of 30 m. Overall, 20 sampling pairs (each with a high- and low-disturbance site) were established along the two channels, resulting in 40 transects in total. Constraints in habitat type (large regions of sand and extremely shallow water that would have heavily driven variation in fish assemblages) and the minimum separation distance between survey sites meant that the Matautia channel was restricted to four sampling pairs; there were 16 sampling pairs along the Vaipahu channel.

Benthic surveys were undertaken to assess substrate composition along the transects. Benthic video recordings were made for each 50 m transect by one surveyor (HRH) swimming 1 m above the reef and filming with a GoPro Hero 4 from a standardised mounted-camera position. The point-intercept method (Ohlhorst *et al.* 1988) was then used on these video recordings to quantify the benthic composition. Using a consistent midpoint of the video panel (VLC Media Player), the substrate type at 1 m intervals along the transects was categorised as one of the following: live coral (soft and hard), dead coral (algal symbionts visibly absent), turfing/macroalgae, sand, rubble, bedrock, anemone or human material. Benthic composition did not vary significantly between high- and low-disturbance sites (PERMANOVA: Pseudo-$F$ = 0.083, $p$ = 0.953, Fig. S1). Depth was measured at 5 x 10 m intervals along each transect using a dive computer (Zoop, Suunto Oy, Vantaa, Finland). High-disturbance sites were 16 ± 0.1 cm deeper than low-disturbance sites (paired t-test: $t$ = 3.12, df = 19, $p$ = 0.006). However, this difference in depth was well within the tidal range (0.3 m from MHWS to MLWS) and similar to the resolution of the dive computer (± 1% accuracy; 0.1 m resolution), and thus is unlikely to influence fish assemblages.

Non-cryptic fish were visually surveyed along transects by snorkelers and classified to species. The first of two surveyors (EW) documented transient mobile fish species within a 4 m-wide belt. After a period of 3 min, allowing fish to resume typical behaviour, the second surveyor (HRH) documented site-attached fishes within a 2 m-wide belt. Surveys were conducted between 09:00

and 16:00 to avoid crepuscular periods of high temporal variation in fish assemblages (Mallet *et al.* 2016). Each site was surveyed three times, with a minimum of 24 h between repeats.

*Fish community differences in relation to experimental manipulation of motorboat disturbance*

Baseline community assemblages were censused at 12 sites before the experimental regime of chronic motorboat disturbance or an equivalent control period. The 12 sites were clustered in groups of three (minimum separation distance of 40 m within a cluster), with the four clusters separated by a minimum distance of 170 m, along the back reef within the lagoon (Fig. 1c). Clustered grouping of reefs aided boat operations during the experimental manipulation. The disturbance regime consisted of driving motorboats at two of the clusters (hereafter chronic-motorboat sites), with the other two clusters acting as controls and receiving no experimental motorboat disturbance (chronic-ambient sites). The driving regime involved repeated passes 10–50 m from the site for 5 min before moving onto the next site in the cluster. The boat was driven in reverse for safe navigation of coral bommies. Three 25 hp motorboats were used in a randomised order over the course of the disturbance regime to minimise pseudoreplication. Motorboat exposures were carried out for 15 min at each chronic-motorboat cluster (5 min at each of three sites within a cluster), twice per day for 22 days and once per day for 7 days (depending on weather and boat availability) during the course of one month. Therefore, each chronic-motorboat cluster received 12.25 h total experimental motorboat exposure; each site received ~4 h of close-proximity motorboat disturbance and ~8 h of varying levels of motorboat disturbance from motorboats driving around the other sites in the cluster.

Fish surveys were carried out at the 12 chronic-manipulation sites using the same methods as for the existing motorboat-disturbance sites. The 50 m transects passed through the immediate vicinity of the *S. nigricans* territories selected for the behavioural experiment. A single survey was conducted at each of the 12 sites before the chronic-manipulation period. Transects were visibly

marked to enable easy return and repeat of an equivalent survey 40 days later (post-chronic-manipulation period). Benthic composition was assessed at each site, following the methods described above; benthic composition did not differ significantly between the chronic-motorboat and chronic-ambient sites (PERMANOVA: Pseudo-$F$ = 0.172, $p$ = 0.955, Fig. S2). The depth ranged from 1–2 m, measured with the same method as above. There was no significant difference in depth between the chronic-motorboat and chronic-ambient sites (independent-samples t-test: $t$ = -0.28, df = 7.17, $p$ = 0.79).

*Acoustic stimuli and analysis*

To characterise the soundscape experienced by the fish communities at the existing high- and low-disturbance sites, representative examples of passes by motorboats routinely using the channels and of ambient conditions were recorded. Recordings were made in both acoustic-pressure (Fig. 2a) and particle-acceleration (Fig. 2b) domains at sites across the two boat channels. To characterise experimental-manipulation acoustic conditions, representative examples of ambient sound and motorboat noise at individual sites, equivalent for both the short-term experimental behavioural trials and the chronic driving regime carried out at each site, were recorded in both acoustic-pressure (Fig. 2c) and particle-acceleration (Fig 2d) domains. To ensure that experimental noise from the chronic-motorboat sites was not propagating to the control sites, representative acoustic conditions at adjacent control clusters were recorded in the particle-acceleration domain whilst driving boats at chronic-motorboat sites (Fig. 2d).

Acoustic pressure was measured using a calibrated omnidirectional hydrophone (HiTech HTI-96-MIN with inbuilt preamplifier, manufacturer-calibrated sensitivity -164.3 dB re 1 V/µPa; frequency range 0.02–30 kHz; High Tech Inc., Gulfport MS) and a digital recorder (PCM-M10, 48 kHz sampling rate, Sony Corporation, Tokyo, Japan). Particle acceleration was measured using a calibrated triaxial accelerometer (M20-040; sensitivity 0–3 kHz; Geospectrum Technologies, Dartmouth, Canada) and a 4-track recorder (Boss BR-800, 44.1 kHz sampling rate, Roland Corporation, Los Angeles, CA). All

recorded levels used were calibrated using a 1 kHz pure sine wave signal of known voltage, measured in-line with an oscilloscope. Artefacts (external noise from equipment knocking) detected in the recordings were removed following manual inspection of spectrograms using Audacity 2.3.0 software (www.audacityteam.org). Due to the close proximity of our hydrophone to fish territories, fish vocalisations formed a large part of the soundscape below 600 Hz; in order to gain an accurate assessment of the contribution of motorboat noise to high- and low-disturbance sites, these vocalisations were manually removed after inspection of spectrograms (Fig. 2a–b; see Fig. S3a–b for power spectral density plots of recordings before removal of fish vocalisations).

