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Ocean acidification and elevated temperature effects on New Zealand snapper

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EXECUTIVE SUMMARY

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Ocean acidification (OA), caused by the uptake of anthropogenic carbon dioxide (CO_2) from the atmosphere, will affect the performance of many marine organisms, populations, and ecosystems. Until recently, fish were thought to be minimally affected by OA, but evidence demonstrating significant OA effects on fish is growing. This report investigates the effects of OA (and elevated temperature) on snapper (*Chrysophrys auratus*), an abundant coastal fish species in northern New Zealand that is highly important to Māori, recreational, and commercial fishers alike.

A review of the literature highlighted the wide variety of effects that fish are likely to experience as a result of OA. Although direct effects on growth and mortality were not the norm, sensory and behavioural effects (which can result in population level consequences) were widespread, and a neurotransmitter receptor disruption mechanism has now been proposed. Beyond the direct effects of OA, understanding the responses of fish in a multiple stressor environment and incorporating the ecosystem connections that will occur via elevated CO_2 (i.e., indirect effects) is an important, but challenging consideration. Complex ecosystem models are an attractive option in this regard but are limited by the information available to inform them. A more pragmatic approach is to adjust parameters to account for OA (and elevated temperature) within existing single species fishery models.

Tank experiments were conducted at the National Institute of Water and Atmospheric Research (NIWA) Northland Marine Research Centre to assess the response of snapper larvae to ambient vs. elevated levels of CO_2 (400 vs. 1000 µatm) and temperature (18 °C vs. 22 °C) expected to occur at the end of the century (these stressors will co-occur under climate change). A range of responses were measured, with some of the most notable being: (1) a strong positive effect of elevated temperature on growth, (2) a positive effect of elevated CO_2 on survival in the absence of other real-world factors, (3) negative effects of elevated CO_2 on swimming ability and metabolic performance, (4) a positive effect of temperature on swimming ability, and (5) a negative effect of elevated CO_2 on hearing ability.

Results from these tank experiments, and other studies describing snapper response to climate change, were used to adjust parameters within a stock assessment model of the SNA 1 (North Cape to East Cape) Quota Management Area snapper population. Parameters adjusted to account for climate change effects included larval survival (R_0), initial size, and adult growth rate. Due to opposing effects from the tank experiments (e.g., positive survival vs. a negative metabolic performance effect) and uncertainty from other information sources (e.g., growth), sensitivities were conducted on some parameters. Results suggested that larval survival was the most important parameter considered, accounting for the majority of the change in fishery yield for a population projected to equilibrium (40% of unfished population biomass (B_0)) abundance. Overall, the most pessimistic scenario

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predicted about a 29% reduction in yield, and the most optimistic about a 44% increase. As such, changes to larval survival, are predicted to translate into a similar magnitude effect on fishery yield, although the direction of this change is uncertain.

Although a first of its kind and valuable step forward in our understanding of how a New Zealand fish population will respond to climate change, these results also highlight how little is known even for New Zealand's most well understood fish, especially when considering the importance of indirect effects (e.g., changes to habitat availability, predator/or prey abundance, or changes potentially stemming from altered behaviour or sensory ability such as reduced hearing ability documented for snapper) which were not considered in this model. There are options to address this information shortage including: (1) fine scale climate projections to address how physical variables (wind and mixing patterns) may change in coastal systems, and (2) experiments to understand how climate change will impact key ecosystem components and processes (i.e., a multi-species approach). Iterative data collection in this regard could then be used to better inform more complex, and realistic, models. Beyond gathering new information, there are other important considerations such as potentially mitigating for climate change effects by reducing other stressors on fish populations. Part of any management response relies on frequent monitoring to identify when change is occurring, which will become increasingly important in times of increasing uncertainty.

1. INTRODUCTION

Ocean acidification (OA), caused by the uptake of anthropogenic carbon dioxide (CO_2) from the atmosphere, will affect the performance of many marine organisms, with implications for population dynamics, community structure, and ecosystem function (Doney et al. 2009, Gaylord et al. 2015). Atmospheric CO_2 concentrations were 300 µatm at the start of the 20th century, but have been rising steadily since then due to continued anthropogenic CO_2 emissions, reaching 400 µatm (here we use microatmospheres (µatm) to describe CO_2 concentrations, which are roughly equivalent to units reported in parts per million (ppm)) in 2014 (www.esrl.noaa.gov/gmd/ccgg/trends/), with a 0.1 unit reduction in pH occurring over the same period (Rhein et al. 2013). Furthermore, models predict that CO_2 concentrations in the surface ocean (dissolved CO_2) will reach c. 900 µatm by the end of this century under a business-as-usual (RCP 8.5) emission scenario (Meinshausen et al. 2011).

Until recently, fish were thought to be minimally affected by OA because they lack a calcium carbonate skeleton and possess well developed mechanisms for acid-base regulation (Melzner et al. 2009). At elevated CO_2 conditions fish are able to compensate for acidosis (which can be detrimental to cellular processes) through ion transport, mostly across the gills (Brauner 2008). This acid-base regulation maintains extra and intra cellular pH allowing cellular functions to continue, but may require higher energy expenditure to do so (Ishimatsu et al. 2008). For adult fish, concentrations of CO_2 that cause mortality are generally much higher (10,000 µatm) than those predicted to occur by the end of the century (Ishimatsu et al. 2008). Conversely, the early life stages of fish are expected to be more sensitive to elevated CO_2, potentially because they have a higher surface area to volume ratio and less well developed mechanisms for acid-base regulation (Brauner 2008). Consequently, much of the recent work has focused on these stages (eggs and larvae). Amongst these studies, a large range of different effects have been observed across a number of different life history and behavioural characteristics. Predominantly, elevated CO_2 does not result in increased mortality or decreased growth (although there are exceptions; see below and Section 3 for details). The most dramatic influences of OA on fish early life stages are disruptions to 'normal' sensory ability and behaviour. One of the first pieces of research to document these effects investigated olfactory discrimination of the orange clownfish (*Amphiprion percula*). Under normal CO_2 conditions, when clownfish were offered a choice of two different water streams they had clear preferences or avoided water with certain odours (e.g., they preferred water containing the odour of some rainforest trees, but avoided water containing the odour of other trees, and they also avoided water with the odour of their own parents). When clownfish were reared in water that had CO_2 levels expected at the end of the century (c. 1050 µatm) this olfactory discrimination was disrupted, and, in some cases, clownfish even showed preference for odours they avoided under control conditions (Munday et al. 2009b). Because these olfactory cues are likely to be connected to the ability of clownfish to detect and successfully recruit to suitable adult habitat, the consequences of this sensory disruption could be severe. In an even more dramatic example, Dixson et al. (2010) observed that under elevated CO_2 conditions clownfish became attracted to the odour of their fish predators. Since these initial studies there was a rapid expansion of studies, many of which focused on behaviour and tropical species (Clements & Hunt 2015, Heuer & Grosell 2014).

The present report focuses on snapper (*Chrysophrys auratus*), an abundant coastal fish species in northern New Zealand that is highly important to Māori, recreational, and commercial fishers alike (Parsons et al. 2014). With so little known about the effects of OA or climate change on New Zealand fish species (with the exception of an acidification experiment conducted on kingfish, *Seriola lalandi*, (Watson et al. 2018)), expanding this knowledge via a species that is important at cultural, economic, and ecological levels was a logical place to start. Furthermore, some locations that are very important to snapper spawning, such as the Firth of Thames (Zeldis & Francis 1998), are now understood to already have elevated CO_2 levels from microbial respiration of organic matter, with increasing atmospheric CO_2 expected to lead to further increases in dissolved CO_2 and decreases in pH (Green & Zeldis 2015). This implies that the distribution of snapper larvae (the life stage most likely to be

vulnerable to acidification effects) will overlap with locations where pH declines will be the worst (see Appendix 1 for an indicative map of the distribution of snapper spawning and low CO_2 areas within the Hauraki Gulf).

This report has three main sections. Section 2 aligns with Specific Objective Two and describes a review of the literature on OA effects on fish, with consideration given to New Zealand fish and fisheries, specifically snapper. Section 3 aligns with Specific Objective Three and describes the results of tank experiments conducted to assess the effect of elevated temperature and CO_2 on snapper larvae. Section 4 aligns with Specific Objective Four and describes the potential consequences of acidification and climate change effects on snapper populations. In addition, the purpose and outcomes of a workshop (Specific Objective One) are detailed in Appendix 2.

1.1 Objectives

Specific Objective One: To host a workshop introducing the issue of ocean acidification effects on fish in New Zealand

Specific Objective Two: To conduct a review of international literature on the effects of ocean acidification on fish with consideration for potential consequences for New Zealand fish and fisheries.

Specific Objective Three: To assess the sub–lethal impacts of pH change on different life stages of up to 2 species of fish (e.g., snapper, kingfish).

Specific Objective Four: Model the potential effects at the population level and explore the implications for fish stock productivity.

2. REVIEW OF LITERATURE ON EFFECT OF OCEAN ACIDIFICATION ON FISH

2.1 Introduction

The literature review found 120 studies in the primary literature on OA and fish. Seventy-four of these studies were published after 2013, illustrating the recent growth of this branch of OA research. About half of these 120 publications have now been conducted on temperate species (a reversal of the initial focus on tropical species), and a number of commercially important species have also been investigated. Together, these studies clearly show that fish can be negatively influenced by OA.

In section 2.2, the direct effects (and potential consequences) of OA that have been observed for fish (nearly always early life history stages: eggs, larvae, or juveniles) within several different physiological, life history, and behavioural categories are documented. A description is also given for a physiological mechanism which may explain why such a wide variety of behaviours and sensory systems are all effected by OA. Section 2.3 describes the real-world context for the influence of OA on fish, which includes the existence of multiple stressors, indirect effects of OA on fish, and the capacity of fish populations to respond to these changes through acclimation and adaptation. Finally, the last half of section 2.4 describes recent advances in modelling that can help in piecing this complex information together, to understand the impact of OA at the population and fishery level. Throughout this review, the findings within the literature are discussed as they apply to snapper (*Chrysophrys auratus*), the focal fish species for the ZBD2014–03 project.

2.2 Direct impacts of OA on fish

The direct impacts of OA on fish include effects on survival, and on physiological, behavioural, and neurosensory responses. Experiments investigating these effects are usually conducted in replicated tank systems, where CO_2 levels or pH are manipulated, usually by bubbling or diffusing CO_2 gas into a header tank that supplies the replicated treatment tanks where fish are contained. After exposure to experimental conditions for periods ranging from days to months, fish responses are then measured.

The CO_2 levels that fish are exposed to in these studies do vary, but usually authors attempt to compare current day ambient conditions (~380–400 µatm CO_2) with a level that is expected to occur around the end of this century (c. 700–1000 µatm CO_2). For some species and geographic locations, testing at even higher CO_2 levels may also be relevant, considering that upwelling and coastal eutrophication can elevate CO_2 levels beyond that expected from climate change (to 1700–3200 µatm CO_2) (Feely et al. 2008, Melzner et al. 2013). Below is a summary of some of the different types of direct physiological and behavioural responses to elevated CO_2 conditions that have been observed in fish (a summary of these direct effects is given in Appendix 3).

Survival

Many of the early studies investigating OA effects at relevant CO_2 levels did not observe significant negative effects on survival. Two early exceptions included decreased survival (and growth) of the inland silverside (*Menidia beryllina*) (Baumann et al. 2011) and the cinnamon anemonefish (*Amphiprion melanopus*) (Miller et al. 2012) (although the effects in this later study were mediated by parental exposure to OA). More recently, however, a number of studies have identified negative effects of OA on survival, including some studies that focused on commercially important fish, such as: yellowfin tuna (*Thunnus albacares*) (Bromhead et al. 2015, Frommel et al. 2016), Atlantic cod (*Gadus morhua*) (Stiasny et al. 2016), *Solea senegalensis* (Pimentel et al. 2014b), and summer flounder (*Paralichthys dentatus*) (Chambers et al. 2013). Of particular relevance to the present review, Pimentel et al. (2016) observed that the combined effect of warming and acidification caused a decrease in the hatching success and survival of two commercially important species, meagre (*Argyrosomus regius*) and a species from the Sparidae family to which snapper belong, the gilthead seabream (*Sparus aurata*). Negative survival effects have also been observed in a number of non-commercial species including: Atlantic silverside (*Menidia menidia*) (Murray et al. 2014) and the two-spotted goby (*Gobiusculus flavescens*) (Forsgren et al. 2013). Overall it appears that acidification levels that will be reached by the end of the century could elicit a negative survival response, but this response is species specific.

Otoliths

Fish otoliths, or 'earbones', are calcified ($CaCO_3$) structures important in sound detection and gravity sensing (Hara & Zielinski 2006). While acidified conditions are generally associated with reduced calcification of the $CaCO_3$ exoskeleton or shell of invertebrates, fish otoliths generally grow faster and to a larger size under acidic conditions. This was first demonstrated by Checkley et al. (2009) for white sea bass (*Atractoscion nobilis*), but has since been shown for a range of other species (Bignami et al. 2013b, Hurst et al. 2012, Maneja et al. 2013, Munday et al. 2011b), and is probably the most consistent response of fish to OA (although see Franke & Clemmesen (2011), Munday et al. (2011a) for studies that observe no effect). The increased otolith growth likely reflects elevated CO_2 and bicarbonate (HCO_3^-) in the otolith endolymph (fluid that surrounds the otolith) fish plasma that occur as a result of acid-base regulation in elevated CO_2 conditions (Heuer & Grosell 2014). The impact of the increased otolith growth resulting from exposure to OA conditions is not clear, but effects on hearing have been suggested (Bignami et al. 2013a).

Growth

Although the additional energy fish must allocate to acid-base regulation when they are exposed to elevated CO_2 conditions would be anticipated to have a cost, this does not appear to be expressed via a consistent reduction in growth rate. For example, although acidified conditions resulted in a decrease in the standard length and daily growth rate of cobia (*Rachycentron canadum*), no effect was observed for mahimahi (*Coryphaena hippurus*) that were also assessed as part of the same study (Bignami 2013). In some studies, elevated CO_2 conditions have even led to an increase in standard length or weight (Miller et al. 2012, Munday et al. 2009c). Overall there is a lack of any consistent pattern in terms of how fish growth responds to elevated CO_2. As a result of this variability, the formulation of a mechanistic understanding of what drives this growth response to OA is not possible (Heuer & Grosell 2014).

Development

As for growth, there was no clear pattern in the development of fish larvae exposed to elevated CO_2 conditions, with effects noted for some species but not others. For example, cobia (*Rachycentron canadum*) did not show any developmental delays (here the timing of flexion of the notochord) relative to fish reared under ambient conditions when exposed to end-of-century CO_2 levels, but development was delayed at more extreme CO_2 levels (Bignami et al. 2013b). Similarly, development of larvae of summer flounder (*Paralichthys dentatus*) exposed to end-of-century CO_2 levels was not affected, but under extreme CO_2 conditions they initiated larval metamorphosis earlier and at a smaller size (Chambers et al. 2013). No effect of elevated CO_2 was observed on the embryonic duration of orange clownfish (Munday et al. 2009c). Developmental abnormalities, such as severe tissue damage to a number of organs and associated changes to growth and survival, however, have been observed under end-of-century CO_2 levels in Atlantic cod (*Gadus morhua*), yellowfin tuna (*Thunnus albacares*), and Atlantic herring (*Clupea harengus*) (Frommel et al. 2012, Frommel et al. 2014, Frommel et al. 2016).

Reproduction

The effect of OA on the reproductive attributes expressed by fish has also produced contrasting results without clear pattern. For example, reproductive output (number of clutches and the number of eggs per clutch) increased under elevated CO_2 for the orange clownfish *Amphiprion percula*, but decreased for the spiny chromis damselfish *Acanthochromis polyacanthus* (Welch & Munday 2016). No effect of elevated CO_2 was observed on the sperm motility of Baltic cod (*Gadus morhua*), the spawning occurrence or clutch size of the two-spotted goby (*Gobiusculus flavescens*) (Forsgren et al. 2013), or on the mating propensity of the broad-nosed pipefish (*Syngnathus typhle*) (Sundin et al. 2013). In potentially the most comprehensive reproduction study to date, elevated CO_2 was observed to stimulate breeding activity in the cinnamon anemonefish (*Amphiprion melanopus*), with an overall reproductive output that was 82% higher relative to breeding pairs held under control conditions (Miller et al. 2013). In a follow-up study that investigated the combined effect of elevated CO_2 and elevated temperature on the same species, however, only minimal effects of elevated CO_2 alone on reproductive output were noticed, with a decline in offspring quality occurring when combined with elevated temperature (Miller et al. 2015).