The acoustic-pressure and particle-acceleration recordings taken at the high- and low-disturbance sites were cut into 20 s clips for each treatment—high-disturbance sites with a boat pass (10 s either side the peak of the pass), high-disturbance ambient conditions, and the equivalents at the low-disturbance sites—and appended together. Recordings of experimental manipulations from boat sites were cut into 5-min clips to reflect exposures during short-term trials; two recordings to test for acoustic transfer of motorboat noise between chronic-motorboat and chronic-ambient clusters were assessed over 3 min.
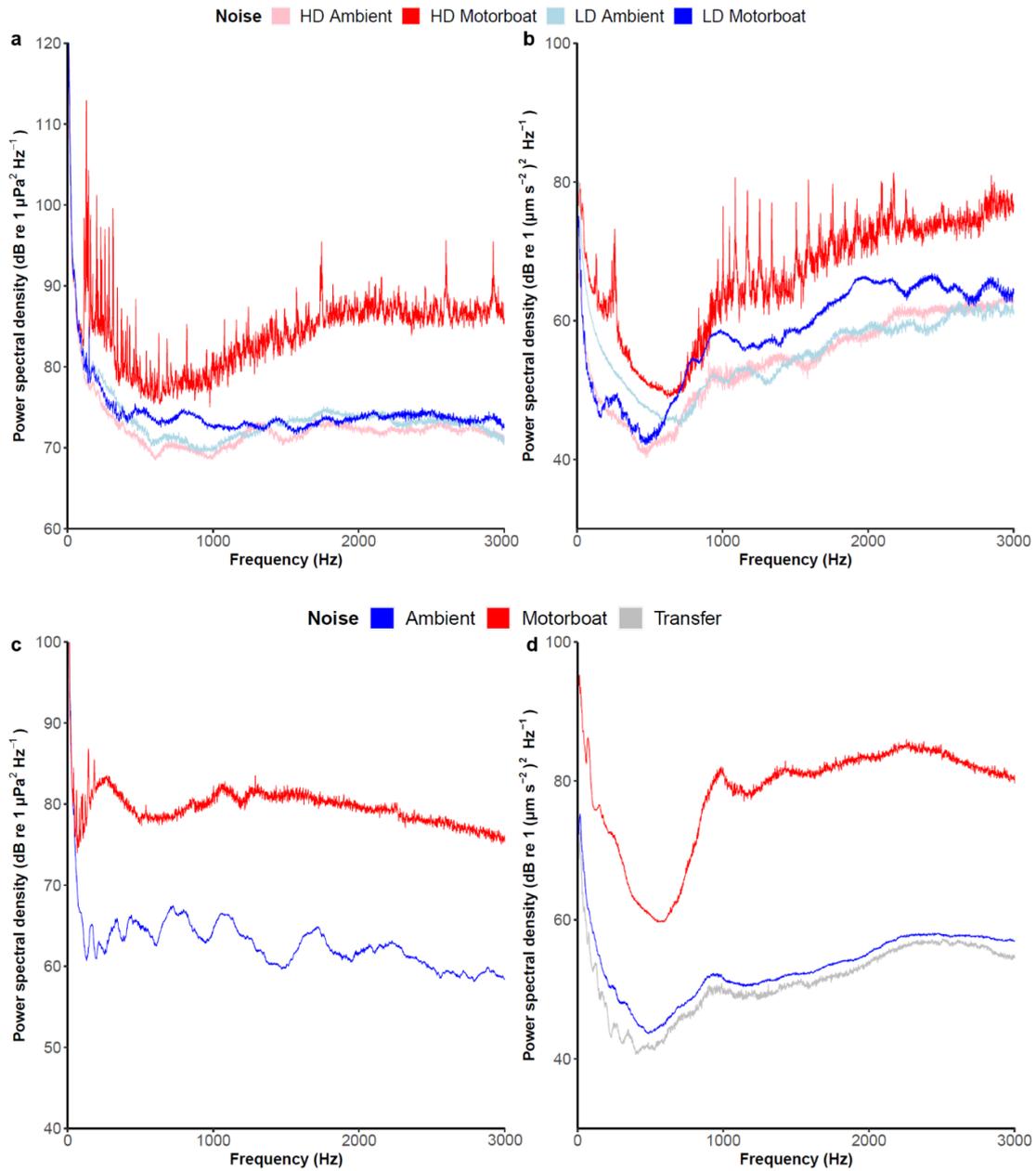
**Figure 2**. Power spectral density plots (PSD) of sound measurements from the motorboat channels and chronic-manipulation sites. All recordings were analysed using PaPAM acoustics analysis package in MATLAB (Nedelec *et al.* 2016a), with a sampling rate of 44.1 kHz, Hamming window, 50% overlap, window length = sampling rate. HD = High-disturbance sites, LD = Low-disturbance sites. Acoustic pressure at the **a**) boat-channel sites ($n_{high-disturbance}$ = 14; $n_{low-disturbance}$ = 14) and the **c**) chronic-manipulation sites ($n_{ambient}$ = 4; $n_{motorboat}$ = 4), and monoaxial particle acceleration at the **b**) boat-channel sites ($n_{high-disturbance}$ = 4; $n_{low-disturbance}$ = 4) and the **d**) chronic-manipulation sites ($n_{ambient}$ = 8; $n_{motorboat}$ = 2; $n_{transfer}$ = 2). Lines represent the mean power spectral density for each treatment condition.

*Data analysis*

All multivariate analyses were performed in PRIMER v6 with +PERMANOVA add-on package (Clarke & Warwick 1994). All univariate analyses were performed in R (www.cran.r-project.org, version 3.5.2) using linear mixed models (LMM) or generalised linear mixed models (GLMMs), with the error structure determined using AICc selection (R package: *lme4*; *DHARMa*). Levels of significance were determined for fixed terms and the interaction via comparisons to models without the term of interest. Residual plots from all binomial GLMMs were checked using the *DHARMa* package in R (Hartig 2017). Model residuals for the continuous data were assessed for normality, homogeneity of variance, collinearity and influential outliers via Cook's distance.

*Fish community differences in relation to existing variation in motorboat disturbance*

All fish survey data were standardised to abundance per 100 m$^2$. Convict surgeonfish (*Acanthurus triostegus*) were either absent or appeared as >200 individuals per transect due to their schooling behaviour (Randall 1961); this caused difficulties in statistical analysis due to the resulting violations to test assumptions, therefore they were excluded from the dataset. Total fish abundance, species richness and Shannon Wiener diversity index were calculated for each transect and assessed with GLMMs. All GLMMs incorporated motorboat disturbance (fixed), repeat (random) nested within sampling pair (random) and channel (random) as factors. Species assemblages were compared between high- and low-disturbance sites using an unrestricted one-way nested PERMANOVA (maximum permutations = 9,999), with motorboat disturbance (high, low) as a fixed term and sampling pair (1–20) and repeat (1–3) nested within sampling pair as random factors. Variation in fish species assemblages between high- and low-disturbance sites was visualised using non-metric Multidimensional Scaling (nMDS) based on a Bray-Curtis similarity matrix of the survey data.

A percentage similarity analysis (SIMPER) was carried out to identify particular fish species that consistently contributed to the greatest dissimilarity between high- and low-disturbance sites. The species identified as most influential on the variation in fish assemblages between the high- and low-disturbance sites in the SIMPER analysis were then assessed in separate GLMMs, here the original unstandardised counts were used to fit a Poisson distribution. Our hypothesis tests were conducted across 22 species which risks inflating Type 1 error rate. Often, the traditional Bonferroni-type multiple comparison procedures are used to account for such error inflation, but are highly conservative risking the increase of wrong rejections of true hypotheses (Pike 2011). We used a False Discovery Rate (FDR) procedure (the 'graphically sharpened method') which corrects for multiple comparisons without risking the same loss of power. FDR-adjusted $p$-values were calculated using automated computation from Appendix S1, Pike 2011.

*Fish community differences in relation to experimental manipulation of motorboat disturbance*

Fish survey data were standardised to abundance per 100 m$^2$, and *A. triostegus* was excluded, as per the boat-channel surveys (above). Abundance, species richness and Shannon Wiener diversity index were also analysed using non-parametric Wilcoxon's signed-rank tests. Variation in species assemblages across pre-manipulation sites was compared in an unrestricted one-way PERMANOVA (maximum permutations = 9,999) with manipulation treatment as the single fixed factor, and visualised with an nMDS, based on a Bray-Curtis similarity matrix. The same analysis was then conducted on the post-manipulation survey data to observe any changes to the community composition between the sites exposed to chronic-ambient and chronic-motorboat treatments. A SIMPER analysis was also carried out on the post-manipulation census data to identify fish species that consistently contributed the greatest dissimilarity in distributions between treatments. Species identified as most responsible for variation between chronic-ambient and chronic-motorboat sites were analysed separately using non-parametric Wilcoxon's signed-rank tests. FDR multiple

comparisons corrections were applied to the 22 hypotheses tested via the Wilcoxon's signed-rank tests.

## 2.3 Results

*Fish community differences in relation to existing variation in motorboat disturbance*

There was no significant effect of natural motorboat-disturbance level on the total fish abundance (GLMM: $\chi^2 = 0$, df = 1, $p = 1$), species richness ($\chi^2 = 1.16$, df = 1, $p = 0.28$) or Shannon Wiener diversity index ($\chi^2 = 0.09$, df = 1, $p = 0.77$). However, there was a significant difference between the high- and low-disturbance sites in the composition of their fish communities (PERMANOVA: Pseudo-F = 2.69, df = 1, $p = 0.03$, 9948 Permutations). An nMDS plot provided a visual representation of the disparity in the fish community composition between the high- and low-disturbance sites (Fig. 3a). A SIMPER analysis identified 24 species cumulatively contributing to 90% of dissimilarities between high- and low-disturbance fish assemblages (Table S1; Fig. 3b).
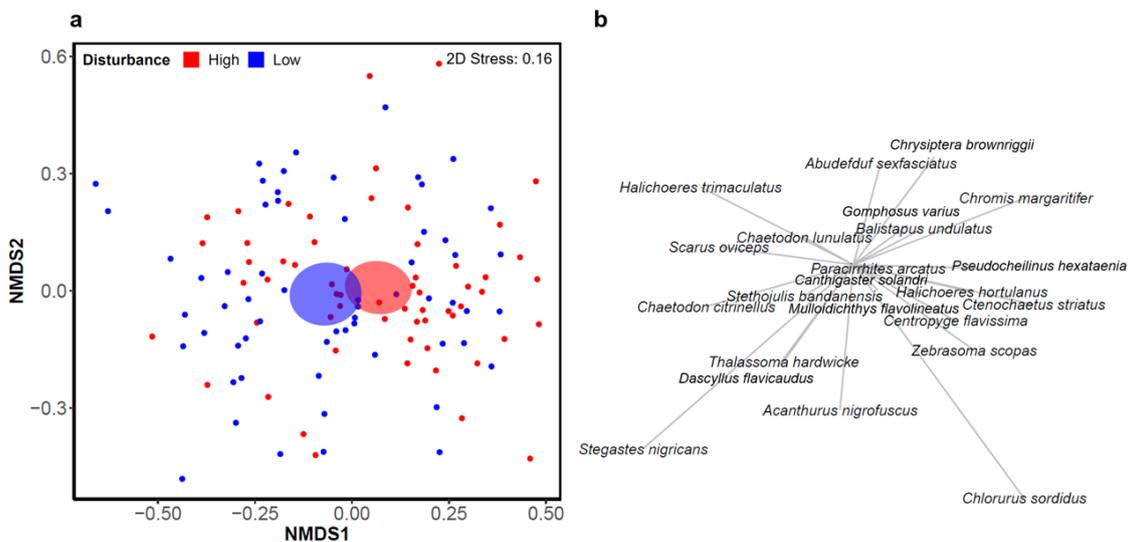


**Figure 3.** a) Nonmetric multidimensional scaling ordination (nMDS) showing variation in fish community composition between sites exposed to high and low

levels of natural motorboat disturbance. Individual dots represent survey repeats at each site (n = 40 sites); shaded ellipses represent the standard error of the weighted average of each disturbance group. b) Species-loadings plot from the SIMPER output indicating the relative contribution of species to the observed variation in fish community assemblages between sites of low and high levels of natural motorboat disturbance.