Metabolism and swimming performance

The metabolic rate of a fish (often measured as aerobic scope, the difference in oxygen consumption between resting and maximum metabolic rate) is considered a measure of whole animal fitness (Heuer & Grosell 2014). As such, if exposure to elevated CO_2 conditions diverts energy to acid-base regulation, then this may negatively affect metabolic rate or critical swimming speeds that fish are able to reach. Research conducted on metabolic rate and swimming performance to date, however, provides mixed results. In some studies no effect of elevated CO_2 on metabolic rate or critical swimming speed was observed (Bignami et al. 2013b, Melzner et al. 2009, Munday et al. 2009c, Silva et al. 2016, Strobel et al. 2012); in others metabolic rates were negatively affected (Miller et al. 2012, Munday et al. 2009a, Pimentel et al. 2014a, Pope et al. 2014), or increased (Grans et al. 2014, Rummer et al. 2013). The measurement of metabolic rates is inherently difficult, however, and some of this variability might be explained by methodological differences. Regardless, even in studies that used the same facilities and methods to assess metabolic rates for multiple species, variable responses have been observed (Couturier et al. 2013, Enzor et al. 2013).

Neurosensory and behaviour

The most well-established direct effects of elevated CO_2 on fish relate to neurosensory and behavioural disruption. Unlike the other direct effects described above, behavioural disruption resulting from elevated CO_2 occurs across a wide variety of different behaviours and senses. Below is a list of some of the behavioural effects that elevated CO_2 has been observed to elicit.

- *Activity*: Increased activity (or distance moved within a certain time period) of Ward's damselfish (*Pomacentrus wardi*) (Munday et al. 2012) and the freshwater largemouth bass

(*Micropterus salmoides*) (Hasler et al. 2016) were observed, but no effect was observed on three day old yellowtail kingfish (*Seriola lalandi*) (Munday et al. 2015).

- *Aggression*: The competitive relationship between two coral reef fish was reversed due to decreased aggression by the usually dominant *Pomacentrus amboinensis* and increased aggression by the usually submissive *Pomacentrus moluccensis* (McCormick et al. 2013).
- *Anxiety*: Increased anxiety, as measured by increased preference for dark environments and decreased proximity to an object, was noted for Californian rockfish (*Sebastes diploproa*) (Hamilton et al. 2014).
- *Auditory ability*: The normal auditory preferences of orange clownfish (*Amphiprion percula*) (usually avoid daytime reef sound) and barramundi (*Lates calcarifer*) (usually attracted to settlement habitat noise) were reversed (Rossi et al. 2015, Simpson et al. 2011).
- *Boldness*: The majority of studies that have investigated boldness have observed an increase in riskier behaviours such as decreased association with shelter, reduced response to threats, and more aggressive feeding interactions (Ferrari et al. 2011a, Munday et al. 2012, Munday et al. 2010). Alternatively, Jutfelt et al. (2013) observed decreased curiosity of stickleback (*Gasterosteus aculeatus*) in response to a novel object, suggesting reduced boldness.
- *Escape response*: How fish react to a startle stimulus (reaction time, distance moved, maximum speed reached, and duration of movement) is likely to be relevant to understanding the ability of a fish to escape a predator. The majority of studies investigating escape responses under elevated CO_2 conditions have observed reactions that would translate into a decreased ability to evade a predator (i.e., reduced movement or speed, increased reaction time) (Allan et al. 2013, Allan et al. 2014, Munday et al. 2016). Alternatively, Munday et al. (2015) observed no change in escape response of three day old kingfish (*Seriola lalandi*) exposed to elevated CO_2, although this lack of response may be due to the age and developmental status of the larvae.
- *Olfactory ability*: How fish respond to olfactory stimuli is the most frequently conducted assessment of the effects of OA on fish. Many studies have revealed decreased olfactory discrimination, or a reversal of olfactory preferences. For example, spiny damselfish (*Acanthochromis polyacanthus*) lost their innate avoidance of a chemical alarm cue under elevated CO_2 conditions (Welch et al. 2014), adult gobies (*Paragobiodon xanthosomus*) lost their preference for odour cues emanating from their host coral (Devine & Munday 2013), and the predatory brown dottyback (*Pseudochromis fuscus*) responded by avoiding the odour of preferred prey items (Cripps et al. 2011).
- *Visual ability*: Damselfish (*Pomacentrus amboinensis*) exposed to elevated CO_2 and the visual threat of a predator demonstrated a reduced anti-predatory response; specifically, they did not change time spent in shelter (Lönnstedt et al. 2013), or reduce foraging, activity levels, or the overall area used (Ferrari et al. 2012b) as much as control fish presented with the same visual threat. In spiny damselfish (*Acanthochromis polyacanthus*), the maximal flicker frequency of the retina was reduced, potentially decreasing their ability respond to fast events, such as interactions with predators (Chung et al. 2014).

In addition to the behavioural and sensory disruptions described above, the cognitive ability of fish also appears to be affected by elevated CO_2 conditions. For example, Ward's damselfish (*Pomacentrus wardi*) exhibited a reversed bias for behavioural lateralisation (turning preference) (Domenici et al. 2014). Using a clever experimental design that separated learning ability from odour detection ability, Ferrari et al. (2012a) demonstrated that damselfish (*Pomacentrus amboinensis*) were not able to learn to recognise predator odour under elevated CO_2 conditions.

The ultimate consequence for fish populations affected by OA is higher mortality, potentially impacting population replenishment. By assessing the survival of settlement stage damselfish (*Pomacentrus wardi*) in a natural setting, Munday et al. (2010) were able to demonstrate that elevated CO_2 treated damselfish experienced five to nine times higher predation mortality, likely due to their inability to discriminate predator odour and the riskier behaviours they were undertaking. Likewise, Ferrari et al. (2011a) observed a similar increase in predation mortality for *Pomacentrus chrysurus*.

Because OA will affect both predators and prey, Ferrari et al. (2011b) assessed the predation mortality of four damselfish species (with large and small size classes from each species) where both predator and prey had been exposed to elevated CO_2. Small damselfish still experienced higher predation mortality, but this did not occur for the large damselfish. Interestingly, however, elevated CO_2 exposure reversed the species preference of the predator (Ferrari et al. 2011b). In a similar study, Allan et al. (2013) observed that the performance of both predator and prey were affected, suggesting that the outcome of predator-prey interactions will be determined by the extent of the OA effect on each species.

A universal physiological mechanism?

The variety of neurosensory and behavioural effects listed above, together suggest that elevated CO_2 causes widespread dysfunction throughout the central nervous system. As such, it seems likely that inhibition of some overarching function links these diverse behavioural effects. The potential for a link between behavioural disturbance and alterations to sensory system structures has been investigated (e.g., a link between modified nasal structures and olfactory disturbance or enlarged otoliths and hearing disruption), but not established (Munday et al. 2009b, Munday et al. 2011b). Therefore, as a potential alternative explanation, Nilsson et al. (2012) suggested that increased HCO_3^- and reduced Cl^- resulting from acid-base regulation in fish may disrupt the gamma-Aminobutyric acid-A ($GABA_A$) receptor, the major inhibitory neurotransmitter receptor common to vertebrate brains. The $GABA_A$ receptor is likely to be connected to this behavioural dysfunction because under normal CO_2 conditions it is an ion channel that enables a net inflow (across the neural membrane) of the same negative ions that are part of acid-base regulation (HCO_3^- and Cl^-). This generates a hyperpolarising (inhibitory) current as the GABA neurotransmitter binds to the $GABA_A$ receptor, reducing neural activity. Conversely, when exposed to elevated CO_2 conditions, a depolarising (excitatory) current resulting from the outflow of negative ions associated with acid-base regulation (HCO_3^- and Cl^-) is likely to occur. Nilsson et al. (2012) provided evidence supporting this hypothesis by treating high CO_2 exposed fish with gabazine, a $GABA_A$ antagonist that blocks the binding of the GABA neurotransmitter to the $GABA_A$ receptor. When high CO_2 exposed damselfish (*Amphiprion percula* and *Neopomacentrus azysron*) were treated with gabazine their abnormal olfactory (*A. percula*) and lateralisation (*N. azysron*) preferences were reversed to that expected under ambient CO_2 conditions. Several similar experiments showing the reversal of abnormal behaviours at high CO_2 following treatment with GABA antagonists have since been conducted on a range of species and behaviour types (Chivers et al. 2014a, Chung et al. 2014, Hamilton et al. 2014, Lai et al. 2015, Ou et al. 2015). Together, these studies suggest that disruption of the $GABA_A$ receptor during acid-base regulation may provide an explanation for the behavioural alterations seen across a wide range of fish species at high CO_2 conditions.

2.3 Real-world context

Multiple stressors and a variable CO_2 environment

Although the direct effects outlined above are likely to generate deleterious consequences for some fish populations, they must be put in the context of real-world conditions. The majority of the results described above are derived from experiments within a controlled tank environment where a single fish species is exposed to a constant high CO_2 concentration. In reality, however, OA will not occur in isolation, average CO_2 levels will rise slowly over coming decades, and local CO_2 conditions will not be constant. Climate change will deliver other stressors, including (but not limited to) an increase in temperature and a depletion in dissolved oxygen. Beyond climate change, additional stressors such as sedimentation and eutrophication will provide further environmental stress. This is particularly true for some coastal areas. A local example that is highly relevant to New Zealand's inshore fisheries, especially snapper, is the Firth of Thames. The firth is one of the main spawning areas for New Zealand's largest snapper population and was likely a historically important nursery area for juvenile fish (Parsons et al. 2014, Zeldis & Francis 1998, Zeldis et al. 2005). In the firth, land-derived nutrients have led to increased sedimentation and phytoplankton production. By late summer/autumn microbial respiration associated with the sinking of this organic matter reduces the level of dissolved oxygen (to

c. 60–70% saturation or 4.9–5.7 mg L^{-1}) and introduces additional CO_2 into the system, reducing pH (from ~8.05 to ~7.9) (Green & Zeldis 2015). When combined with atmospheric CO_2, pH is expected to fall even further (potentially doubling CO_2 in eutrophic coastal systems; (Melzner et al. 2013)).

Multi-stressor scenarios such as this are the reality for marine fish populations. The combined effect of multiple stressors will not always result in additive negative effects, and scenarios are possible where there will be no additional or increased negative effects, or even possibly mitigation of effects. To date, most multi-stressor experiments involving fish have investigated the combined effect of elevated temperature and OA (Cattano et al. 2018). For example, Nowicki et al. (2012) observed no effect of OA alone on food consumption in cinnamon anemonefish *Amphiprion melanopus*, but food consumption did increase when fish were also exposed to higher temperatures. Alternatively, Domenici et al. (2014) observed that the OA effect on behavioural lateralisation in Ward's damselfish *Pomacentrus wardi* was mitigated when temperature was increased. Allan et al. (2017) demonstrated that when both predators and prey were exposed to elevated temperature and OA, the effect of temperature had a much stronger influence on prey survival than OA, and in some instances acted antagonistically. Recently, the combined effect of OA and hypoxia (highly relevant to the Firth of Thames situation) has also been investigated for three different species, with highly variable results. For the inland silverside *Menidia beryllina*, OA and hypoxia had an additive negative effect on survival (DePasquale et al. 2015). For the Atlantic silverside *Menidia menidia*, a synergistic negative effect on survival occurred (DePasquale et al. 2015). Survival of the sheepshead minnow *Cyprinodon variegatus* was not affected by OA and hypoxia (DePasquale et al. 2015).

Another important real-world context relates to the temporal variability in CO_2 conditions, particularly in coastal regions where land-derived nutrients, water circulation, and variable biomass of living organisms create complex and often cyclical patterns in CO_2 conditions (Duarte et al. 2013). It is not clear how CO_2 will vary in the future, so it is difficult to factor this into experimental conditions; it nonetheless may be important. For example, in the isopod *Paradella diane*, negative effects of OA on behaviour were elicited only when exposed to variability in CO_2 concentration rather than constant concentrations (Alenius & Munguia 2012), the latter being the standard conditions tested in most OA experiments.

Indirect effects of OA on fish

In addition to the direct effects of multiple spatially and temporally variable stressors, there are an almost endless number of potential indirect effects that stem from the influence of OA on ecosystem components with which fish populations interact. In fact, these indirect effects have the potential to be more influential (and less predictable) on fish populations than the direct effects themselves (Branch et al. 2013, Le Quesne & Pinnegar 2012, Nagelkerken & Connell 2015). The most obvious indirect effects include alterations/reductions to food web dynamics and system productivity, the abundance of important predator or prey species, competitor relationships, the extent and value of biogenic habitats that fish are dependent on, and nutrient recycling and bentho-pelagic coupling. Because phytoplankton provide the majority of primary production for marine ecosystems (including fish), the influence of climate change (of which OA is one part) on phytoplankton is especially relevant. Plankton community structure and productivity, however, is the result of a complex interplay among species (all with different sensitivities to climate change) and multiple environmental drivers, making predictions difficult (Nagelkerken & Connell 2015). For New Zealand, climate change is expected to decrease phytoplankton production by 6%, with greater decreases expected in north-eastern New Zealand, which is an area especially relevant for snapper populations (Law et al. 2016). As a result the flux of particles falling to the seabed and fuelling benthic ecosystems (and associated fisheries) will also decrease (Law et al. 2016). Furthermore, OA is generally expected to decrease secondary productivity (because many zooplankton species are expected to suffer negative effects under acidification; (Koenigstein et al. 2016). This may result in a scenario where higher level predators have increased energy demand due to higher temperatures, but reduced productivity is available to them (Nagelkerken & Connell 2015).

Beyond impacts on system productivity and phytoplankton and zooplankton community composition, inter-species relationships within marine communities are likely to be altered. For some fisheries this may be beneficial; for example when a top predator is negatively affected by climate change relative to its prey (Allan et al. 2013). Alternatively, where climate change increases the structuring force exerted by a key predator, this could cascade through the remainder of the community causing dramatic alterations to community composition (Harley 2011). Competitive relationships have the potential to be affected too. Changes in aggression of damselfish, *Pomacentrus amboinensis* and *Pomacentrus moluccensis*, reversed competition outcomes, forcing the species that was originally dominant in that habitat to the fringes of its preferred habitat where it succumbed to higher mortality (McCormick et al. 2013). Many fish species have the potential to be highly adaptable to these changes, however, adjusting diet depending on food availability; this could potentially buffer some of these effects, but makes predictions of the outcome of climate change and OA for community composition highly challenging (Le Quesne & Pinnegar 2012).

Habitat change or degradation resulting from climate change and OA are other indirect effects which could be of critical importance (Chivers et al. 2014b, McCormick & Allan 2017, McCormick et al. 2017, McCormick et al. 2013), especially where fish species have habitat dependent life stages, such as juvenile nursery occupying species. This may be especially true for calcifying biogenic habitats likely to be impacted by OA (such as coral, shellfish beds, or calcifying algae including rhodoliths) (Branch et al. 2013, Wilson et al. 2006). Alternatively, seagrass is expected to be an OA winner (Branch et al. 2013), which is of particular relevance to snapper due to its nursery habitat function (Parsons et al. 2014). Again, it is important to emphasise that the indirect effects of OA stemming through food-web connectivity and habitat dependence will again not occur in isolation from broader environmental change effects, so these also need to be taken into consideration when trying to understand the impact on particular fish populations or fisheries.

Understanding the consequences of OA on fish populations given the complexities of interacting direct and indirect effects is challenging, but areas where CO_2 levels are naturally elevated, such as CO_2 seeps, may provide some insight. Munday et al. (2014) demonstrated that fishes at a CO_2 seep in Papua New Guinea had the same behavioural abnormalities (reduced odour discrimination and bolder behaviour) as observed in laboratory experiments; however, fish community structure was not largely different between CO_2 seep and control sites, with the differences that did exist likely explained by differing coral habitat (Munday et al. 2014). The importance of habitat (and the capacity of elevated CO_2 to change habitats) was further emphasised by the investigation of fish responses conducted at CO_2 seeps in Italy and at New Zealand's White Island (Nagelkerken et al. 2016). Again, negative direct effects of elevated CO_2 on fish behaviour were observed, here reducing predator escape responses. However, when conducted within habitats that provide shelter, this effect was minimised. Furthermore, elevated CO_2 drove habitat shifts (at White Island this was from a mosaic of kelp, urchin barrens, and turfing algae to a habitat dominated by just turfing algae), which in turn increased food abundance, reduced predator abundance, and actually led to an increase in the abundance of the focal species (*Forsterygion lapillum* at White Island) (Nagelkerken et al. 2016).

Capacity of fish populations to acclimate or adapt to OA

Although there are many ways OA might impact fish populations, there is potential for fish to acclimate and/or adapt. For example, when parents are exposed to elevated CO_2 levels before spawning, the resulting juveniles may show no negative effects in response to elevated CO_2 (e.g., for reactivity, locomotor performance, growth, condition, survival) when they would have been expected if parents had spawned in ambient CO_2 conditions (Allan et al. 2014, Miller et al. 2012). This transgenerational plasticity (acclimation) is likely to stem from non-genetic (epigenetic) inheritance (Jablonka & Raz 2009). Specifically, changes in gene expression related to acid-base regulation (i.e., up or down regulation of specific genes) might be able to be passed on between generations, resulting in improved performance. Although these epigenetic parental effects may provide substantial capacity for fish populations to acclimate to OA, it is important to note that such effects have not been

observed for all behaviours/life history characteristics or species, and in some cases do not fully compensate for the effect of elevated CO_2 (Allan et al. 2014, Welch et al. 2014).

In addition to acclimation, fish populations contain substantial individual variation in their response to stressors such as OA, which suggests that adaptation may be possible (Munday et al. 2012). Whether this variation represents adequate genetic diversity to allow for adaptation that keeps pace with the rate of change in CO_2 levels is unknown (Munday et al. 2013). Empirically addressing adaptation poses a huge logistical hurdle. In one of the few studies conducted to date, Malvezzi et al. (2015) investigated the evolutionary potential of Atlantic silverside (*Menidia menidia*), finding that early life survival in the face of high CO_2 levels had a genetic component. This suggests that *M. menidia* do have potential to adapt to OA, but the real-world conditions required to invoke such rapid adaptation may be somewhat restrictive. For example, selection pressure might occur too gradually, and other environmental changes may alter the strength or even direction of selection pressure (Malvezzi et al. 2015, Tasoff & Johnson 2019)

Scaling up: understanding the consequences to populations and fisheries

Extrapolating the effects noted above to whole populations is challenging. In light of this, how can we estimate the impact of OA on fish populations and fisheries? A variety of modelling approaches offer a way to incorporate the complexities required to address this question.

The simplest way of modelling the effects of OA on fisheries is to adapt existing **single species stock assessment models** to incorporate the direct effects of acidification on fish (Koenigstein et al. 2016, Le Quesne & Pinnegar 2012). This can be achieved by altering model parameters such as growth, mortality, and the stock recruit relationship. Such alterations could be conducted for whatever life cycle partitions are deemed necessary but are likely to be limited by the availability of experimental data and/or the coarseness of existing single species models. Because determining direct effects of OA on finfish is relatively rare, there are few examples where this approach has been implemented specifically for OA effects. Stiasny et al. (2016), however, documented a doubling of daily mortality experienced by Atlantic cod in experiments conducted to represent end-of-century acidification levels. When this increase in mortality was incorporated into Ricker stock-recruit models, population recruitment was estimated to be reduced to 8 and 24 % of current-day recruitment levels for the two populations that were modelled (Stiasny et al. 2016).

An additional level of complexity can be incorporated into a modelling approach through **multi-species models**, which link population models for a small number of species groups through diet relationships. Plagányi et al. (2011) presents a number of examples relevant to climate change scenarios (although not explicitly OA). These examples illustrate the importance of incorporating additional complexity, namely the potential indirect effects of OA on the species of interest which proliferate through feeding relationships.

Mass balance models, which track the flow of energy/biomass through ecological networks (often conducted using the *Ecopath with Ecosim* software package; (Christensen & Walters 2004), offer an alternative approach to adapting existing fish population models. The effect of environmental drivers such as OA can be accommodated within these models by altering values for the production and consumption of biomass. A New Zealand example exists for the Wellington South Coast ecosystem (Cornwall & Eddy 2015). In this study, the authors assumed that OA would have a minimal impact on the productivity of fish groups, and as a result small negative effects were observed for fish. Greater negative impacts of OA were predicted for the more sensitive lobster, and as a result positive effects were predicted for lobster prey species such as pāua.

A number of modelling studies have addressed the impacts of climate change and OA on fisheries using **species distribution models** (Koenigstein et al. 2016). This type of model predicts habitat suitability in spatial cells under climate change scenarios (and therefore geographic range for different fish species) and links the population dynamics of each fish stock to population growth, movement,

and the ecophysiological effects of environmental variables such as OA. Indirect effects of OA stemming from species interactions can also be included in more advanced versions of these models (Koenigstein et al. 2016). Cheung et al. (2016) developed such a model for 500 fish stocks worldwide and observed a 3 to 13% decrease in fishery catch resulting from climate change by 2050. The biggest impacts were observed in tropical fisheries, where fish species are on the edge of their thermal tolerance (so not an OA effect). Using a similar model targeted at Arctic fisheries, Lam et al. (2016) observed a 39% increase in fishery catch resulting from climate change by 2050 resulting from shifts in the geographical distribution of fish as temperatures rose. However, when OA effects were explicitly considered, and modelled as increased metabolic costs and higher mortality for fish larvae, Arctic fishery increases were reduced to 34% (Lam et al. 2016). In an earlier version of these distribution models, Cheung et al. (2011) investigated the effect of climate change on north-eastern Atlantic fisheries. OA effects were specifically incorporated as reduced growth and asymptotic weight of fish, which resulted in faster range shifts and decreased catch potential by 20–30% (Cheung et al. 2011). Including the impact of OA on phytoplankton communities reduced the catch potential by a further 10% (Cheung et al. 2011).

The most complex method of modelling OA and climate change effects is to incorporate them into **end to end models** (often using the Atlantis marine ecosystem modelling framework developed by CSIRO, Australia), which link or couple a series of models that together encompass entire systems. Using this approach, Griffith et al. (2012), Fulton (2011), and Kaplan et al. (2010) modelled the impact of climate change (including OA) on south-eastern Australia, three different Australian marine systems, and west coast United States fisheries, respectively. Although the direct effects of OA were only incorporated for benthic invertebrates, this impact flowed through to negative effects for finfish fisheries in all cases due to trophic linkages. In southern-eastern Australia, these negative OA effects synergistically compounded with warming and fishing to negatively affect fish population biomass (Griffith et al. 2012). Fulton (2011) observed a c. 40% reduction in biomass across all functional groups (including fish) specifically due to OA. These effects were most pronounced in tropical systems where OA impacted coral habitat and associated assemblages. Declines of 20–80% were predicted for west coast United States groundfish fisheries, including English sole, arrowtooth flounder, and yellowtail rockfish, purely as a result of the loss of shelled prey items from their diet (Kaplan et al. 2010). Other end to end models have addressed the impact of climate change on pelagic tuna fisheries by forward projecting environmental conditions (and the response of tuna to these conditions) expected over the remainder of this century within spatial cells that cover entire ocean basins (Lefort et al. 2015, Lehodey et al. 2015). Both of these models predicted range shifts, and reduced biomass/catch potential in low latitude areas, in response to ocean warming. Model results, however, were sensitive to uncertainty around dissolved oxygen concentrations and the level of genetic selection imposed by climate change (Lehodey et al. 2015).

An alternative approach to modelling OA effects is to conduct a **risk assessment** that identifies the probability of climate change, OA, or some other stressor leading to certain undesirable outcomes for particular fish populations, marine ecosystems, fisheries, and the human communities dependent on these resources (Hobday et al. 2011). Pecl et al. (2014) conducted a risk assessment describing the effects of climate change on important fishery species in south-eastern Australia by: (a) identifying the most important fishery species, (b) conducting a literature review for each of these species to describe the habitat and environmental drivers relevant to all species life stages, and (c) using expert workshops to judge sensitivity of each species to different climate change factors. Although some species were identified as being at risk of climate change, limited information on the direct or indirect effects of OA on the finfish species relevant to that study limited the insights possible for future populations. Alternatively, Mathis et al. (2015) conducted a risk assessment of the specific impact of OA on Alaska's fisheries, with a focus on how these risks would impact human communities heavily dependent on these fisheries. Again, there was a lack of information on the direct effects of OA on finfish, but indirect effects (specifically the dependence of salmon on pteropods, which are known to be vulnerable to acidification), were identified as important considerations (Mathis et al. 2015).

2.4 Conclusions

This review highlights the wide variety of effects that fish could potentially experience as a result of OA. Although fish have generally been regarded as less vulnerable than shelled invertebrates, this review demonstrates that they can be affected in multiple ways, with potentially serious consequences. Direct effects on growth and mortality are not always apparent but have been established for a number of species (including fish that support important fisheries) in recent years (Chambers et al. 2013, Stiasny et al. 2016). Sensory and behavioural effects have now been established for a variety of species and sensory systems and behaviours (Briffa et al. 2012, Nagelkerken & Munday 2016), though not all species and traits are affected. Although it can be difficult to predict consequences, a number of studies have demonstrated that this can result in increased predation mortality in natural settings (Ferrari et al. 2011a, Munday et al. 2010), and it seems likely that ecological processes will be disrupted (Nagelkerken & Munday 2016).

Potentially even more important than the impact of OA alone is the multiple stressor environment that will result in interacting direct and indirect effects on fish. The Firth of Thames provides an example that is relevant to New Zealand inshore fisheries (and especially to snapper, the focus of this project). The firth receives heavy loads of land-derived sediment and nutrients that lead to seasonal decreases in dissolved oxygen and pH. Climate change will exacerbate this situation by increasing temperature and decreasing pH (through absorption of atmospheric CO_2) even further. How temperate New Zealand fish species like snapper will respond is unknown. The only New Zealand fish species where OA effects have been investigated is the yellowtail kingfish, which are relatively tolerant up to 21 days post-hatch (dph) (Watson et al. 2018). The gilthead seabream (*Sparus aurata*), an Atlantic species from the Sparidae family to which snapper also belongs, experiences increased mortality under elevated temperature and CO_2 conditions (Pimentel et al. 2016), but responses can be variable, even amongst very similar species (Ferrari et al. 2011a). Relevant indirect effects of OA for New Zealand inshore fish species are not well established. Nevertheless, modification of plankton community structure and productivity as well as negative effects on shelled invertebrate prey items (e.g., horse mussels) and the biogenic habitats (including those that they create) on which fish depend are possible and are likely to affect finfish such as snapper in multiple ways.

Understanding what the combination of these effects will look like for fish populations in a high CO_2 environment is not straightforward. There are a range of modelling options with varying complexities. End to end models are an attractive choice because they incorporate impacts from whole ecosystems, but this approach is limited by the poor understanding of how stressors like OA may manifest across an ecosystem. A more pragmatic approach is to initially establish what the direct effects of OA conditions on a fish species are. This information can then be used within existing fishery models to conduct sensitivity analyses on appropriate parameters (e.g., growth, survival, stock-recruit relationship). Although insight would be limited to the direct effects of OA for one population, this would be a good starting point as more empirical information becomes available and more complex modelling options can be considered in the future.

3. TANK EXPERIMENTS TO ASSESS THE EFFECT OF OCEAN ACIDIFICATION ON SNAPPER

3.1 Introduction

The literature review undertaken in the 2016–17 financial year demonstrated that some fish species (and usually the larval stages) can be negatively influenced by OA (section 2). Section 3 (Specific Objective Three) describes empirical results from a manipulative tank experiment that assessed the response of larval snapper, the focal fish species for the ZBD2014–03 project, to elevated temperature and CO_2. Snapper is a widely distributed inshore fish species in New Zealand that is highly accessible and valued by a variety of stakeholders (Parsons et al. 2014). Snapper also has an important role in maintaining ecosystem structure in some systems (Babcock et al. 1999). Snapper is also a likely

candidate to respond to climate change, with a strong response of year class strength to water temperature having already been established (Francis 1993). Further to this, snapper spawning areas are focused around harbour mouths, some of which have already been shown to have seasonal increases in CO_2 levels connected to land-based nutrients input (Green & Zeldis 2015). As such, the distribution of snapper larvae (the life stage likely to be affected by OA) is likely to overlap with land- and climate-derived increases in CO_2 levels. For these reasons, snapper is an ideal species to investigate the direct effects of climate change (here elevated temperature and CO_2).

3.2 Methods

This study was conducted at the NIWA Northland Marine Research Centre, Ruakākā, New Zealand. A spawning stock of snapper was captured in May 2017 via longline and maintained indoors in two 20-m^3 circular tanks. Each broodstock tank contained c. 20 locally sourced, wild-caught snapper and was supplied with 130 L/min ultraviolet treated seawater filtered to 50 µm, maintained at 15 °C (approximately winter water temperature) and a photoperiod of 10 hr of light and 14 hr of dark. Broodstock were fed a mixture of pilchard (*Sardinops sagax*) and squid (*Nototodarus* spp.).

In December 2017, an attempt was made to initiate spawning by increasing the water temperature in the broodstock tanks to 18 °C and adjusting the photoperiod to 14 hr of light and10 hr of dark. Although some egg production occurred over separate spawning events over a period of weeks (with eggs retained from the broodstock tanks via 300-µm mesh nets over the surface overflow), the number of eggs produced was not sufficient to stock the experiment that was initially planned. The eggs from one of the larger spawning events were reared as a practice run under ambient conditions within a single 400-l conical incubation tank and transferred to a single 1500-l grow-out tank (the resulting larvae were used to stock experiment 2, see below).

By January 2018 (the time scheduled to initiate tank experiments), spawning events were infrequent. Therefore, to improve the volume of eggs produced and the predictability of spawning events, each broodstock fish received a hormone implant. Fish were initially sedated with 10 ppm Aqui-S (Aqui-S® New Zealand, Ltd., Lower Hutt, New Zealand), before being given a single intramuscular implant of a pellet containing 500 µg GnRHa. This resulted in two successive spawning events, the eggs from which were captured to stock the experiment. After checking the quality of the eggs produced (assessment of fertilisation and normal egg development), a 16-tank experiment (experiment 1) was initiated from the two spawning events over two days. On each day eggs from both of the broodstock tanks were mixed, rinsed with oxygenated seawater for 5 min, and disinfected with tosylchloramide (chloramine-T) at 50 ppm for 15 min. Eggs were then rinsed with seawater and distributed into 8 conical 400-l incubation tanks. Each incubation tank received flow-through seawater at either 18 or 22 °C with a photoperiod of 14 hr of light and 10 hr of dark and at a flow rate of 3 l/min. Gentle aeration was maintained within each tank with a weighted 4-mm airline. All tanks were at ambient ocean temperature at stocking. Temperature control was turned on after stocking and allowed to slowly adjust to the treatment set points of 18 and 22 °C. This process was then repeated the next day so that 16 incubation tanks were stocked. The average number of eggs stocked per tank was 23 075 ±11 491 (standard deviation).

Eggs hatched c. 1 day after stocking and larvae were reared for a further 1 day in the incubation tanks before transfer to grow-out tanks. Dead eggs, larvae, and eggshells were removed daily from the incubation rearing tanks by draining from an outlet at the bottom of each tank and counted. At 1 dph, larvae were transferred from their rearing tanks into 16 replicated grow-out tanks at a density of approximately 30 larvae per litre (6000 larvae per tank). Grow-out tanks were 200-l circular tanks with slightly sloping bottoms and a black internal surface. Each grow-out tank received flow-through seawater at either 18 or 22 °C with a photoperiod of 14 hr of light and 10 hr of dark and at a flow rate of 3 l/min. Gentle aeration was maintained within each tank with a weighted 4-mm airline. Larvae were fed with enriched rotifers up to 4 times per day. Dead larvae were removed daily from the grow-out tanks by siphoning into a bucket and the number of dead larvae from each tank were counted

daily. The intention was to terminate experiment 1 at 25 dph, but due to higher than expected mortality it was terminated at 15 dph.