Five species were significantly lower in abundance in high-disturbance compared to low-disturbance sites (Table S1; Fig. 4): *Stegastes nigricans* (GLMM: $\chi^2$ = 4.81, df = 1, FDR-adjusted $p$ = 0.028), *Thalassoma hardwicke* ($\chi^2$ = 11.90, df = 1, FDR-adjusted $p$ = 0.001), *Chaetodon citrinellus* ($\chi^2$ = 8.31, df = 1, FDR-adjusted $p$ = 0.005), *Gomphosus varius* ($\chi^2$ = 14.40, df = 1, FDR-adjusted $p$ < 0.001) and *Dascyllus flavicaudus* ($\chi^2$ = 11.20, df = 1, FDR-adjusted $p$ = 0.001). Seven species had significantly higher abundances at the high-disturbance compared to low-disturbance sites (Table S1; Fig. 4): *Ctenochaetus striatus* ($\chi^2$ = 9.69, df = 1, FDR-adjusted $p$ = 0.003), *Chromis margaritifer* ($\chi^2$ = 72.50, df = 1, FDR-adjusted $p$ < 0.001), *Zebrasoma scopas* ($\chi^2$ = 15.30, df = 1, FDR-adjusted $p$ < 0.001), *Centropyge flavissima* ($\chi^2$ = 7.70, df = 1, FDR-adjusted $p$ = 0.007), *Abudefduf sexfasciatus* ($\chi^2$ = 11.70, df = 1, FDR-adjusted $p$ = 0.001), *Pseudocheilinus hexataenia* ($\chi^2$ = 5.94, df = 1, FDR-adjusted $p$ = 0.016) and *Mulloidichthys flavolineatus* ($\chi^2$ = 12.80, df = 1, FDR-adjusted $p$ = 0.001).
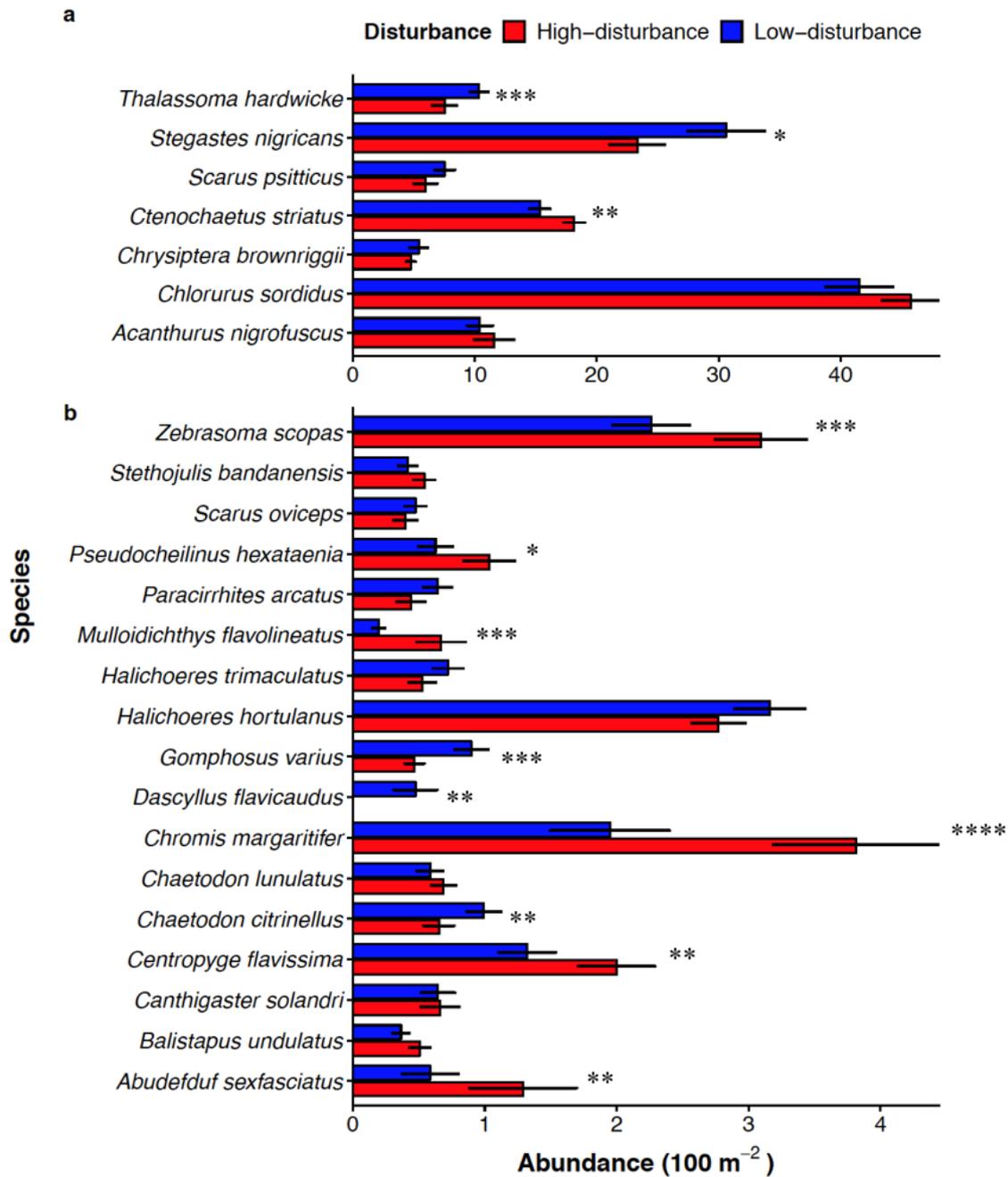
**Figure 4.** Mean fish abundance per 100 m$^2$ for each of the 24 species identified from the SIMPER analysis as explaining 90% of the cumulative variation between high- and low-disturbance sites at the boat channels: (a) abundant species (>5 per 100 m$^2$) and (b) less abundant species (<5 per 100 m$^2$). Error bars represent SE. Asterisks represent significance level: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ and **** = $p < 0.0001$.

*Fish community differences in relation to experimental manipulation of motorboat disturbance*

There was no significant difference between the chronic treatments, before or after the one-month manipulation period, in total fish abundance (Wilcoxon signed-rank test, before: W = 19, n = 6, $p$ = 0.94; after: W = 18, n = 6, $p$ = 1), species richness (before: W = 16.5, n = 6, $p$ = 0.87; after: W = 18, n = 6, $p$ = 1) or diversity (Shannon Wiener index; before: W = 15, n = 6, $p$ = 0.70; after: W = 13, n = 6, $p$ = 0.49). Overall, the fish community composition did not differ significantly between treatment sites before (PERMANOVA: pseudo-f = 0.457, df = 1, $p$ = 0.925) or after (pseudo-f = 1.41, df = 1, $p$ = 0.189; Fig. 5a–b) the chronic-manipulation period. An nMDS plot visually indicated the lack of separation in the fish community composition between the chronic-motorboat and chronic-ambient sites following the one-month manipulation period (Fig. 5a). In keeping with the boat-channel community census, a SIMPER analysis was used to explore whether some individual species were still affected, despite no significant change in the overall community. SIMPER analysis conducted on post-manipulation survey data indicated that there were 22 species cumulatively contributing to 90% of the dissimilarity that existed in community composition between the chronic-motorboat and chronic-ambient sites (Table S2; Fig. 5b).
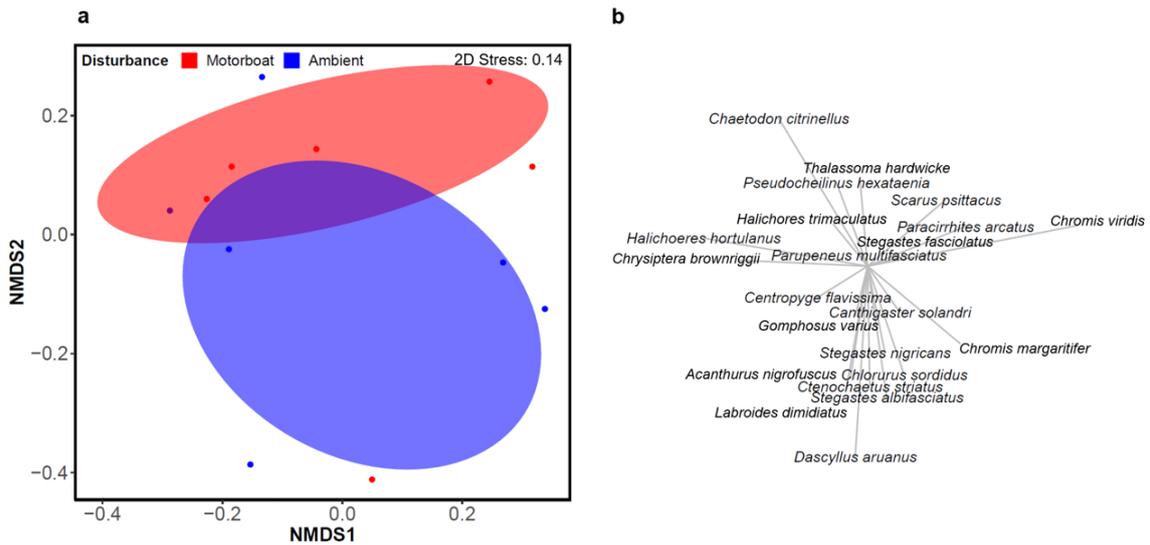
**Figure 5.** (a) Nonmetric multidimensional scaling ordination (nMDS) describing the variation in fish species composition between sites exposed to chronic-motorboat or chronic-ambient conditions. Dots represent transects surveyed at each site (n = 12 sites). Shaded ellipses represent the standard error of the weighted average of each treatment group. (b) Species loadings plot from the SIMPER output indicating relative contribution of species to observed variation in fish community assemblages between chronic-ambient and chronic-motorboat exposures.

The 22 species identified in SIMPER were analysed independently using Wilcoxon signed-rank tests. There were no significant differences in species abundances between the treatment sites prior to the one-month manipulation (Wilcoxon signed-rank tests: all W < 25, n = 6, all $p$ > 0.05). However, consistent with the observational findings from the boat channels, there was a post-manipulation decline in *S. nigricans* abundance at the sites exposed to motorboat disturbance compared to ambient sites (W = 31, n = 6, $p$ = 0.04; Fig. 6). In addition, there was a post-manipulation increase in *C. margaritifer* abundance at sites exposed to motorboat disturbance compared to ambient sites (W = 5, n = 6, $p$ = 0.03; Fig. 6). However, after FDR correction, the significance for both *S. nigricans* and *C. margaritifer* is lost (for both FDR adjusted $p$ = 0.48). The abundance of all other species were not significantly affected by the motorboat manipulation (all W < 28, n = 6, all FDR-adjusted $p$ > 0.1; Fig. 6).
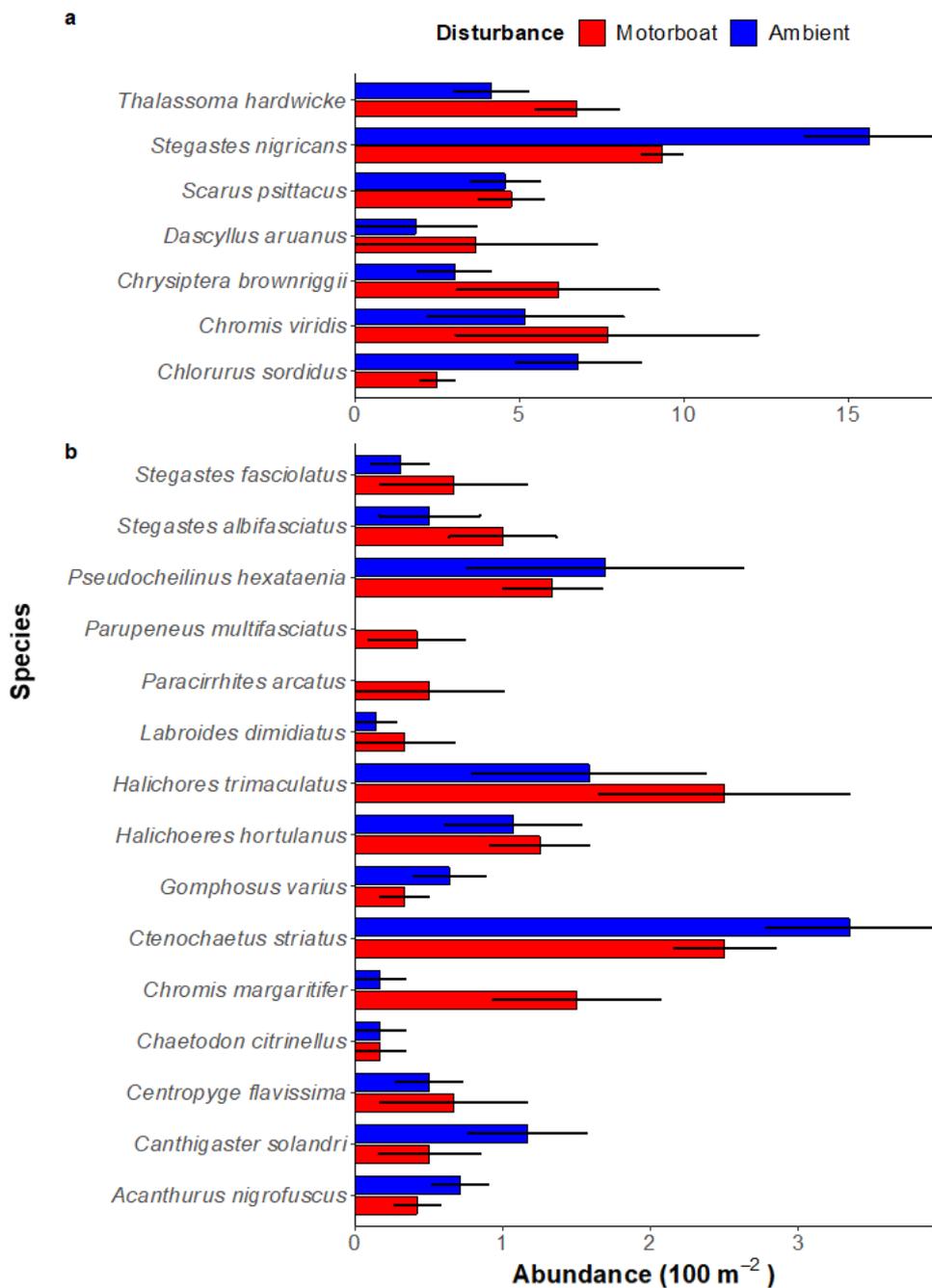
**Figure 6.** Total abundance per 100 m$^2$ for each of the 22 species identified from the SIMPER analysis as explaining 90% of the cumulative variation between chronic-ambient and chronic-disturbance sites after the manipulation: a) abundant species (>5 per 100 m$^2$) and b) less abundant species (<5 per 100 m$^2$). Error bars represent SE. Asterisks represent significance level: * = $p < 0.05$.

## 2.4 Discussion

Twelve common fish species had significantly different abundances between

areas exposed to chronic high and low motorboat disturbance, such that there was a difference in the overall coral reef fish community composition. A month-long manipulation of motorboat disturbance, in previously minimal-disturbance sites, had no significant effect on species distributions. We found that motorboat disturbance, existing or experimentally manipulated, did not result in any overarching differences in the total abundance, species richness or diversity of the fish community. This study, to our knowledge, is the first major assessment of the impact of chronic motorboat disturbance on a fish community. It addresses this gap in the literature by using both the existing spatial variation along with an experimental manipulation of motorboat disturbance on coral reef fish assemblages.

Species vary in their functional traits, ecology, life histories (Thorson *et al.* 2017), vocalisation activity (Tricas & Boyle 2014) and hearing sensitivities (Popper & Fay 2011) which may all play a part in determining how they respond to anthropogenic noise. Differences in the fish community composition identified in this study were evident only at the species level rather than at broader ecological metrics (total abundance, species richness and diversity), suggesting that impacts of vessel noise on marine communities may be more intricate than predicted. This somewhat contrasts terrestrial studies, whereby overall bird species richness was lower in habitats disturbed by noise (Francis *et al.* 2009; Herrera-Montes & Aide 2011). Nevertheless, some bird species had higher reproductive success in noisy habitats due to disrupted predator–prey interactions, suggesting that, despite broad changes in overall richness, intricate species interactions should not be neglected (Francis *et al.* 2009). It is important to note that the north fringing reef-lagoon system of Mo'orea lack biodiversity compared to healthier reefs nearby due to a history of spearfishing, agricultural runoff, crown-of-thorns outbreaks, cyclones and coral bleaching (Faurea 1989; Gillett & Wayne 2006; Chin *et al.* 2011; Rouzé *et al.* 2015). The common species found here heavily dominate the reef community and may possess higher stress tolerances. Thus, anthropogenic noise could have a stronger influence on healthier reef communities with fewer historical disturbance events.