As experiment 1 did not utilise all the available tanks, a second experiment was initiated utilising the larvae that were reared in a single tank from the December spawning event described above. These eggs and larvae were treated exactly the same as the eggs and larvae in experiment 1, as described above, except they were reared within a single tank until 21 dph. They were then evenly divided amongst eight 200-l circular grow-out tanks (as above). At 29 dph, enriched *Artemia* was also introduced to the feeding regime (with feeding occurring up to four times per day). The density of larvae within the grow-out tanks for experiment 2 was approximately c. 8 larvae per litre (1623 larvae per tank). Experiment 2 was terminated at 46 dph.

Experimental design, water temperatures, and chemistry

Seawater pumped from the ocean was filtered through mixed media (sand), bag filtered to 5 µm, UV light treated to 150 mW/cm, and delivered to large header tanks. Oxygen diffusers in the header tanks maintained baseline minimum dissolved oxygen (100% saturation) and foam fractionators removed any additional organics. Seawater from each header tank was gravity-fed into eight separate 200-l sump tanks where temperature was maintained at ambient control (18 °C) or elevated (22 °C) temperature and CO_2 was maintained at ambient control (c. 400–500 µatm) or elevated (c. 1000 µatm) CO_2 in a fully crossed 2 × 2 experimental design with two replicate sumps for each treatment. Although long-term mean summer temperatures for the region are 21 °C (Shears & Bowen 2017), 18 °C represents the long-term average for December, when snapper spawning peaks (Crossland 1977). The experiments used pCO_2 (partial pressure of carbon dioxide) levels and water temperatures consistent with projections for the open ocean by the year 2100 under RCP 8.5 (projected to exceed 900 ppm by the end of this century) (Collins et al. 2013). This will lead to ocean warming in the range of 2–4 °C (Collins et al. 2013), which is also consistent with the 22 °C temperature treatment. Therefore, our nominal experimental treatments were (a) current-day average spring temperature of 18 °C and ambient CO_2 of 400–500 µatm, (b) current-day average spring temperate of 18 °C and projected future CO_2 of 1000 µatm, (c) projected future spring temperature of 22 °C and ambient CO_2 of 400–500 µatm, and (d) projected future spring temperature of 22 °C and projected future CO_2 of 1000 µatm.

For experiment 1, seawater from each of the eight treatment sumps was pumped into two of the 400-l incubation tanks during the egg incubation stage and two of the 200-l rearing tanks during the grow-out stage, so that there were four replicate experimental tanks at each temperature and CO_2 level throughout the experiment. For experiment 2, after the experiment was stocked with 21 dph larvae seawater from each of the eight treatment sumps was pumped into one of the 200-l rearing tanks during the grow-out stage, so that there were two replicate experimental tanks at each temperature and pCO_2 level throughout the experiment. An aquarium pump (Hailea HX-6540) circulated water from each treatment sump to the experimental rearing tanks containing snapper eggs or larvae. A second aquarium pump (AquaOne Maxi 103) in each sump ensured that the water was well mixed and served as the dosing point for the elevated CO_2 treatments. Elevated pCO_2 seawater was achieved by dosing treatment sump tanks with CO_2 to the desired pH set point using a pH computer (Aqua Medic, Germany). The CO_2 was introduced to the pump inlet where it was immediately dissolved by the impeller. A needle valve was used to regulate the flow of CO_2 into the powerhead to ensure a slow, steady stream of CO_2 into the sump. This slow dosing and rapid mixing in the treatment sump tanks ensured that each experimental rearing tank received a steady supply of well-mixed water. All treatment sump tanks and experimental rearing tanks were housed in environmentally controlled rooms.

The pH on the total hydrogen scale (pH_{total}) of each rearing tank was measured daily by spectrophotometry (Hach, DR3900) with cresol purple dye (Clayton & Byrne 1993). Temperature was measured daily with a digital thermometer (Comark C22). Water samples were taken from each tank multiple times throughout the experiment for total alkalinity (TA) analysis. Water samples were

immediately poisoned with a saturated solution of mercuric chloride (0.05% of the sample volume) and later analysed at the University of Otago Research Centre for Oceanography, Dunedin, New Zealand. Alkalinity was determined by potentiometric titration in a closed cell (Dickson & Millero 1987) using a Metrohm Dosimat burette (model 765, Metrohm, Switzerland), a Fluke model 8846A voltmeter, and with 0.2M HCl (nominal concentration, fortified with NaCl to the ionic strength of seawater) added in 0.1-ml steps. Samples were water-jacketed at 25 °C. The TA was determined from the titration data using a least squares minimisation technique and calibrated with certified reference material (Prof. A.G. Dickson, Scripps Institution of Oceanography, U.S.A.). The salinity of each sample was measured with a YSI Pro30 salinity probe. The daily pCO_2 of each rearing tank was then calculated in CO2SYS (Pierrot et al. 2006) from the measured values of pH_{total}, temperature, TA, and salinity and using the constants of Mehrbach et al. (1973), refit by Dickson & Millero (1987) (Table 1).

Table 1: Mean (± 1 standard deviation) of experimental seawater chemistry parameters for the experimental treatments that snapper were exposed to. Temperature, salinity, and pH_{total}, were measured daily in each rearing tank. Total alkalinity was measured multiple times during the experiment. pCO_2 was estimated from these parameters in CO2SYS.

Treatment	Salinity (ppt)	Temperature (°C)	Total Alkalinity (mmol/kgSW)	pH (Total)	pCO_2 (µatm)
Ambient Temperature Ambient CO_2	35.39 ±0.29	18.05 ±0.06	2299 ±9	8.02 ±0.02	425 ±19
Ambient Temperature Elevated CO_2	35.27 ±0.28	18.05 ±0.07	2308 ±8	7.69 ±0.02	1011 ±47
Elevated Temperature Ambient CO_2	35.34±0.21	22.03 ±0.07	2313 ±9	7.99 ±0.02	465 ±26
Elevated Temperature Elevated CO_2	35.29 ±0.16	21.96 ±0.20	2316 ±10	7.69 ±0.01	1027 ±32

Sampling protocol

For experiment 1, the number of fish remaining in each tank (i.e., survivorship) at 1 dph was estimated during transfer from the larval rearing tanks to grow-out tanks and by absolute counts at the end of the experiment at 15 dph. The 1 dph count involved mixing the fish within each rearing tank using aeration and gentle mechanical mixing with a hand-held agitator. Five samples of 3000 ml were then taken with a beaker and larvae counted on a 300-µm mesh flat screen. The average of the five counts was then used to calculate the total number of fish in each rearing tank (using the sample volume to tank volume ratio). Throughout the experiments, no sampled fish were returned to tanks. Survival percentage for each component of experiment 1 was calculated as proportional survival from initial numbers at egg incubator stocking to 1 dph and from 1 to 15 dph, respectively. The overall survival percentage was then calculated by multiplying the survival percentage from the second component of the experiment (i.e., 1 to 15 dph) by the number of individuals that survived the first component of the experiment (i.e., egg to 1 dph) and dividing by the original number of eggs stocked at the beginning of the experiment. The total number of fish sampled from each tank for other purposes (e.g., morphometric traits and physiological and behaviour tests) was added to the final count because it was assumed that these fish would have otherwise survived to the end of the experiment. A random subset of 30 fish was sampled from each tank at 1 and 15 dph and preserved in ethanol. At a later stage an observer (blinded to the treatments) measured a range of standard

morphometric traits that are indicators of growth and performance in larval fishes: wet mass (weight), standard length (SL), total length (TL), body length (BL), muscle depth at vent (MDV), total depth at vent including fins (or 'fin depth at vent') (FDV), eye diameter (ED), yolk area (YA), oil globule length (OGL), oil globule depth (OGD), mandible length (ML), head length (HL), head depth (HD), swim bladder area (SBA). Morphometric measurement landmarks followed Chambers et al. (2014). Each sampled larva was photographed with a Leica DFC 420 camera fitted to a Leica MZ7.5 stereo microscope or, for larger individuals, a Canon G16 series camera fitted to a stand. Morphometric traits were extracted from the photographs using ImageJ software with the image displayed on a high-resolution computer screen.

For experiment 2 survivorship was calculated from an estimate of the number of fish originally stocked into the experiment (21 dph) and absolute counts at the end of the experiment (46 dph). The 21 dph count involved taking five 72-ml subsamples from the concentrated transfer vessel (12 l total) after gentle mechanical mixing with a hand-held agitator. The larvae from each of these samples were counted on a 500-µm mesh flat screen and the average of the five counts was then used to calculate the total number of fish in each rearing tank (using the sample volume to tank volume ratio). A sample of 30 fish were also weighed at the termination of the experiment.

Behavioural, physiological, and swimming performance assessments

For the larvae reared to 46 dph in experiment 2, behavioural, physiological, and swimming performance assays were conducted. All assays were conducted on larvae between 40 and 46 dph. Juvenile snapper were sampled randomly from experimental rearing tanks for these assays. All assays were conducted in seawater at the same temperature and CO_2 level as the experimental treatment of the individuals tested. These assays were conducted by researchers and students from James Cook University and the University of Auckland.

Swimming ability and oxygen physiology

Aerobic performance was measured using intermittent flow respirometry (Clark et al. 2013, Svendsen et al. 2016) in 15 fish from each treatment (60 fish total). Fish were tested in their respective rearing treatment. Resting oxygen consumption (MO_{2Rest}) was used as a proxy for Resting Metabolic Rate (RMR) and maximum oxygen uptake (MO_{2Max}) was used to estimate Maximum Metabolic Rate (MMR), and absolute aerobic scope was calculated by subtracting MO_{2Rest} from MO_{2Max} for each fish. Respirometry was conducted in purpose-built intermittent-flow respirometry chambers for juvenile fish (between 13 and 14.5 ml per closed system), submerged in aquaria within the fish's respective experimental treatment water. Submersible pumps fitted to each chamber supplied a continuous water flow from the surrounding water bath through the chambers. A purpose built python program, AquaResp V3.0, was used to control the timing measurement cycle. This consisted of a four-minute measurement period, two-minute flushing period, and a one-minute wait period, which was repeated over a 4-hour trial duration. The O_2 consumption rates were measured during the intervals of interrupted water flow with a Firesting Optical Oxygen Meter (Pyro Science e. K., Aachen, Germany), which the AquaResp program recorded during the measurement periods. Immediately before respirometry commenced, each fish was swum for 5 minutes at 10 body lengths per second in a swimming flume (see below). Five minutes was enough to illicit unsteady swimming and anaerobic muscle use. Fish were then placed immediately into respirometry chambers allowing for MO_{2max} to be measured immediately following exercise. Fish then remained in the chambers while recovering back to MO_{2rest} over 4 hours, with the majority of juveniles reaching stable MO_{2rest} by the first hour. At the end of each trial, wet mass was taken for each individual to adjust the MO_2 calculations for the individual's specific weight. MO_2max, MO_2rest, and total aerobic scope of individuals in mg O_2 kg^{-1} h^{-1} were calculated using the equation:

$$1) \qquad MO_2 = K*V*\beta / M$$

where K is the linear rate of decline ($kPah^{-1}$) in the oxygen content over time (h) in the respirometer; V is the volume of the respirometer in litres, which is adjusted for the volume of the fish; β is the

solubility of oxygen in water at a specific temperature and salinity (mg O_2 l^{-1} kPa^{-1}); and M is the body mass of the fish (kilogram).

Critical swimming speed (Ucrit) was measured to compare swimming performance among treatments. Individual fish (13 fish per treatment, 52 fish total) were swum against a water current in a Brett type swimming tunnel (Brett 1964). The water was maintained at the desired temperature and CO_2 by constant flow-through of the respective treatment water of each fish from the main system. A single fish was placed into the swim tunnel and allowed 10 minutes to habituate at a water speed of one body length per second (bl s^{-1}). Following standard procedure (Brett 1964), the water flow was then increased by increments of ~2 bl s^{-1} (~3 cm s^{-1}). Each flow speed was maintained for 10 minutes, after which the water speed was increased by another 2 bl s^{-1}. These 10-minute intervals, increasing by 2 bl s^{-1} each time, were conducted until the fish was no longer able to maintain its position in the water current. The trial was stopped when an individual rested against the rear screen of the flume for 5 seconds, because fish have the potential to rest momentarily and then burst back into swimming. After fatiguing, the water flow was stopped and the fish was allowed 10 minutes to recover before it was removed from the swim tunnel. Ucrit was calculated following Brett (1964):

2) $$U_{crit} = U + U_i * (t/t_i)$$

where U is the penultimate speed before the fish stopped swimming; U_i is the flow speed increment; t is the time elapsed in the final increment during which the fish stopped swimming; and t_i is the amount of time individuals were maintained at each speed.

Separate linear mixed effects models (LMEs) were used to test for differences in aerobic scope and Ucrit across the experimental treatments. Temperature and CO_2 were fixed factors in the models. Rearing tank and testing day were included as random factors. An additional random factor of respiration chamber was used in aerobic scope LMEs. Fish weight was included as a covariate in LMEs for aerobic scope. Standard length was included as a covariate in the LME for Ucrit. All assumptions for the LMEs were met. Statistical analysis was conducted with a statistical significance of $\alpha = 0.05$. Analyses were done in SPSS V.25 (IMB).

Escape performance

To assess the escape response of snapper larvae to a repeatable startle stimulus, individual fish were transferred to a test arena and a protocol similar to that described by Watson et al. (2018) was followed. After a habituation period, fast-start responses were elicited by the release of a black, cylindrical weight with a tapered end onto the water surface at the centre of the arena. The metal weight was controlled by a lanyard that was just long enough to allow the tapered tip to touch the surface of the water. This was achieved by remotely turning off an electromagnet to which the metal weight was attached. To provide a sudden stimulation and allow calculation of the escape latency, the stimulus was released through a white PVC tube (550 l × 40 Ø mm) suspended above the experimental arena, with the bottom edge at a distance of 10 mm above the water level. The cylindrical weight was released when the fish moved to the middle portion of the tank, allowing it to move an equal distance in any direction and standardising for the fish's position relative to the stimulus. Escape responses were recorded at 240 frames per second (Casio EX-ZR1000) as a silhouette from below obtained by pointing the camera at a mirror angled at 45°. Fish escape variables were measured only when a C-start (a very quick startle or escape reflex employed by fish) was initiated. The water in the test arena was the same temperature and CO_2 as the corresponding treatment water in which the fish was reared. To minimise any effect of any change in temperature and CO_2 in the arena water, the arena was drained and reset with fresh treatment water every 20 min. From the recorded videos, the proportion of reactors and response distance of those fish that reacted were measured/recorded. The number of fish that responded to the startle stimulus was compared between treatments with a Chi-square test, whereas the distance that the responders moved after the startle stimulus was compared across the two treatments with a 2-way ANOVA.

Olfaction

The response of snapper larvae to olfactory cues was tested in a two-channel choice flume following methods similar to that of (Munday et al. 2009b). Larvae were placed in the downstream end of the flume where they were free to move to either side of the chamber. A constant gravity-driven flow of water was maintained throughout all trials. Flow rates were measured using a flow meter and dye tests were conducted at each water change to ensure that the two channels exhibited separate and parallel water flow, with no turbulence or eddies. For each trial, a single fish was placed into the centre of the downstream end of the choice flume and acclimated to the two water choices. In each trial, a larva was given a choice in the flume chamber between a water source with the odour of a potential predator (live hāpuku *Polyprion oxygeneios* were held in header tanks with the same water temperature and CO_2 as that which the larvae had been reared) and an identical water source without that cue. Fish position relative to the odour cue was then recorded every five seconds for two minutes. The side of the choice flume that the odour cue was released into was then swapped, and the two-minute observation period repeated. Trials were video-recorded from above. The percentage of the five-second intervals that the snapper larva was recorded in the odour cue was the overall response variable produced. A total of 30 replicates per treatment level were conducted.