*Stegastes nigricans* have a 24% lower abundance at existing high-disturbance compared to low-disturbance sites (Fig. 4, Table S1). *S. nigricans* are one of the most common species of this reef-lagoon system and so the

disparity in their abundance was responsible for driving the greatest difference observed between the high- and low-disturbance communities. *Stegastes nigricans* is a soniferous species producing low frequency pops and pulse trains, with acoustic communication playing a key role in reproduction, feeding, nest defence and predator avoidance (pers. obs. HRH & EW, see Weimann *et al.* 2018 for other *Stegastes spp.*). Thus, factors that reduce vocalisation efficiency and detection may have indirect deleterious fitness consequences. Auditory masking—whereby sound level and frequency of an interfering noise directly competes with biotic signals emitted by marine fauna—represents one such mechanism. High noise levels associated with boat channels may mask courtship calls, conspecific alarm calls, intruder sounds, and aggressive and deterrent vocalisations. Motorboat noise has been found to alter predator–prey dynamics in other coral reef damselfish resulting in increased mortality by predation (Simpson *et al.* 2016b); it is possible that elevated predation risk could underpin the lower *S. nigricans* abundances observed in this study.

Changes in *S. nigricans* distributions may be driven by direct impacts of motorboat noise on early life stages. Exposure to motorboat noise has been found to reduce the natural ability of damselfish and cardinalfish larvae to move towards reef sound (Holles *et al.* 2013; Simpson *et al.* 2016a), a key settlement cue for larval coral reef fish (Simpson *et al.* 2005; Holles *et al.* 2013). *Stegastes nigricans* often aggregate in large colonies, increasing the cooperative defence of algal turf from herbivores and broods from predators, as well as increasing spawning efficiency (Karino & Nakazono 1993). Thus, a reef soundscape with a large presence of *S. nigricans* calls may be most attractive to settlement-stage larvae. Acoustic masking of vocalisations by motorboat noise may reduce the attractiveness of a reef resulting in fewer larval recruits. Recruitment success is not possible to monitor in one–month manipulations; but it could, over multiple generations, explain the long-term alterations to *S. nigricans* distributions near boat channels.

Two common predators on this reef system, the sixbar wrasse (*Thalassoma hardwicke*) and the Pacific bird wrasse (*Gomphosus varius*), were also observed at significantly lower abundances in high-noise disturbance areas. While there has been substantial focus on the detrimental impact of anthropogenic noise on vigilance and predator avoidance in prey species

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(Bruintjes & Radford 2013; Simpson *et al.* 2015; Purser *et al.* 2016; Spiga *et al.* 2017; Ferrari *et al.* 2018; McCormick *et al.* 2018a), few studies have focussed on the predators within predator–prey relationships (Simpson *et al.* 2016b; McCormick *et al.* 2018b). These studies have generally assessed a predator's capture success when presented with prey in noisy conditions. However, the effects of motorboat noise on the ability of a predator to seek out and correctly identify prey in the wild, which is arguably more demanding of the sensory system and cognitive ability, are not yet known. Predators may rely heavily on sound generated by prey during hunting (Holt & Johnston 2011), which could make them more vulnerable than herbivores, detritivores and planktivores in a noisy environment.

Community-level responses to an environmental disturbance are usually the result of interference with functional traits and complex interspecific interactions, rather than equal impacts across all species (Skagen *et al.* 2006; Williams *et al.* 2010). Adult *T. hardwicke* prey upon the eggs of *S. nigricans* (Shima & Osenberg 2003); and so, their distributions may be driven by *S. nigricans* abundance, which would explain the lower abundances of both species in the high-disturbance areas. If this is indeed the case, once *S. nigricans* populations decline in response to the introduction of noise we could expect a lag before predator distributions follow (Lotka 1925). The lack of response from *T. hardwicke* to motorboat disturbance observed in the month-long experimental motorboat manipulation would support this hypothesis; if the manipulation were to continue for longer, *T. hardwicke* distributions may begin to follow similar trends to *S. nigricans*. This indirect response would be the first indication that motorboat disturbance could have the potential to trigger trophic cascades within a marine community.

Some species were found to have a greater abundance in areas of high motorboat-disturbance compared to those with low acoustic disturbance. The bicolor chromis (*C. margaritifer*)*,* lemonpeel angelfish (*C. flavissima*)*,* scissortail sergeant (*A. sexfasciatus*) and sixline pygmy wrasse (*P. hexataenia*) all had significantly higher abundances in areas exposed to motorboat disturbance. Like *S. nigricans,* all these fishes are site-attached, meaning they remain tightly associated to small areas of reef. Yet, unlike *S. nigricans*, these species do not farm turfing algae, and so have a reduced requirement to aggressively defend

their territory. Thus, in areas of high *S. nigricans* densities these less confrontational species are likely outcompeted for space. Where high motorboat disturbance leads to lower *S. nigricans* abundance, the alleviated competition for space could allow these sedentary, and potentially more noise tolerant, species to persist in greater abundances.

Two common acanthurids, the striated surgeonfish (*Ctenochaetus striatus*) and the brushtail tang (*Zebrasoma scopas*), were also observed in significantly greater abundances in areas of high motorboat disturbance. Acanthurids produce sounds during courtship and agonistic interactions (Tricas & Boyle 2014), but do not rely on sound to forage on algae and detritus. Moreover, it is suggested that they possess relatively low hearing sensitivity (Colleye *et al.* 2016); which may confer greater tolerance to anthropogenic noise than other families. *Ctenochaetus striatus* and *Z. scopas* also likely experience agonistic chases from *S. nigricans,* for their diets form components of the epilithic algal matrix (EAM)—detritus, sediment, filamentous algae and invertebrates (Wilson & Bellwood 1997)—that is maintained by *S. nigricans* inside their farmed territories. Thus, reefs with fewer *S. nigricans* may present *C. striatus* and *Z. scopas* with greater opportunities to graze on unguarded EAM, alleviating competition for food.

In our study the month-long experimental manipulation of a reef to daily boat disturbance showed indications of two fish species showing signs of following similar trends as identified in the previous observational study; with an increased abundance of *C. margaritifer* and a reduced abundance of *S. nigricans* in regions of reef manipulated with chronic boat disturbance. However, False Discovery Rate corrections for multiple comparisons eliminated the significance of the difference identified in these species. This secondary experiment lacked the statistical power of the previous observational study due to lower replication level, which may have caused a hinderance in uncovering any changes to the community. In addition, the boat manipulation of one month may not have been sufficient to elicit enough of a change in the fish community that can be detectable by visual census techniques. Nonetheless, the trends of *S. nigricans* and *C. margaritifer* populations emerging from experimental study to complement the findings of the observational study should not be ignored, but should encourage further investigation.

Species vary, with their ecology, life history, functional traits, soniferous activity and hearing sensitivity likely dictating winners and losers in environments polluted by anthropogenic noise. To date, the majority of studies have assessed short-term effects of anthropogenic noise on single species, with few addressing interspecific interactions. This study suggests that species may be affected differently by motorboat noise and impacts may only begin to emerge after chronic disturbance. Here we highlight the need for caution when translating impacts of anthropogenic noise on single species to wild communities; as functional diversity combined with complex interspecific interactions may well govern community-wide responses to chronic noise disturbance. Understanding the bigger picture of ecological implications from anthropogenic noise is essential for predicting future ecosystem functioning and stability in the face of a plethora of interacting local and global anthropogenic stressors. Further research on the community-wide effects of noise will help develop a stronger basis for implementing mitigation policies in boating zones and engineering low-disturbance engine and propeller systems, with the ultimate goal of reducing our acoustic footprint on vulnerable ecosystems in the marine environment.

## 2.5 Supplementary information
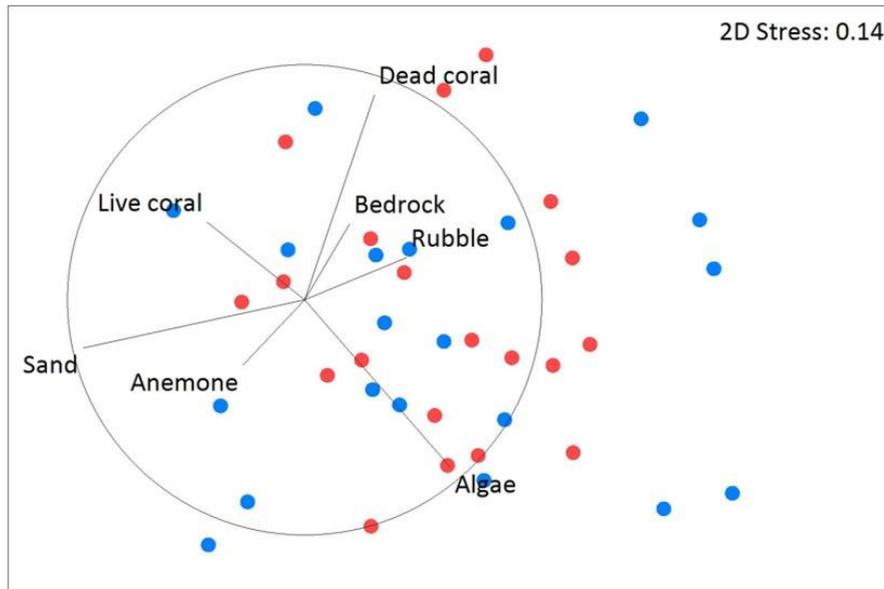


**Supplementary Figure S1.** Non-metric multidimensional scaling ordination (nMDS) of benthic composition variation among survey sites of the boat channel study. Blue circles represent low-disturbance sites, red circles represent high-disturbance sites. Overlaying loadings indicate contribution of substratum types to the variation in benthic composition.
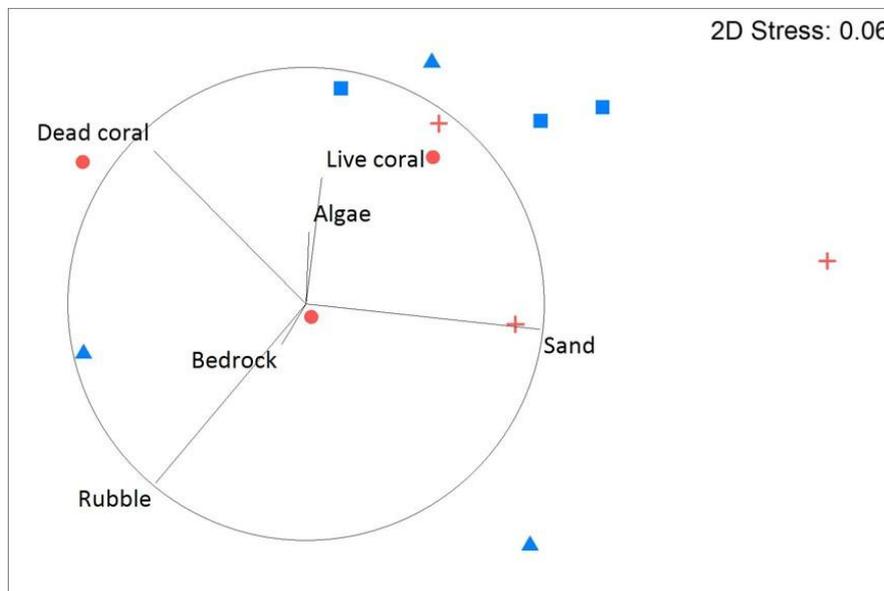


**Supplementary Figure S2.** Non-metric multidimensional scaling ordination (nMDS) of benthic composition variation among motorboat manipulation sites. Colour represents manipulation treatment: ambient (blue) and motorboat (red). Symbol shape represents clusters 1 (triangle), 2 (circle), 3 (square) and 4 (cross). Overlaying loadings indicate contribution of substratum types to the variation in benthic composition.
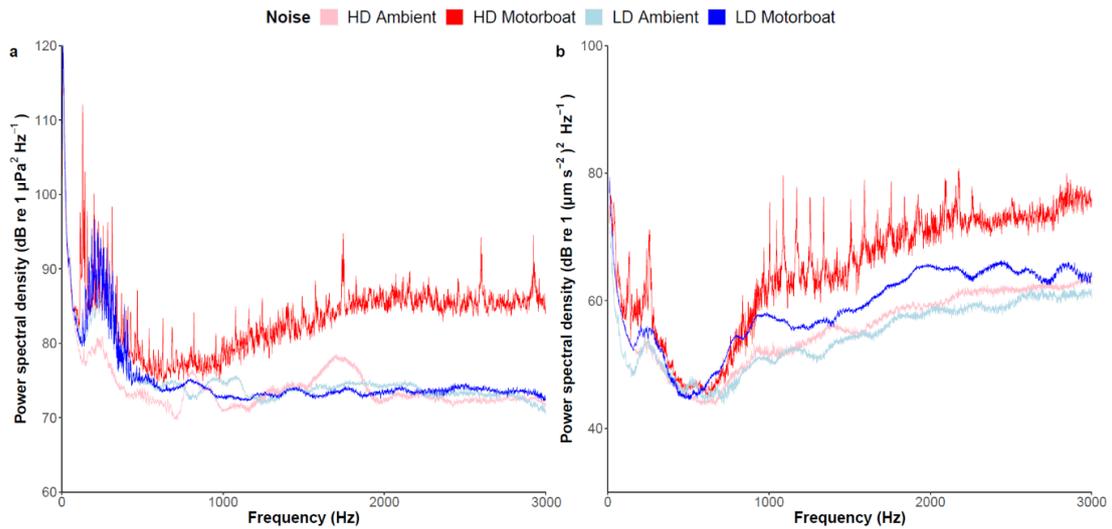
**Supplementary Figure S3**. Power spectral density plots (PSD) of sound measurements from the boat channels prior to exclusion of fish vocalisations. All recordings analysed using PaPAM acoustics analysis package in MATLAB (Nedelec *et al.* 2016a), with a sampling rate of 44.1 kHz, Hamming window, 50% overlap, window length = sampling rate. Sound pressure (**a**) and Monoaxial particle acceleration (**b**). Lines represent the mean power spectral density for each treatment condition.

**Table S1.** SIMPER analysis of species contributions to dissimilarities between high- and low-disturbance fish community assemblages, percentage difference in fish abundance from low to high-disturbance sites, GLMM output *p*-values and FDR adjusted *p*-values.

| *Species* | Mean diss | SD | Contrib (%) | HD vs LD (%) | GLMM *p*-value | FDR adjusted *p*-value |
|---|---|---|---|---|---|---|
| Stegastes nigricans | 7.78 | 1.28 | 19.94 | 76 | 0.028* | 0.028* |
| Chlorurus sordidus | 7.74 | 1.37 | 19.82 | 110 | 0.11 | 0.078 |
| Ctenochaetus striatus | 2.75 | 1.33 | 7.05 | 118 | 0.002** | 0.003** |
| Acanthurus nigrofuscus | 2.67 | 0.66 | 6.84 | 111 | 0.26 | 0.16 |
| Thalassoma hardwicke | 2.33 | 1.06 | 5.98 | 73 | 0.0006*** | 0.001** |
| Scarus psitticus | 2.26 | 1.01 | 5.79 | 79 | 0.33 | 0.19 |
| Chrysiptera brownriggii | 1.63 | 1.04 | 4.17 | 88 | 0.11 | 0.078 |
| Chromis margaritifer | 1.56 | 0.93 | 4.00 | 196 | <0.0001*** | <0.0001*** |
| Zebrasoma scopas | 0.94 | 1.27 | 2.41 | 137 | <0.0001*** | 0.0006** |
| Centropyge flavissima | 0.68 | 1.00 | 1.75 | 151 | 0.005** | 0.007** |
| Halichoeres hortulanus | 0.68 | 1.22 | 1.73 | 87 | 0.069 | 0.059 |
| Abudefduf sexfasciatus | 0.66 | 0.51 | 1.69 | 220 | 0.0006*** | 0.0014** |
| Pseudocheilinus hexataenia | 0.41 | 0.86 | 1.04 | 165 | 0.015* | 0.016* |
| Chaetodon citrinellus | 0.36 | 1.10 | 0.93 | 66 | 0.004** | 0.005** |
| Canthigaster solandri | 0.33 | 0.83 | 0.85 | 103 | 0.91 | 0.45 |
| Halichoeres trimaculatus | 0.31 | 0.98 | 0.80 | 73 | 0.057 | 0.053 |
| Gomphosus varius | 0.30 | 0.96 | 0.77 | 52 | 0.0001*** | 0.0006*** |
| Chaetodon lunulatus | 0.28 | 1.02 | 0.71 | 117 | 0.39 | 0.21 |
| Paracirrhites arcatus | 0.28 | 0.88 | 0.70 | 68 | 0.15 | 0.09 |
| Mulloidichthys flavolineatus | 0.25 | 0.55 | 0.64 | 343 | 0.0003*** | 0.001** |
| Scarus oviceps | 0.22 | 0.87 | 0.56 | 84 | 0.38 | 0.2 |
| Stethojulis bandanensis | 0.22 | 1.05 | 0.56 | 131 | 0.16 | 0.1 |
| Dascyllus flavicaudus | 0.20 | 0.39 | 0.51 | 0 | 0.0008*** | 0.0014** |
| Balistapus undulatus | 0.19 | 1.04 | 0.49 | 140 | 0.09 | 0.072 |