Hearing

Auditory abilities of snapper larvae were determined using auditory evoked potentials (AEPs) following similar methods to those described by (Radford et al. 2012). For AEP testing, fish were completely submerged underwater in a PVC tank, positioned laterally, and restrained in place. A micromanipulator was used to position the fish holder in the tank. An underwater speaker was placed near the opposite end of the tank, which produced auditory stimuli with frequencies of 80, 100, 200, 400, and 800 Hz. The presentation order of the frequencies was conducted randomly. Sound levels were increased for each frequency. Stainless steel subdermal electrodes were used to collect AEPs. The recording electrode was positioned dorsally, just anterior to the operculum, whilst the reference electrode was placed dorsally in the nasal region, with a ground electrode positioned under the body of the fish. Each electrode was insulated with nail varnish, except the tip, and was positioned using a micromanipulator. The auditory threshold was defined as the lowest level at which a clear response could be detected visually and with AEP.

Vision

The visual ability of snapper from different temperature and CO_2 treatments was assessed by measuring the ability of snapper to visually resolve fine-scale detail on a moving background. Visual ability was measured via the presence (or not) of an optomotor response to visual stimuli in a similar fashion to that described by Herbert & Wells (2002). The optomotor response is an innate behaviour in fish that enables them to stabilise their view of the environment.

The optomotor device consisted of a wooden cabinet with circular holes on the top that provided the frame through which recording cameras and fish holding containers were suspended. Individual larval snapper were held in clear 50-ml plastic bottles, suspended on monofilament fishing line 100 mm below a camera housed within a PVC pipe. This setup allowed snapper to be suspended within a striped rotating drum whilst the camera provided a clear view of snapper activity. The optomotor device comprised a circular drum (height = 215 mm, diameter = 250 mm) with a patterned paper strip of alternating black and white vertical bars housed atop a motorised spinning plate. Motors were set to spin in a clockwise direction, at a fixed rate of four revolutions per minute. The paper strips had a residual distance (RD, linear distance from midpoint of the bottle to the patterned strips) of 105 mm and six variants of the paper strips (with different bar widths) were used. The width of the black and white bars was calculated to provide a subtended acuity angle of 2°, 4°, 6°, 8°, and 10°, assuming fish reacted to the stimulus across the residual distance. A white paper strip with no black bars was used to provide a control condition (0° acuity angle).

Larval snapper were transferred into test bottles containing water at the same CO_2 conditions as their source tank. Fish were then exposed to all of the patterned strips in turn by manually replacing the patterned strips between tests.

At the start of each test sequence, the camera and bottle on the PVC pipe were lowered into a rotating optomotor device, and the fish was allowed to acclimate within stimulus-active conditions for five minutes before data recording was initiated. Snapper behaviour within bottles was digitally recorded for three minutes, as well as observed in real time. The behavioural response of snapper was quantified using angular swimming velocity (net revolutions per minute) over the three-minute observation period. Net revolutions per minute (revs min^{-1}), either positive (clockwise) or negative (anti-clockwise) were determined according to:

$$revs\ min^{-1} = \frac{(total\ clockwise\ revs - total\ anticlockwise\ revs)}{T}$$

Where T is the observation period of three minutes. The minimum acuity angle at which optomotor responses were initiated (where revs min^{-1} first increased significantly from the control 0° behaviour) was defined as the visual acuity threshold. A total of 20 fish for each of the four experimental treatments were tested.

Statistical analysis

Statistical analysis methods specific to some particular data types are described within the methods above. Morphology was assessed with a Canonical Analysis of Principal coordinates (CAP). Before performing these analyses, datasets were individually normalised so all variables were on a similar scale, and a Euclidean distance resemblance matrix was calculated. The number of axes used was set to the number that achieved the maximum allocation success in leave one out analysis. An hypothesis test for differences between treatments was performed with 999 permutations and the influence of individual variables was assessed by calculating Pearson correlations with canonical axes. Permutation-based multivariate ANOVA (PERMANOVA) was used to test for differences in morphology between the treatment groups, with temperature and CO_2 as factors, and the temperature × CO_2 term was also included.

Other data were analysed with 2-way ANOVAs (with temperature and CO_2 as fixed factors, as well as a temperature × CO_2 interaction term). Where required, data were transformed to ensure the assumptions of homogeneity of variances and normality were met. In some of these analyses, incorporating fish size as a co-variate and the specific tank fish were from as a random factor would have produced a more thorough analysis, but this was not conducted here.

3.3 Results

Despite some initial problems with broodstock spawning, a replicated tank experiment was successful in assessing the impact of elevated temperature and CO_2 on snapper larvae, rearing some larvae through to 46 dph in the process (Figure 1).

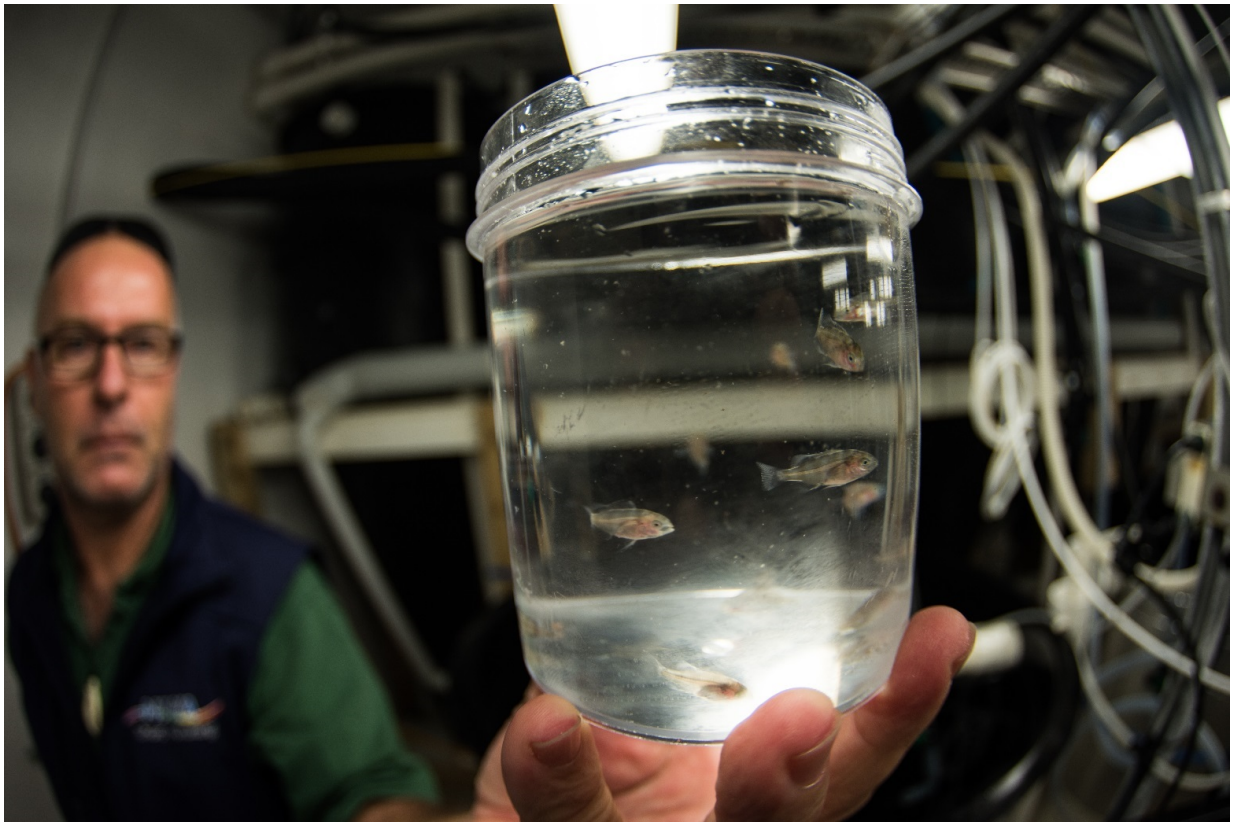

Figure 1: Aquaculture technician Yann Gublin holds a sample of snapper larvae reared during the tank experiments (Photo: Crispin Middleton).

Survival

Both experiments allowed assessment of the survival of snapper by treatment. For experiment 1, survival estimates from two different time periods (egg to 1 dph and 1 dph to 15 dph) were combined for an overall survival estimate (as described in section 3.2). Overall survival was positively affected by elevated CO_2 (2-way ANOVA, df = 1, F = 13.75, $p < 0.003$), with no effect of temperature ($p > 0.2$) or the CO_2 × temperature interaction term ($p > 0.3$) (Figure 2).

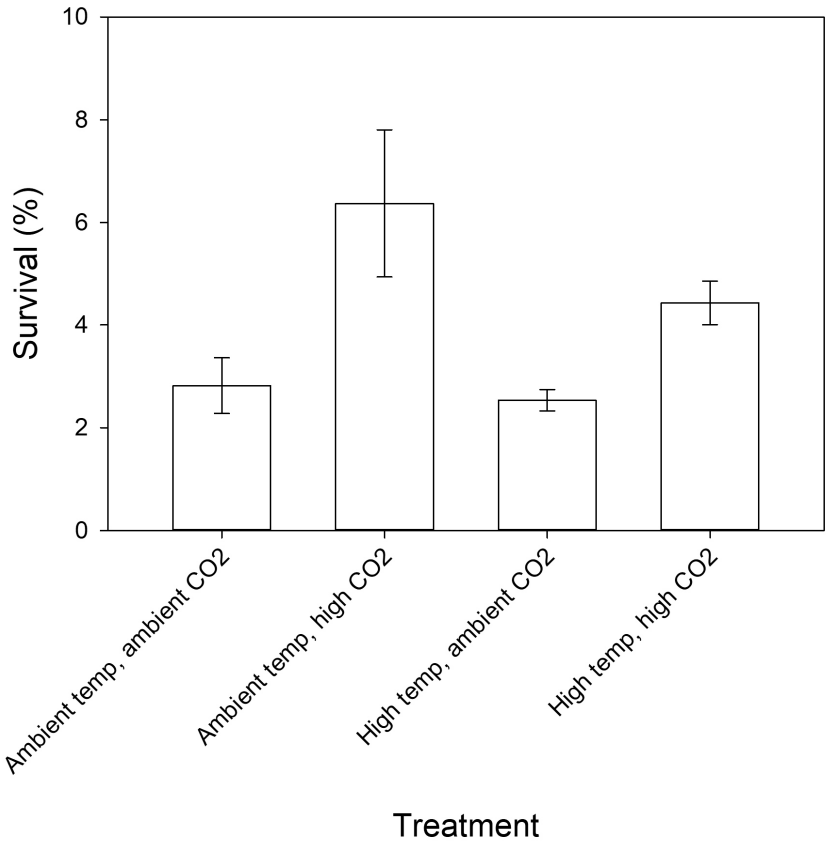

Figure 2: Percentage survival of snapper larvae from experiment 1 between the egg phase and 15 dph. Note: 4 tanks per treatment and error bars are ±1 standard error.

For the period between 21 and 46 dph in experiment 2, there was some indication that high temperature increased survival (Figure 3). This difference was, however, non-significant with both the temperature and CO_2 terms and the temperature × CO_2 interaction term having non-significant p-values (2-way ANOVA $p > 0.22$, $p > 0.81$, $p > 0.63$, respectively). This result was likely influenced by the low level of replication (n = 2 tanks per treatment) and high variation contained within one treatment in experiment 2.

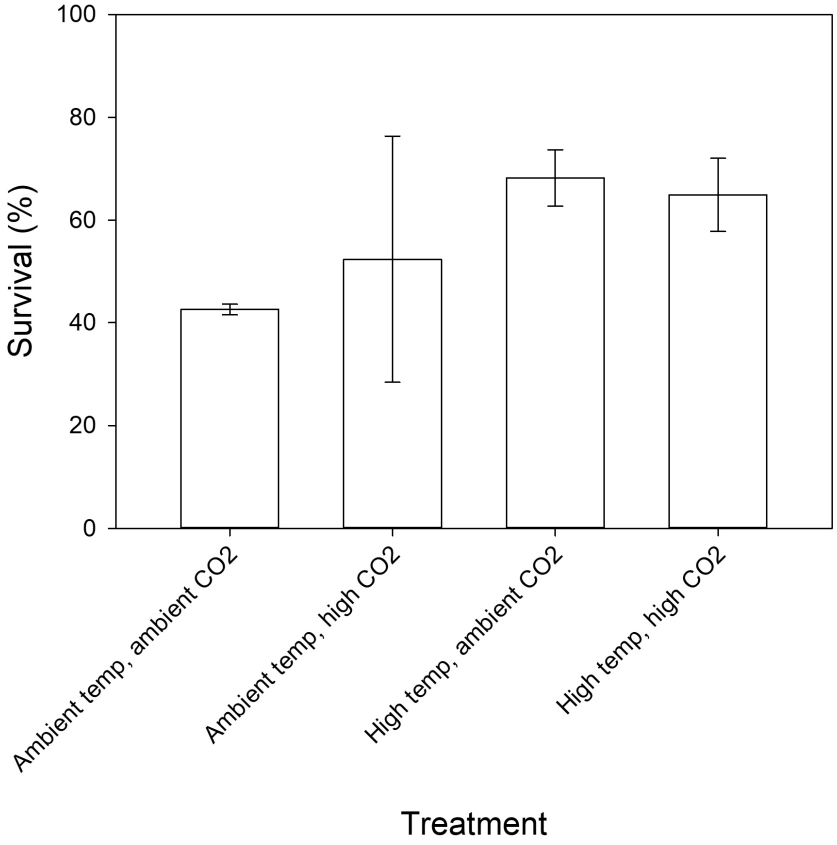

Figure 3: Percentage survival of snapper larvae from experiment 2 between 21 and 46 dph. Note: 2 tanks per treatment level and error bars are ±1 standard error.

Growth

The weights of snapper larvae at the end of experiment 2 were compared to provide insight into the effect of elevated temperature and CO_2 on larval snapper growth. A strong temperature effect on growth was evident, with higher temperatures leading to increased growth (Figure 4). This effect was highly significant (2-way ANOVA, df = 1, $F = 113.94$, $p < 0.0005$), whereas the CO_2 term and the temperature × CO_2 interaction term were non-significant ($p > 0.8$ and $p > 0.9$ respectively). Growth for larvae from experiment 1 was assessed via analysis of morphological features described below.

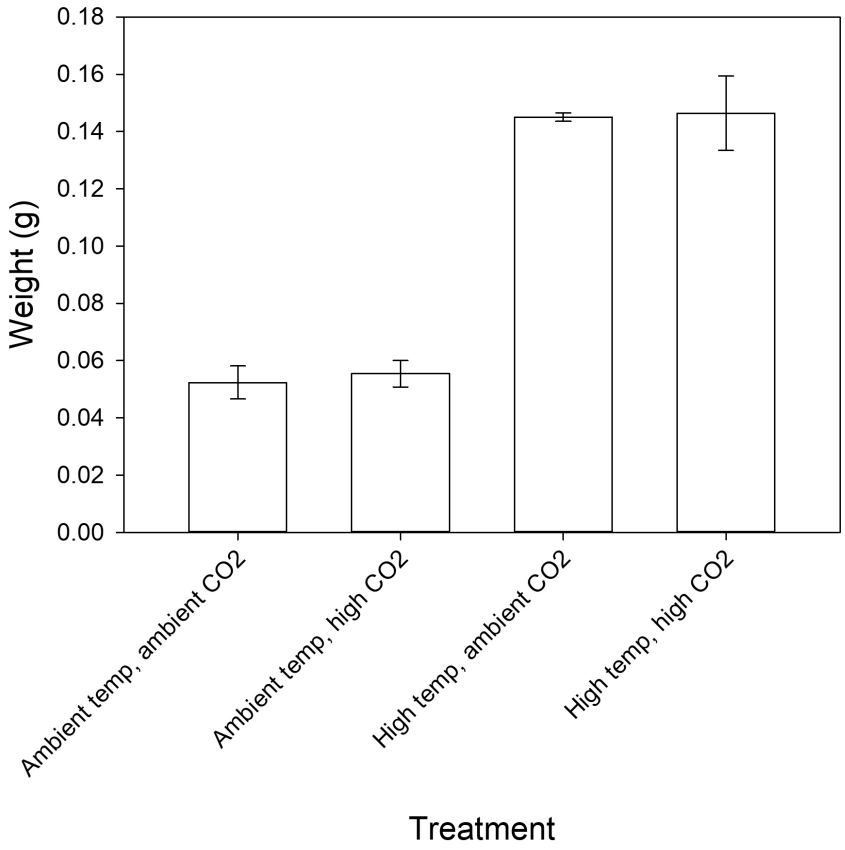

Figure 4: Average weight of snapper at the end of experiment 2 (46 dph). In total, 30 snapper were weighed per tank and tank averages (n = 2 tanks per treatment) are plotted. Error bars are ±1 standard error.

Morphology

A CAP analysis of the morphology of 15 dph snapper (morphological variables listed in section 3.2 but excluded all oil globule and yolk measurements) showed clear separation based on the temperature, but not the CO_2 treatment (Figure 5). PERMANOVA analysis confirmed this pattern, with temperature a significant factor (P(permutation based) = 0.001), whereas the CO_2 term and the temperature × CO_2 interaction term were both non-significant (both P(permutation based) > 0.05). All the morphological variables measured had a positive correlation with temperature. These individual variable correlations ranged from 0.61 to 0.87, with the three strongest correlations plotted as an overlay to Figure 5.

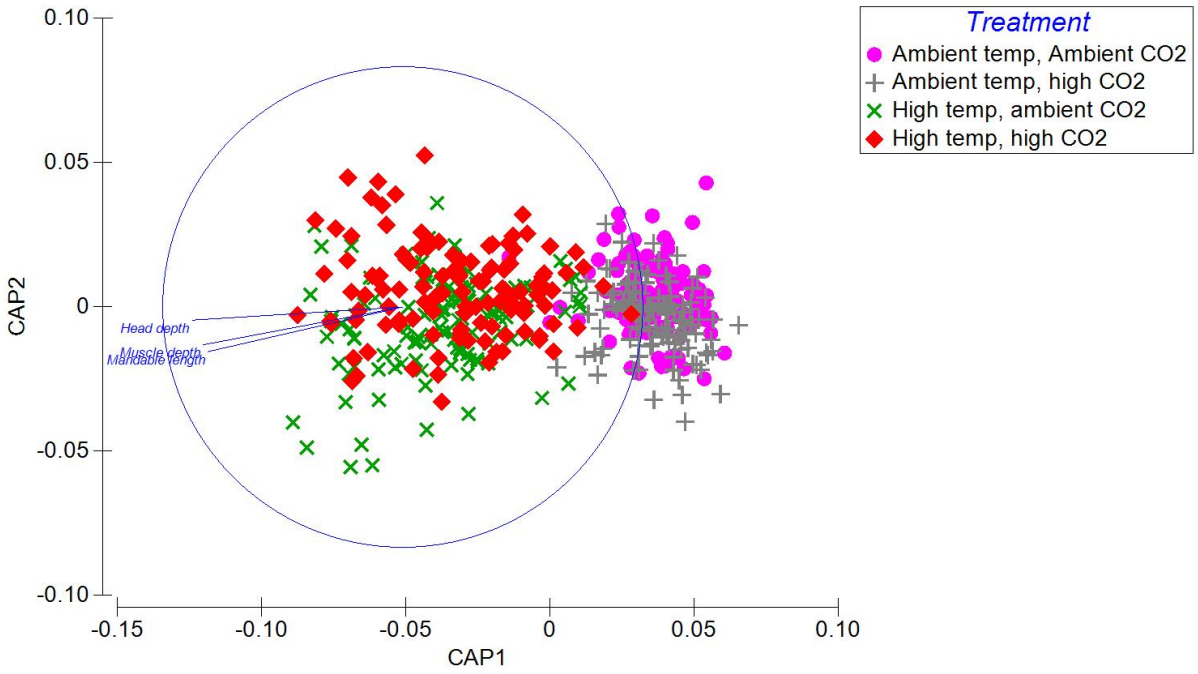

Figure 5: CAP analysis of the morphology of 15 dph snapper. Symbols represent individual fish, with the blue vector overlay representing the direction and strength (length of line) of Pearson's correlations for the three variables with the strongest correlations.

Swimming ability and oxygen physiology

Swimming ability and respirometry trials were successfully conducted by James Cook University students and staff (Figure 6). Elevated temperature significantly increased aerobic scope by 35–77 mg O_2 kg^{-1} h^{-1}, or 8–13% ($F_{1,53}$ = 19.20, p <0.001). The absolute aerobic scope of juvenile snapper was significantly reduced by elevated CO_2 with fish in the ambient CO_2 treatment having an aerobic scope of 591–674 mg O_2 kg^{-1} h^{-1}, compared with 405–440 mg O_2 kg^{-1} h^{-1} for fish in the high CO_2 treatment ($F_{1,55}$=259.95, p < 0.001) (Figure 7) (a 31–35% reduction). There was no interaction between temperature and CO_2 ($F_{1,55}$ = 2.49, p = 0.121).

The *U*crit of juvenile snapper ranged from 14 to 21 cm s^{-1} (7 to 10 body lengths s^{-1}) and speed was dependent on both temperate and CO_2, as well as body length (Figure 8). Specifically, *U*crit significantly increased by 8–12% or 1.2 to 2.1 cm s^{-1}, at high vs. low temperature ($F_{1,47}$ = 30.66, p = 0.001) (Figure 8). Conversely, high CO_2 significantly decreased *U*crit, by 8–11% or 1.3 to 2.1 cm s^{-1} ($F_{1,47}$ = 27.69 p = 0.001). There was no interaction between high temperature and CO_2 ($F_{1,47}$ = 2.375, p = 0.130).

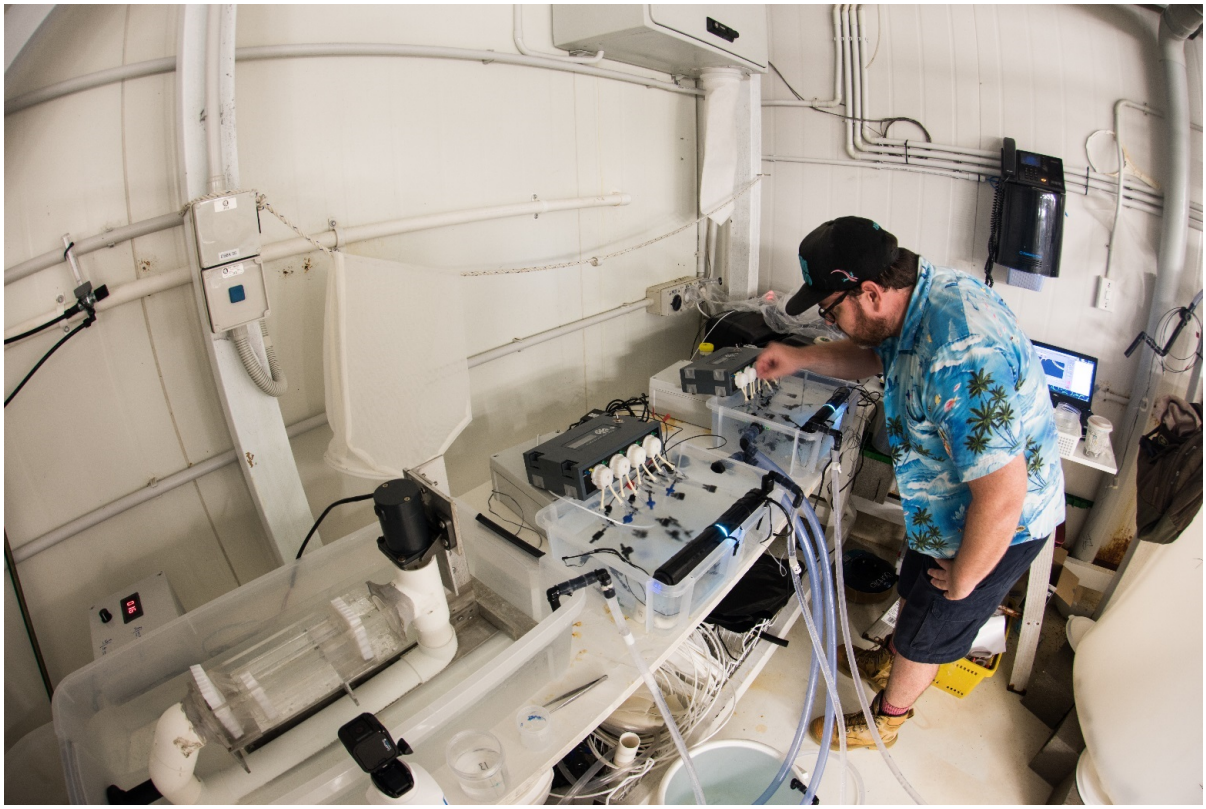

Figure 6: **Shannon McMahon (James Cook University) conducting swimming assessments and oxygen physiological measurements on larval snapper (Photo: Crispin Middleton).**

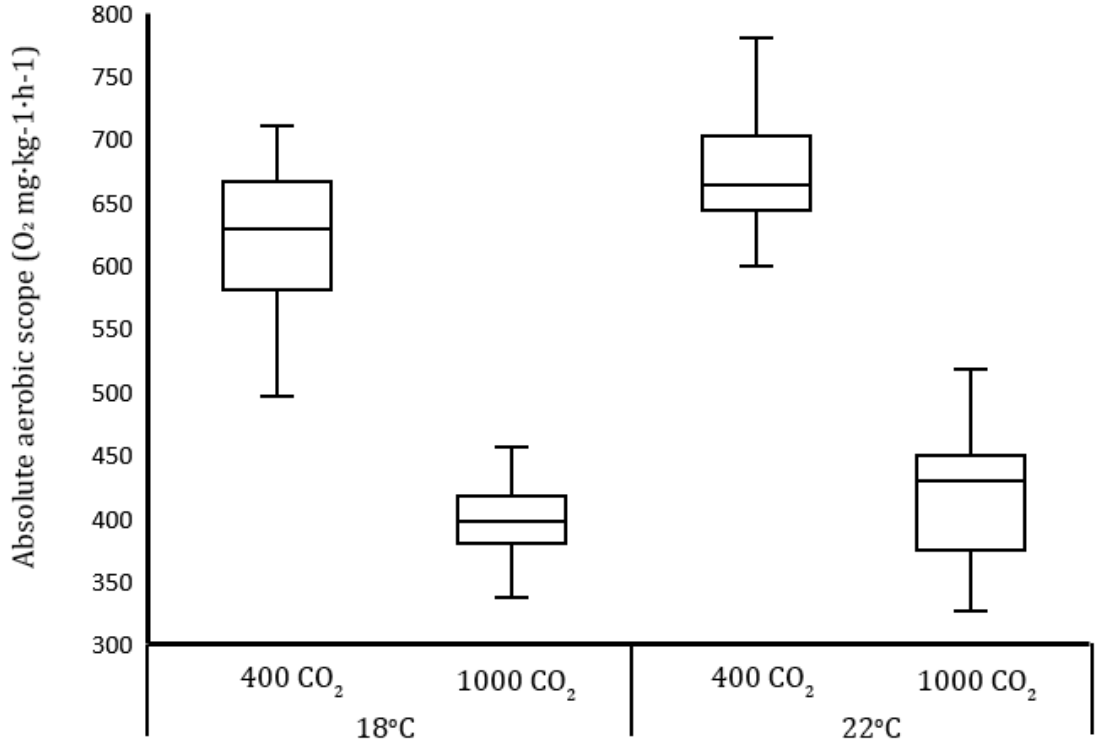

Figure 7: **The factorial aerobic scope of larval snapper held under ambient and high CO_2 and temperature conditions for 21 days (21 dph to 42 dph). Boxes encompass the 25th and 75th percentiles, with the horizontal line representing the median. Whiskers represent the overall range of observations.**

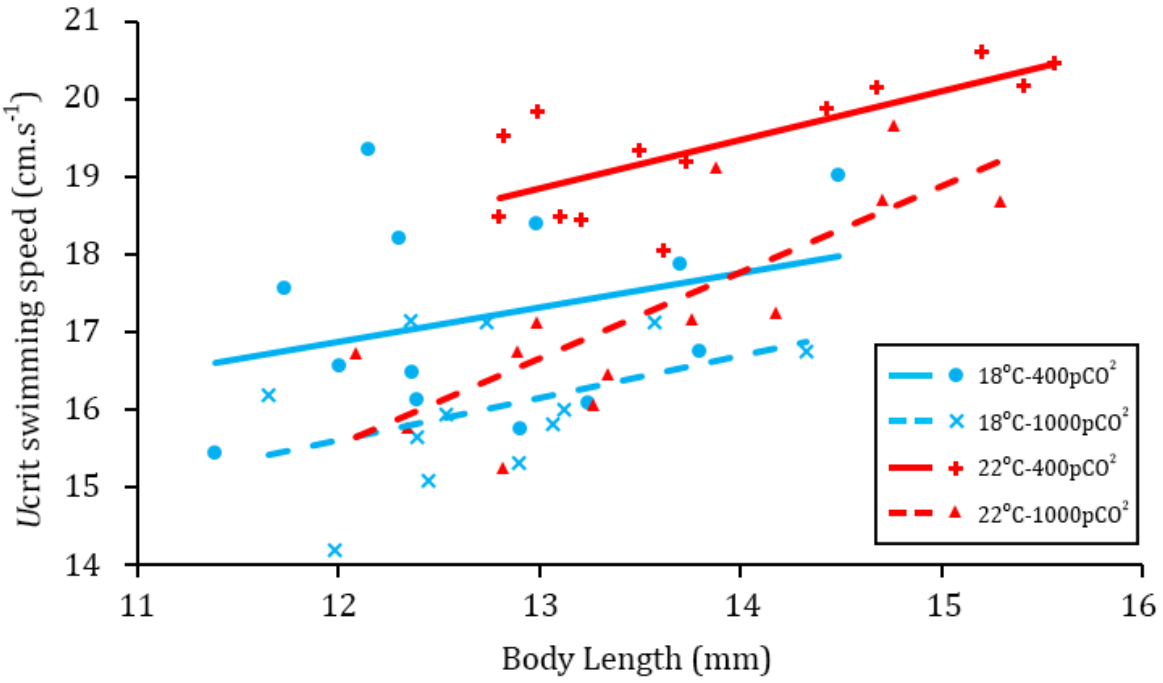

Figure 8: ***U*crit swimming speed of snapper, by standard length of the larvae, across ambient and high CO_2 and temperature treatments that fish were exposed to for 21 days (21 dph to 42 dph).**

Escape response

Escape response assays were successfully conducted using a well-established protocol (Figure 9). The percentage of larval snapper responding to the startle stimulus appeared to be lower for fish raised under high temperature conditions and unaffected by the CO_2 treatment (Figure 10a). Chi-square analysis, however, suggested that this difference was non-significant (χ^2=5.217, $p > 0.15$). For the fish that did respond to the startle stimulus, the distance they moved was higher for fish raised under high temperature conditions (2-way ANOVA, df = 1, $F = 26.503$, $p < 0.000001$) and unaffected by the CO_2 treatment or the temperature × CO_2 interaction term ($p > 0.5$ and $p > 0.7$, respectively) (Figure 10b).