**Table S2.** SIMPER analysis output of species contributions to dissimilarities between high- and low-disturbance fish community assemblages, percentage difference in fish abundance from low to high-disturbance, Wilcoxon signed-rank test $p$-values and FDR adjusted $p$-values.

| Species | Mean diss | SD | Contrib (%) | HD vs LD (%) | Wilcoxon $p$-value | FDR adjusted $p$-value |
|---|---|---|---|---|---|---|
| Chromis viridis | 7.66 | 0.99 | 15.40 | 148 | 0.68 | 0.99 |
| Stegastes nigricans | 5.63 | 1.91 | 11.32 | 60 | 0.04* | 0.48 |
| Chrysiptera brownriggii | 4.70 | 0.94 | 9.45 | 204 | 0.56 | 0.95 |
| Dascyllus aruanus | 4.07 | 0.59 | 8.18 | 200 | 1 | 1 |
| Chlorurus sordidus | 3.84 | 1.27 | 7.71 | 37 | 0.15 | 0.77 |
| Thalassoma hardwicke | 3.16 | 1.30 | 6.35 | 164 | 0.2 | 0.77 |
| Scarus psittacus | 2.29 | 1.37 | 4.61 | 104 | 1 | 1 |
| Halichores trimaculatus | 1.95 | 1.36 | 3.92 | 158 | 0.42 | 0.77 |
| Pseudocheilinus hexataenia | 1.74 | 1.18 | 3.50 | 079 | 0.74 | 1 |
| Chromis margaritifer | 1.20 | 1.12 | 2.42 | 900 | 0.03* | 0.48 |
| Ctenochaetus striatus | 1.20 | 1.35 | 2.42 | 075 | 0.37 | 0.77 |
| Halichoeres hortulanus | 0.98 | 1.55 | 1.96 | 117 | 0.63 | 0.98 |
| Canthigaster solandri | 0.90 | 1.17 | 1.81 | 043 | 0.26 | 0.77 |
| Stegastes albifasciatus | 0.85 | 1.12 | 1.72 | 200 | 0.34 | 0.77 |
| Chaetodon citrinellus | 0.85 | 1.25 | 1.72 | 100 | 1 | 1 |
| Centropyge flavissima | 0.74 | 0.89 | 1.49 | 133 | 0.86 | 1 |
| Stegastes fasciolatus | 0.66 | 0.80 | 1.33 | 218 | 0.85 | 1 |
| Gomphosus varius | 0.50 | 1.21 | 1.00 | 52 | 0.40 | 0.77 |
| Acanthurus nigrofuscus | 0.43 | 1.25 | 0.87 | 59 | 0.27 | 0.77 |
| Parupeneus multifasciatus | 0.41 | 0.53 | 0.83 | Inf | 0.18 | 0.77 |
| Paracirrhites arcatus | 0.41 | 0.44 | 0.83 | Inf | 0.41 | 0.77 |
| Labroides dimidiatus | 0.37 | 0.60 | 0.74 | 240 | 1 | 1 |

# Chapter 3: Discussion

## Discoveries, future directions and solutions

*3.1 Discoveries*

The data chapter of this thesis provides insight into how the noise emitted by motorised vessels may be impacting marine life at the community level. This study found that 30 years of exposure to high levels of motorboat noise had no apparent effect on the overall abundance, species richness and diversity of a coral reef fish community in French Polynesia. However, we found that 12 species, had significantly altered distributions in areas of high noise-disturbance; resulting in a disparity in community compositions between coral reef regions exposed to high and low levels of noise. These findings highlight that the response of a marine community to chronic motorboat noise is complex, and effects on fish are species specific (Kunc *et al.* 2016). The long-term presence of motorboat noise may be interfering with intricate processes and interactions between species and their conspecifics, heterospecifics and abiotic environment, altering the composition of the community. Thus, this study finds that motorboat noise has intricate influences on marine communities, which demand further investigation to disentangle.

Five key coral reef fish species were found in significantly lower abundances, whilst seven species were observed in significantly greater abundances at the high boat noise-disturbance sites. There were no obvious trophic, taxonomic or functional groupings to discern for why certain species had greater success than others. Yet there are possible speculations that can be drawn in light of the results from this and previous studies. The most dominant fish species on this Polynesian reef system is the dusky farmerfish (*Stegastes nigricans*)—a highly soniferous and territorially aggressive damselfish that farms and defends an algal turf upon which it feeds (Wilson & Bellwood 1997; Weimann *et al.* 2018). This species was found in significantly lower abundances at noisy sites, which was the greatest driver of the difference in community composition

between sites exposed to high and low motorboat disturbance. As a brooding species, *S. nigricans* may be less able to defend their clutch of eggs from predation in noisy sites (Picciulin *et al.* 2010; Nedelec *et al.* 2017b). However, it is difficult to pinpoint which exact processes motorboat noise might be interfering with, calling for further investigation.

Two common planktivorous fishes, the bicolour chromis (*Chromis margaritifer*) and the scissortail sergeant (*Abudefduf sexfasciatus*), had significantly greater abundances in high noise-disturbance areas. This was unexpected, as previous studies have indicated that planktivorous species may be particularly vulnerable to noise having exhibited a reduced foraging efficiency when exposed to motorboat noise (Bracciali *et al.* 2012; Voellmy *et al.* 2014a). Furthermore, another small bodied, planktivorous and site attached damselfish, the Ambon damselfish (*Pomacentrus amboinensis*), has been shown to exhibit reduced predator avoidance when exposed to motorboat noise (Simpson *et al.* 2016b; Ferrari *et al.* 2018). Both reduced foraging rates and elevated predation risk would lead to malnutrition and reduced survival from predation; therefore, other factors may be influencing the unexpected positive response to motorboat noise. It could be suggested that the detrimental impact of motorboat noise on *S. nigricans* may have alleviated the competition for space in other site attached damselfish, that would have been otherwise outcompeted by their more aggressive neighbour.

Wrasses, which constitute most of the predators in the coral reef teleost community, are collectively lower in abundance at the high-noise sites. Despite representing one of the largest fish families (Labridae) to inhabit coral reefs (second to gobies, Gobiidae, and above damselfish, Pomacentridae) (Randall *et al.* 1997) wrasses have been highly overlooked in fish bioacoustics research. We know very little on the sound detection mechanisms and hearing thresholds of wrasses. Yet the sixbar wrasse (*Thalassoma hardwicke)* and Pacific bird wrasse (*Gomphosus varius*) had significantly lower abundances in regions exposed to high motorboat-noise levels. This may provide evidence to back the hypothesis that predatory teleosts use the soundscape to eavesdrop on the noise generated by their prey to hunt efficiently (Holt & Johnston 2011), and that acoustic masking from motorboat noise may force predators to hunt in quieter areas. In addition, *T. hardwicke* is known to prey upon *S. nigricans* eggs (Shima & Osenberg 2003),

and so their distributions may be tightly linked with *S. nigricans* distributions on coral reefs.

*Stegastes nigricans* was the only herbivorous species to decline in abundance at noisy sites; all other herbivores either had no distributional difference or had significantly greater abundances at noisy sites. As *S. nigricans* are algal farmers they vocalise to defend their limited resource. Yet, to our knowledge, the free roaming herbivores and detritivores, including the grazers and scrapers, do not require sound production or detection when selecting and locating their food. This could provide an explanation to why non-farming herbivorous species seem to fare better in noisy conditions. Furthermore, the reduced abundance of the dominant *S. nigricans* at noisy sites may free up algal dominated substrate for grazing and scraping without aggressive confrontation; which could result in a greater abundance of transient herbivores and detritivores in a community.

The second study of my data chapter was the first known attempt to experimentally test the response of a marine community to the introduction of long-term motorboat noise. After exposing a coral reef, with little-to-no previous boat disturbance, to a month-long motorboat manipulation there was no impact on the abundance, species richness or diversity of the fish community, nor any significant effect on species distributions. There are many potential reasons for discrepancies between the observed and experimental results. One month may not have been a sufficient disturbance duration to elicit community trends that match those observed at the channels, exposed to a minimum of 30 years of boat disturbance — especially with respect to reproductive seasons and juvenile recruitment. In addition, the frequency and total time of manipulated motorboat disturbance was low relative to the motorboat channels; there may be a threshold disturbance level before it begins to cause changes in the community composition.