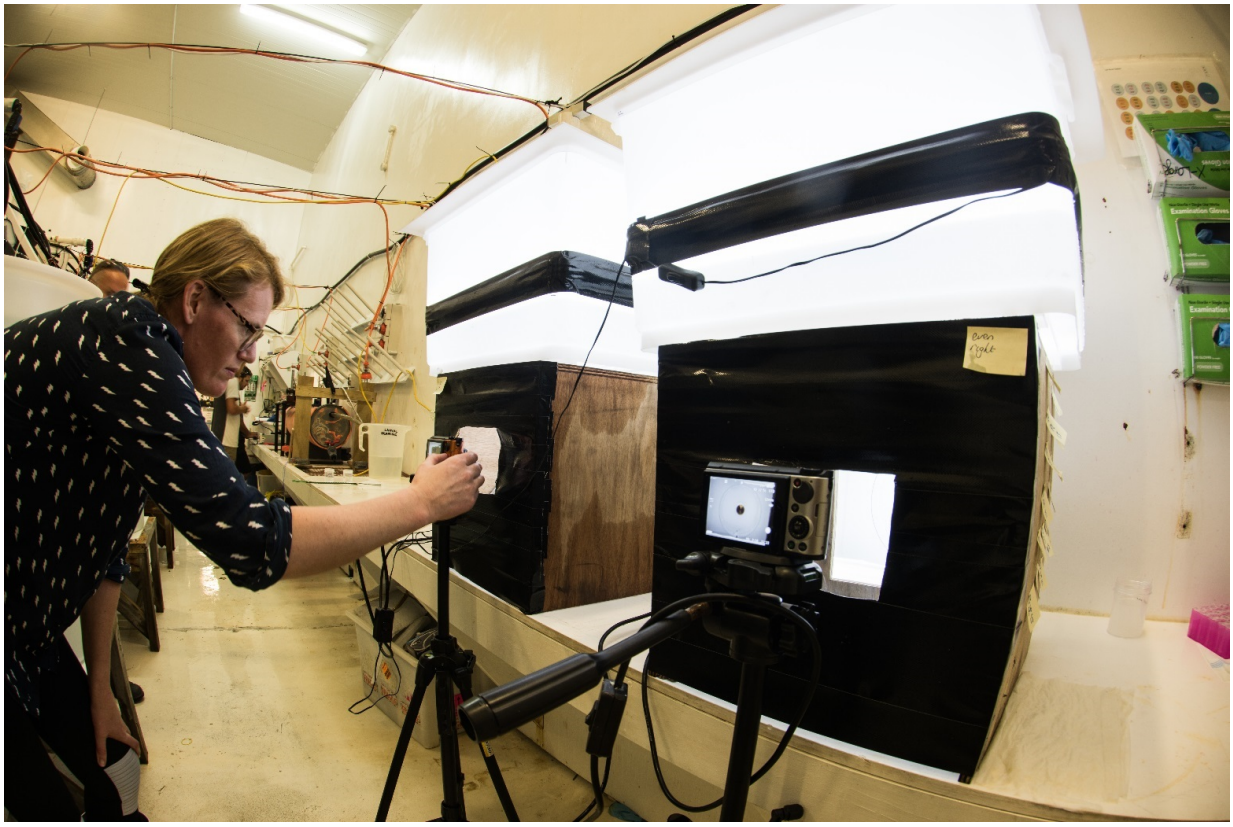

Figure 9: Bridie Allan (University of Otago) conducting an escape response assessment on larval snapper (Photo: Crispin Middleton).

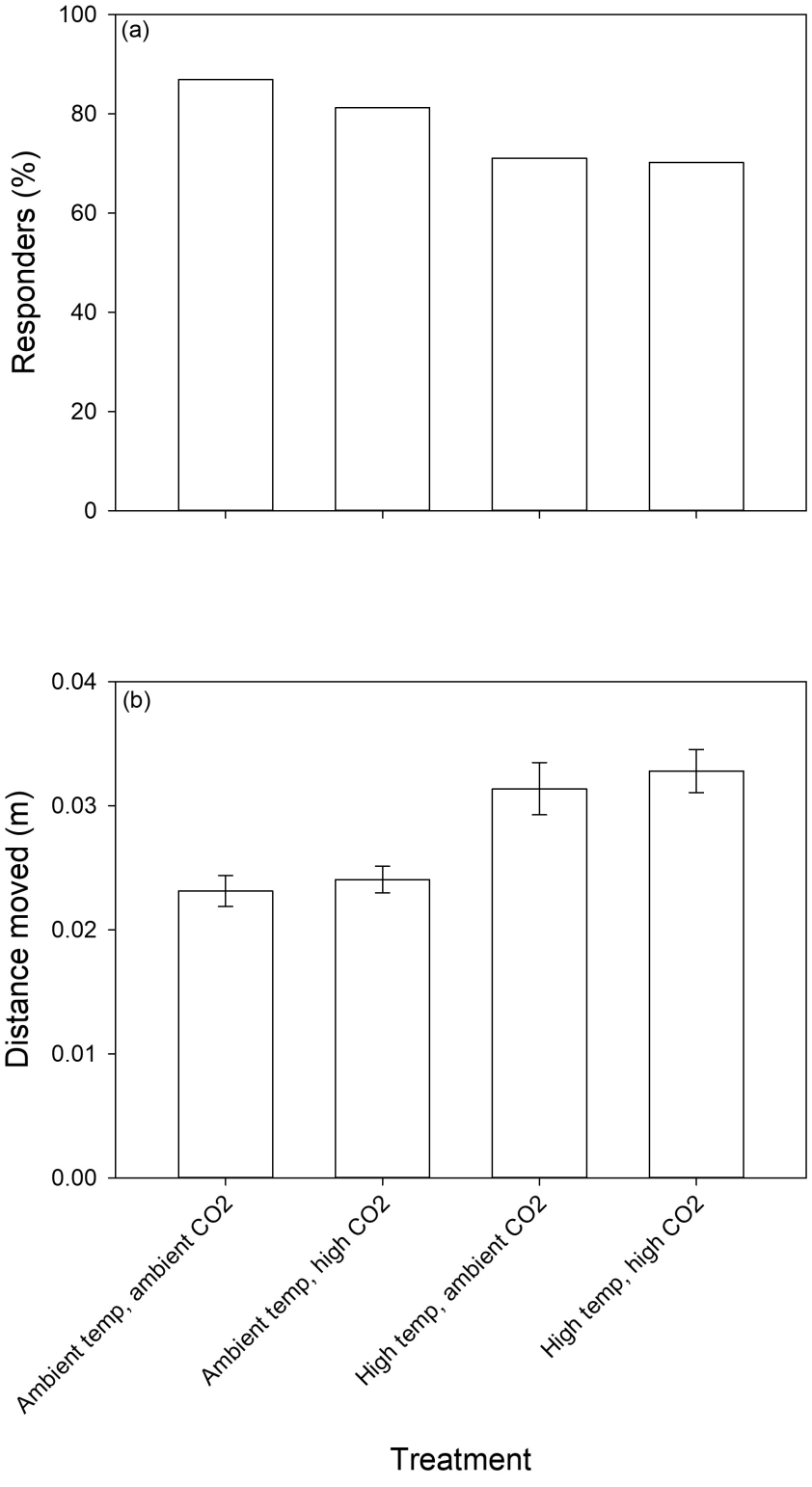

Figure 10: Escape performance, (a) percentage of responders and (b) for individuals that responded, the distance moved (m) (error bars are ±1 standard error).

Olfaction

Snapper larvae exhibited a mild avoidance response to hāpuku odour, spending between 60 and 70% of their time in the water source that did not contain hāpuku odour (Figure 11). This avoidance response also had an overall temperature effect (2-way ANOVA, df = 1, $F = 6.41$, $p < 0.02$), whereas the CO_2 and temperature × CO_2 interaction term were non-significant ($p > 0.6$ and $p > 0.25$, respectively). This temperature effect was driven by reduced avoidance occurring in the high temperature, ambient CO_2 treatment relative to the ambient temperature, ambient CO_2 treatment (Tukey's Honestly Significant Difference, $p = 0.057$)

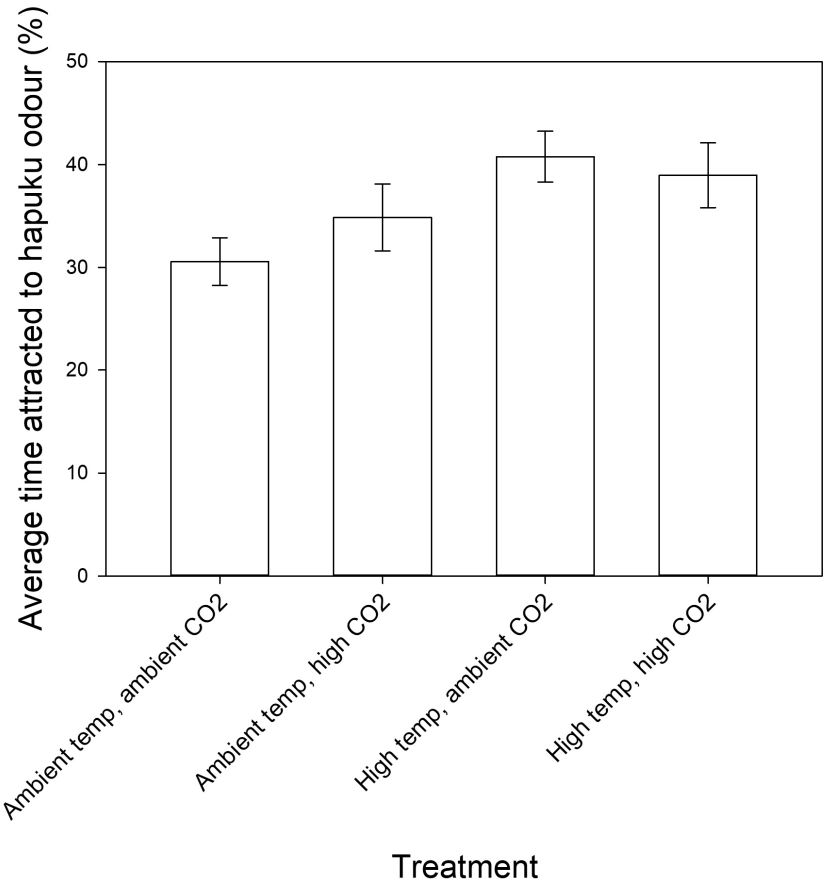

Figure 11: Response of larval snapper reared under different combinations of temperature and CO_2 treatment to hāpuku odour. A value of above 50% on the Y axis would indicate a preference for hāpuku odour, and a value below 50% would indicate avoidance. n = 30 fish per treatment, error bars are ±1 standard error.

Hearing

Snapper larvae reared under high CO_2 had a higher auditory threshold (i.e., sound had to be at a higher level to generate a clear AEP) at low frequencies relative to snapper reared under ambient CO_2 (Figure 12). At high frequencies no difference in auditory threshold was detected between the CO_2 treatments. Only snapper reared at high temperature were assessed because the ambient temperature snapper were too small to properly place electrodes to measure AEPs.

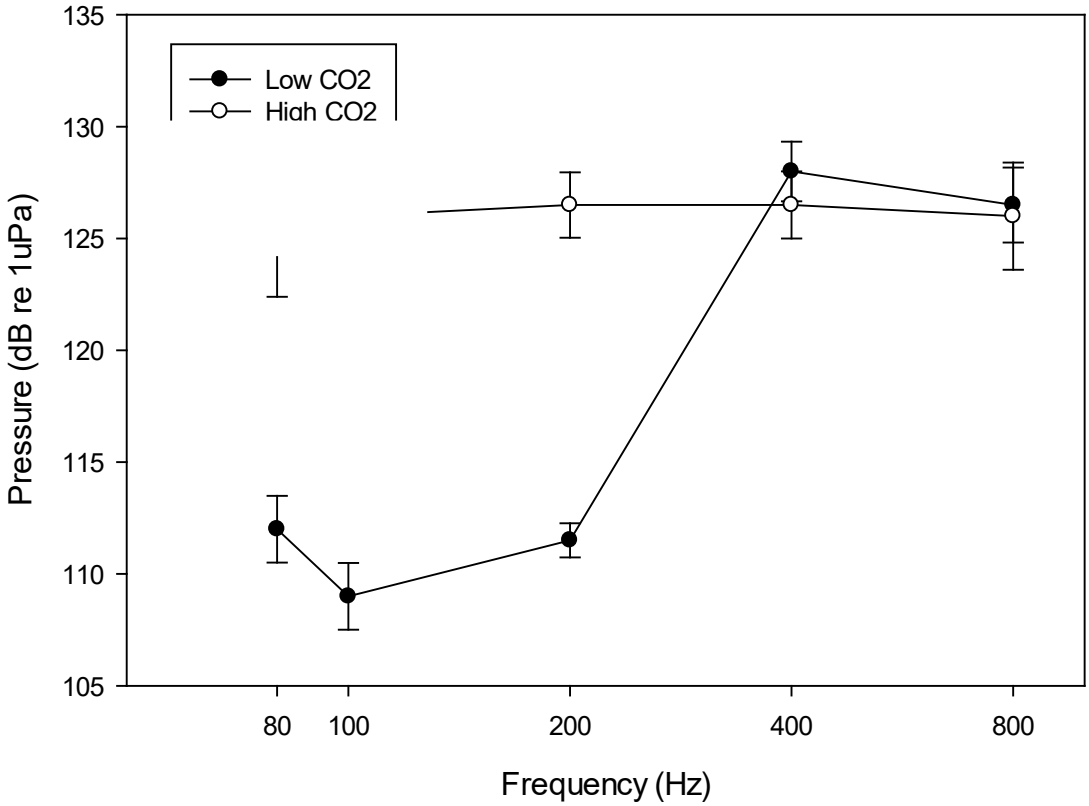

Figure 12: Auditory threshold of snapper larvae across different frequencies (i.e., higher values on the vertical axis indicate that sound needed to be louder before it was registered by the fish). Filled symbols are ambient CO_2; open symbols are high CO_2. Only high-temperature treatment fish were assessed (they were larger, making it possible to position electrodes). Note: 10 fish per treatment, error bars are ±1 standard error.

Vision

Optomotor trials indicated that snapper larvae from all treatments had a visual acuity threshold of 2°, i.e., snapper responded to images once the acuity angle was greater than 2° (Figure 13). Although there was no obvious difference in the angular swimming velocity of snapper between CO_2 treatments, there were some differences in the response between temperature treatments. For snapper reared under ambient temperature their angular swimming velocity plateaued at the 2° threshold. Alternatively, for snapper reared under high temperature their angular swimming velocity decreased at acuity angles greater than 2°. This response was driven by some of the high temperature snapper swimming in a positive direction whereas other high temperature snapper moved in a negative direction relative to the movement of the black and white bars in the optomotor device.