While this study identifies that a coral reef fish community is subject to alteration when exposed to long-term (30 years of) motorboat noise, it does not provide any explanation for the processes behind altered community compositions. It has become apparent from this study that motorboat noise does not affect fish species in the same way, and that there are no obvious functional and taxonomic explanations for the observed responses. Yet, this study

highlights that the interference of motorboat noise with unique functional traits and intertwining interactions and relationships between species that infiltrate an ecosystem may well govern community-level responses to motorboat noise.

## 3.2 Future directions

Fishes are by far the most evolutionarily and genetically diverse of any vertebrate group (Venkatesh 2003); the number of known fish species (31,958) greatly exceeds all vertebrate groups by at least a multiple of 3 (birds – 9,990; reptiles – 9,416; amphibians – 7,694; mammals – 5,750) (Zhang 2013). In addition, fishes possess a wide diversity of sound production and detection mechanisms compared to other vertebrates (Ladich 2000, Popper & Fay 2011). And so, it is imperative that extra consideration should be taken when grouping all fishes for their response to anthropogenic noise. In this study, 25 taxonomic families were surveyed for their responses to noise. So far, only three coral reef fish families have been studied for their physiological and behavioural responses to vessel noise in the nine published studies; of these, Damselfish (Pomacentridae) represented 73% of fish studied. Given the diversity in responses seen across different species in this community assessment, especially within families, we should not treat pomacentrids as a model family to predict the impacts on all fishes. There would be great value in expanding this field to a wider range and diversity of fish families and functional traits, as this would greatly aid in untangling community assessments like the present study, and also provide a greater informational basis for incorporating noise pollution into ecosystem models.

As this is the first community assessment of motorboat noise on fish it has limitations. There were many members of the fish community that were not included for logistical regions. The cryptobenthic fishes, that were so difficult to identify visually, were excluded due to their underrepresentation in our visual census. The cryptobenthic community make up an abundant, diverse and important component of coral reef ecosystems; constituting half of the fish number, 40% of fish species, and contributing largely to the carnivorous and detritivorous pathways in coral reef trophodynamics and energy cycles

(Ackerman & Bellwood 2000; Depczynski & Bellwood 2003). Many members of the cryptobenthic community have either small or absent swim bladders to maintain negative buoyancy (Gibson 1982) making them unable to hear sound pressure compared with other fishes. Yet it is unknown whether cryptobenthic species can detect noise vibrations through the benthos and, if so, whether noise may have any detrimental impacts on their behavioural ecology and physiology. Assessments of noise on the cryptobenthic community would be very challenging to carry-out *in situ*, yet, if made possible it would provide a more complete assessment of noise on coral reef fish communities.

Another limitation, which is neither unique to this study nor easy to overcome, is that the visual census was carried out during daylight hours. This overlooks the entire nocturnal portion of the community. In the majority of all ecological studies, in both terrestrial and aquatic systems, the nocturnal portion of an ecosystem is neglected—coined "The Nocturnal Problem" by an American ecologist Orlando Park over 70 years ago (Gaston 2019). Since then, despite valuable technological advances in tagging, passive acoustic monitoring and night-time infra-red and heat detection cameras, the problem still remains. Motorboat activity exists primarily during the day, and so most studies have considered the effects on diurnal species, for which behaviour and physiology may be directly impacted. Yet, daytime boating could potentially disturb the resting periods of many nocturnal teleosts, including the soldier- and squirrelfish (Holocentridae) and cardinalfish (Apogonidae). This could have knock on effects on their night-time behaviour and activity levels. Nocturnal fishes provide a crucial role in cycling energy and nutrients from surrounding sand flats at night back to the reef during the day (Marnane & Bellwood 2002). It is therefore important that they are considered in future research assessing the impacts of motorboat noise on coral reef fish communities.

This study identified that a couple of common carnivorous wrasses (Labridae) had a lower abundance at sites exposed to high levels of motorboat noise, and I suggested that motorboat noise could interfere with their hunting ability. So far it has been established that motorboat noise can impact foraging efficiency of planktivorous fishes (Bracciali *et al.* 2012; Voellmy *et al.* 2014a). Yet, it remains unknown if wrasses eavesdrop on the sounds emitted by their prey as part of their hunting strategy, and whether the noise of passing motorboats

reduces the success rate in predatory teleosts. A valuable study would experimentally determine the extent to which predatory coral reef fishes use sound to detect prey in the wild. A suggested study could be an *in situ* baited camera set-up, whereby the bait is replaced by an underwater speaker playing back the vocalisations of prey species. Depending on the findings from such a study, nearby motorboat driving could then be implemented to see if successful prey detection is altered. This would provide a greater understanding of how the higher trophic levels of a community may be affected by motorboat noise, and would illuminate a possible explanation for the findings of the present study.

In **Chapter 1** '*1.03 Uses of sound in fish*', I discussed the importance of vocalisations in agonistic and reproductive behaviours. So far, the interference of motorboat noise has been investigated in agonistic behaviours of fishes, yet impacts to courting and spawning behaviours have yet to be investigated. This may be highly logistically challenging as many fishes mass spawn in a single place, at one particular time of the year (Mourier *et al.* 2016). This reduces the means for replication when experimentally manipulating motorboat disturbance or speaker playback. Studies would have to focus on small, site attached, frequent spawners. Successful investigation will allow for a much greater understanding of how motorboat noise may interfere with fundamental behaviours that are essential for future generations of coral reef fish communities.

Developing an ecological understanding of how motorboat noise alters marine communities should go hand-in-hand with developing effective and conscious mitigation strategies and conservation solutions. An essential part of this will involve experimental trailing of strategies. Thus, a crucial area of this field that is just emerging, and has only been considered in a couple of studies in recent years (Jain-Schlaepfer *et al.* 2018; McCormick *et al.* 2018a), is investigations of mitigation strategies and whether they may ameliorate, or eliminate entirely, the impact of motorboats on marine fauna. If future studies were to address the impact of motorboat noise on marine animals with the inclusion of an alternative "mitigation treatment" in addition to the "current motorboat disturbance treatment" it may provide extremely compelling evidence for the implementation of mitigation options in management and policy decisions.

*3.3 Solutions*

Unlike other pollutants, once a noise source is hushed there is no leftover residue contaminating the environment. Thus, reducing our acoustic footprint on the natural environment is attractive proposition to policy makers, as it would provide an immediate relief for acoustically affected ecosystems. The design and engineering of new quiet boat propeller and engine systems is one route to marine noise mitigation. Recent studies have already established that 4-stroke outboard engines are quieter and have a reduced effect on embryonic heart rates and anti-predator behaviour than the older, louder and more common 2-stroke engines (Jain-Schlaepfer *et al.* 2018; McCormick *et al.* 2018a). As the demand for electric car engines grows, so does the push for electric boat motors, which in comparison to combustion engines are very quiet.

Despite alterations to engine type, propeller cavitation remains the dominant sound source in small motorboats (see '*1.02 Motorised vessel noise*'). Therefore, an innovative redesign of propellers could significantly help minimise the noise emitted from small motorboats. Oscar Propulsion, a blade-based propulsion technology innovation company, have been working alongside researchers at Strathclyde University, Scotland, to develop and test a new propulsion system that aims to reduce propeller tip vortex cavitation. They have introduced strategically placed pressure-relieving holes on the surface of propeller blades which reduces the volume of cavitation by 14% and lowers sound levels by up to 21dB. So far this has been proposed for large commercial ships; but Oscar Propulsion CEO, David Taylor, proposed that the 'PressurePores' are suitable for application on all types of propellers on any vessel type (Latarche 2019). Such engineering solutions may allow for the current growing levels of motorised vessel activity to be maintained whilst reducing detrimental impacts on marine communities.

The alternative route to underwater noise mitigation is via behavioural change. In comparison to the slow transition to new propeller and engine systems, the behaviour of motorists can be changed immediately. Boating zones in areas of high ecosystem vulnerability, such as coral reefs, could introduce laws that enforce maximum distances to the reef; vessel type restrictions (i.e. coastguard, lifeboats, patrol and sail boats only); speed limits, as cavitation

intensifies with elevated propeller speed generating more noise (Arveson & Vendittis 2002); and off limits periods to allow for ecologically important events such as mass spawning and fish recruitment.

We are altering the soundtrack of the oceans—the noise we emit as a by-product of human activity may be sending ripples of change through marine communities. The findings of this Masters by Research thesis identifies that motorboat noise, a dominant component of many 21st century coral reef soundscapes, could be impacting marine fauna at a community-scale. Yet, community impacts are more intricate and elusive than previously predicted, and further research is required to disentangle our findings. The sound of the Anthropocene is more unique, pervasive and damaging than any epoch that came before. But, with clear communication of the growing and compelling body of literature to the wider non-scientific maritime community, we can progress further in developing quieter motorised technologies and establishing managed boating zones. Through the successful employment of noise mitigation strategies we have the ability reduce our acoustic footprint on global marine environments and conduct a new soundtrack for the Anthropocene; one that exists in greater harmony with natural marine ecosystems.

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