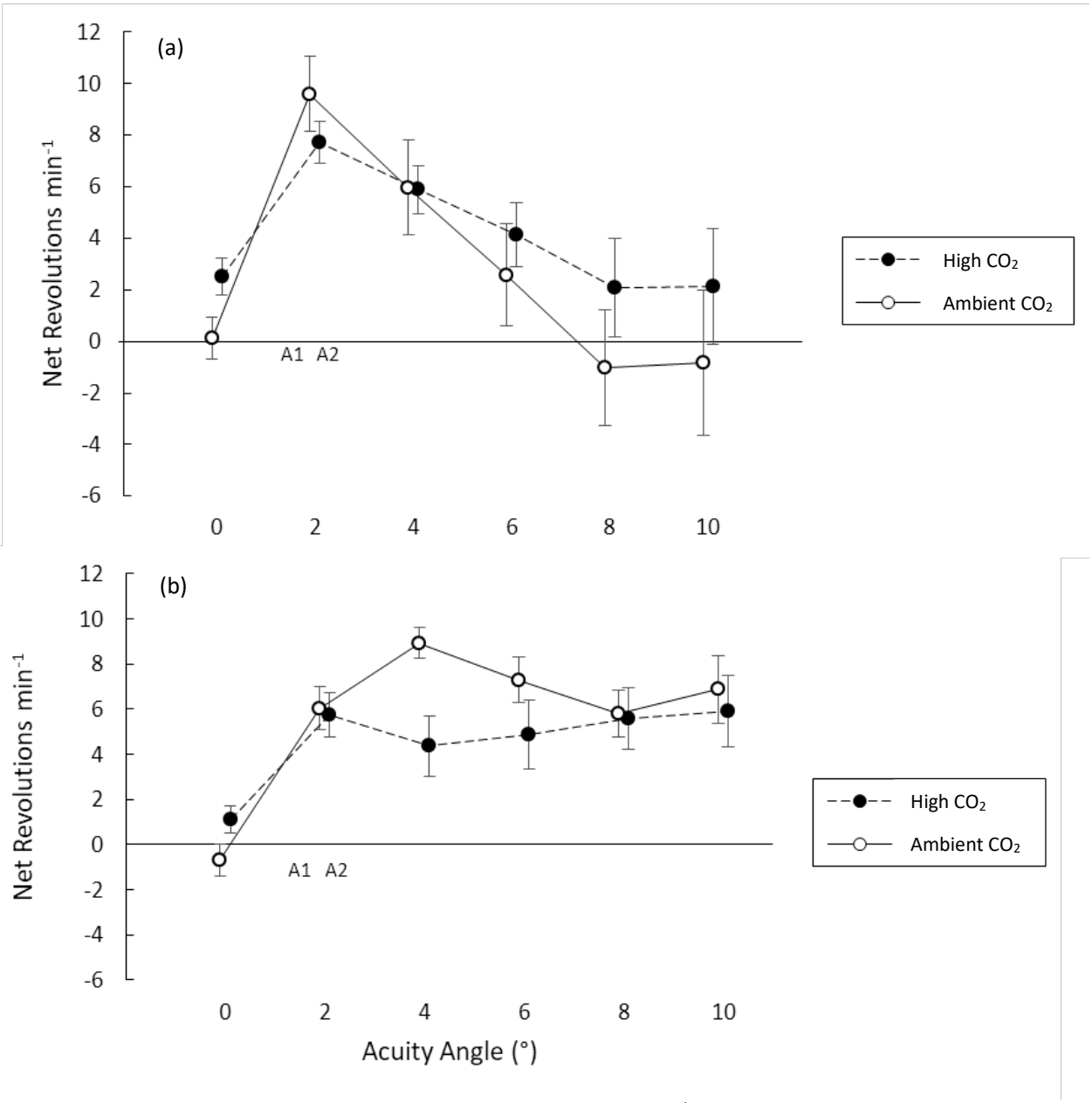

Figure 13: Comparison of angular swimming velocity (Net revs min^{-1}) between: (a) High temperature (22 °C) snapper larvae (elevated vs ambient CO_2 denoted on legend), and (b) Low temperature (18 °C) snapper larvae (elevated vs ambient CO_2 denoted on legend). n = 20 fish per treatment, error bars are ±1 standard error. Data points have been offset from each other along the x-axis to prevent overlap. A1 and A2 labels underneath the data plots denote visual acuity thresholds of ambient and high CO_2 fish, respectively.

3.4 Discussion

Snapper are a species that respond strongly to temperature and climate patterns. Specifically, Francis (1993) demonstrated a strong positive relationship between snapper year class strength measured during their 1+ year and autumn water temperatures the year before. In addition, Zeldis et al. (2005) demonstrated higher larval snapper survival in years where larval food density was higher, which appeared to be driven by climate patterns.

For the first time, the present study experimentally demonstrated the direct effect of not just temperature, but also elevated CO_2, on snapper larvae. These results align well with those of Francis

(1993) and Zeldis et al. (2005), in that a strong positive temperature effect on growth was observed. All the morphological variables assessed were also positively influenced by elevated temperature (and not elevated CO_2), again reflecting the strong growth effect associated with elevated temperature. Although there was some indication that larval survival may also respond to temperature (positively for early stage larvae, negatively for later stage larvae), these were not significant effects. Regardless, the relevance of the strong positive effect of temperature on growth is that, in a natural scenario where food is scarcer and predators are present, faster growth results in less time within the more vulnerable early larval life stage (c. 2% survival from hatching to 8 dph; (Zeldis et al. 2005), and therefore a higher overall survival rate. Essentially faster growth allows larval snapper to outgrow the mouths of their predators. What was more surprising, however, was the positive effect of elevated CO_2 on larval snapper survival (experiment 1). This result is contrary to the majority of studies that have observed either no or a negative effect of elevated CO_2 on larval fish survival (see section 3 and references therein). An exception is Pope et al. (2014), who observed a positive effect of elevated CO_2 on the survival of larval European seabass (*Dicentrarchus labrax*). An explanation for this positive response to elevated CO_2 is not immediately apparent.

In terms of the swimming ability and oxygen physiology of larval snapper, both were negatively affected by elevated CO_2. A lower aerobic scope in juvenile fish can affect any aerobic activity, which would be detrimental to predator avoidance. Reduced swimming ability may also affect the ability to evade predators or find appropriate habitat at the time of settlement. Previous studies investigating aerobic capacity and swimming performance in relation to elevated CO_2 have produced varied results (see Section 2 and references therein), suggesting responses are likely to be species specific. Conversely, elevated temperature had a positive influence on larval snapper swimming ability, but not oxygen physiology. This swimming ability effect is likely to be due to the more advanced developmental state and therefore performance ability of snapper reared under elevated temperature conditions.

Escape performance results were unaffected by elevated CO_2, whereas temperature may have had somewhat opposing effects on the variables measured. For example, the proportion of snapper responding to the startle stimulus was reduced by elevated temperature (although this was non-significant), but of the fish that did respond, the distance they moved was increased. How these results may mediate themselves for snapper populations under a future climate change scenario is unclear, but it is possible that an increased distance moved by responders could result in improved predator avoidance ability.

As far as the authors are aware, for the first time, the effect of elevated temperature and CO_2 was assessed across three different sensory systems. For olfaction, these assays demonstrated that snapper show a weak avoidance response to a potential predator (hāpuku), with the size of this avoidance response further reduced by elevated temperature. There was no effect of elevated CO_2 on the response to the potential predator cue, which contrasts with results for many tropical reef fish, but is consistent with findings for some other temperate water fishes (e.g., Atlantic cod, Jutfelt & Hedgärde 2013).

Elevated CO_2 did not affect the visual acuity of snapper. There was a temperature affect, however, which appeared to be driven by some of the high-temperature-reared snapper responding positively and others negatively to the direction of movement of the black and white bars in the optomotor trial. It is not clear why this occurred, but it could potentially relate to the larger size and competency of the snapper from the high temperature treatment. For example, at a smaller size the fish may be more likely to demonstrate the innate optomotor response to maintain a visual reference point. Alternatively, as the fish grow in size and competency, a rheotactic response (i.e., swimming against the perceived water flow to increase flow over the gills) becomes an option.

A more clear-cut result was obtained from the hearing assay. The hearing ability of larval snapper reared under elevated CO_2 conditions was reduced at lower frequencies compared with snapper reared under ambient CO_2 conditions. This result is potentially consistent with fish having larger otoliths

under elevated CO_2 conditions (because otoliths are involved in hearing), which is an established trend from the literature (see section 2 and references therein). Since this hearing trial was conducted, the authors have quantified the size and shape of the otoliths of the snapper involved (Radford et al. 2021); this is one of the first times where the effect of elevated CO_2 is assessed at a functional (hearing sense) and anatomical (otolith size and shape) level. Negative effects on larval hearing could potentially be significant if hearing function at the frequencies affected is linked to an important life history strategy such as locating suitable settlement habitat (Tolimieri et al. 2000).

Overall the results presented here suggest that the direct effects of climate change on snapper larvae are likely to be both positive (temperature had a positive effect on swimming ability, escape distance in response to a startle stimulus, and growth and elevated CO_2 had a positive effect of on larval survival) and negative (elevated CO_2 negatively affected aerobic scope, swimming ability, and hearing ability). Section 4 considers how all the direct effects of climate change on snapper demonstrated here (along with climate change related effects from other studies on snapper) may combine to affect snapper at the scale of whole populations or fisheries. An important additional consideration, however, is potential influence of the indirect effects of climate change (which are not assessed here). These indirect effects may potentially be more important than the direct effects. A relevant example is the established positive correlation of snapper year class strength to water temperature (Francis 1993). It is possible that this relationship isn't driven by temperature itself, but rather by the availability of food (Zeldis et al. 2005).

4. MODELLING THE EFFECT OF OCEAN ACIDIFICATION AND ELEVATED TEMEPRATURE ON SNAPPER POPULATIONS

4.1 Introduction

Section 4, under Specific Objective Four, describes the use of a model to assess the effects of climate change on snapper populations (here, climate change is defined as elevated temperature and CO_2). In choosing a modeling approach, consideration was given to both the likely impacts of climate change and the level of understanding about these impacts that is available. Most of the experimental studies assessing OA impacts on fish (including those outlined in section 3) are limited to describing the direct effect of OA on physiological processes, growth, and survival of larvae. Understanding the potential impact of OA on fisheries, however, requires scaling these physiological effects up to population- and ecosystem-level processes. Understanding what the combination of these effects will look like for fish populations in an elevated CO_2 environment is not straightforward. As discussed in section 3, there are a range of modelling options with varying complexities (Koenigstein et al. 2016, Le Quesne & Pinnegar 2012). End to end models are an attractive choice because they incorporate impacts from whole ecosystems, but this approach is limited by our poor understanding of how stressors like OA may manifest across an ecosystem. In section 3, it was suggested that the most pragmatic approach given the current level of understanding would be to initially establish what the direct effects of OA on a fish species are. This information can then be used within existing fishery stock assessment models to conduct sensitivity analyses on appropriate parameters (e.g., growth, survival, the stock-recruit relationship). Although insight would be limited to the direct effects of climate change, largely flowing through from impacts on larvae, for one population, this would be a good starting point. As more empirical information becomes available more complex modelling options can be considered in the future. This is the approach described in this section. Specifically, this section considers the aspects of snapper life history traits and physiology which are likely to be affected (using results from section 3 and from the wider literature on snapper), and the parameters that encapsulate these aspects within an existing snapper population model. Because the effects of OA and elevated temperature are likely to be intertwined, temperature effects were also considered, but other factors likely to be part of climate change (e.g., hypoxia, sedimentation, etc.) were not. This assessment was largely based around the likely impact of climate change on the larval life stage (where OA is likely to have an affect), although some temperature effects of older life stages were also incorporated.

4.2 Methods

The effect of climate change on snapper was considered in the context of the snapper population within the SNA 1 (North Cape to East Cape) Quota Management Area. The snapper population in this area is New Zealand's largest and most well understood. The most recent SNA 1 population assessment conducted in 2012/13 was used as the base model. This stock assessment model is described in detail by (Francis & McKenzie 2015a, Francis & McKenzie 2015b), but briefly, it uses a variety of observational data (e.g., catch rate indices, age data, absolute biomass estimates, etc.) to describe the SNA 1 population between 1900 and 2013, with four main fisheries (longline, single trawl, Danish seine, and recreational) operating with different size selectivities and removing fish from SNA 1 population. Some important differences from this 2012/13 assessment model were incorporated in this current model: (1) For simplicity. only one stock was considered (not three as in the original assessment), being the Hauraki Gulf, (2) a length-based proxy of the age-based model (with similar growth, mortality, and gear selectivity characteristics) was used so that OA and temperature effects on growth could be more easily incorporated. The Hauraki Gulf length-based estimation model was then fitted to actual Hauraki Gulf historical observational data (catch-at-length, mark-recapture (tagging), and method specific catch history) to estimate uncertainty on the key productivity parameters of growth and recruitment (i.e., as Bayesian posterior distributions as derived from Markov chain Monte Carlo (MCMC) resampling).

For each different scenario run, as defined in the case table below (Table 2), the Hauraki Gulf snapper population was projected from its 'known' position in 2013 by calculating a total fishing mortality (F) that would bring the population to a deterministic equilibrium target biomass of 40% of an unfished population (B_0). Catch proportions to achieve this $F_{40\% B0}$ were the same for all scenarios and were based on present day method proportions (longline = 25%, Danish seine = 17.5%, single trawl = 17.5%, recreational = 40%). Each $F_{40\% B0}$ projection scenario produced two comparative statistics: (1) the total deterministic equilibrium yield at 40% B_0 (i.e., total catch from all methods in tonnes at B_{40}), (2) the number of years post 2013 taken to reach 99% the B_{40} biomass. Uncertainty was incorporated into the base case (i.e., no change) by running $F_{40\% B0}$ projections pursuant to 1000 unique growth and recruitment parameter combination draws from their MCMC-derived posterior distributions. Each successive scenario run then shifted the median value of the 1000 MCMC generated posterior draws (by the percentage expressed in Table 2) for a particular parameter and scenario. It is important to note that variation was only considered for parameters that were adjusted in the model, so the actual variation expected around model output would likely be higher in reality.

Table 2: Case table for proportional change to parameters incorporated into the SNA 1 stock assessment model to encapsulate climate change effects on snapper. R_0 is the mean number of age-one snapper entering the population at virgin biomass.

Case	R_0	Adult growth	Initial size
1	No change	No change	No change
2	0.70	No change	No change
3	1.30	No change	No change
4	No change	0.94	No change
5	No change	1.06	No change
6	No change	No change	1.48
7	0.70	0.94	1.48
8	1.30	1.06	1.48

Parameters adjusted to incorporate OA and temperature effects on the snapper population

A range of evidence describing the physiological effects of climate change on snapper was considered, some from the experiments described in section 3. In the SNA 1 area, temperature is expected to increase by 2 to 3 °C and CO_2 to c. 1000 µatm by the end of century (Law et al. 2018a, Law et al. 2018b, Meinshausen et al. 2011). These were the environmental conditions considered when assessing the physiological impact of climate change on snapper. An important consideration when modelling climate change effects is that many of the effects of OA on fish are likely to be on larval stages (see section 2 and references therein). Alternatively, fishery stock assessment models generally recruit fish to the modelled population at an older age (one-year- olds for the SNA 1 stock assessment model). As a result, all aspects of larval survival (including how OA and increased temperature may affect larval survival) are encapsulated by the model recruitment parameters; i.e., the mean number of age-one snapper entering the population at virgin biomass (R_0) and the degree of linearity (steepness) between stock size and mean recruitment (h). Other aspects considered likely to be affected by climate change included the mean size of age-one fish recruiting to the model and the growth of adults in the model.

Another consideration was increasing variation in the year class index used to add new recruits to the model based on increased variation in future temperature and the strong link between snapper recruitment strengths and temperature. Further investigation, however, suggested that end-of-century temperatures were not predicted to be more variable (Ministry for the Environment 2018), so no adjustments were made to year class strength variation.

The mean number of age-one recruits at virgin biomass

The 2012/13 SNA 1 stock assessment model used a Beverton & Holt (1957) type stock-recruitment dynamic. The value of steepness (h) assumed in the 2012/13 model was 0.85. In the present study no adjustments were made to steepness, because it was not clear whether OA and temperature may alter this dependent parameter. Alternatively, R_0 (the mean number of age-one snapper entering the population at virgin biomass) has the potential to be affected by OA and temperature. The experiments described in section 3, however, did not provide a clear answer as to the magnitude effect OA and temperature may have on R_0. Larval survival in experiment 1 (where larvae were reared in experimental conditions right from the egg stage) appeared to be positively influenced by OA (with an overall increase of between 157 and 251%), but the aerobic scope of larval snapper (this time from experiment 2) was negatively affected by OA by about 30%. Reduced aerobic scope can reduce physical performance, potentially leading to reduced foraging efficiency and/or reduced ability to evade predators (Pörtner 2010), so would likely translate to some form of negative effect on larval snapper survival. Therefore, with the experiments indicating both positive and negative effects it was not possible to specify a particular value describing the effect of OA and increased temperature on larval snapper survival. Therefore, a sensitivity analysis was conducted to investigate the influence of R_0 on the modelled snapper population in the Hauraki Gulf. Scenarios were run with a 30% increase or decrease applied to R_0 (Table 2). It is important to note, however, that although a 30% reduction in aerobic scope is likely to decrease survival of larval snapper, it is unlikely to translate to a matching 30% reduction in survival. Furthermore, the increase in larval survival indicated from the tank experiments (a 157 to 251% increase) is also unlikely to lead to the same level of increase in overall recruitment because other forms of mortality are likely to act on recruits before they reach age one and environmental carrying capacity limitations would seem unlikely to sustain this magnitude of increase in recruitment. Taking these points into account, 30% represented a change in both the positive and negative direction which allowed assessment of the sensitivity of the modelled snapper population to significant changes in the R_0 parameter. This 30% change was incorporated via a 30% shift to the R_0 parameter estimates generated by the base MCMC runs. Various scenarios were included to incorporate these changes within the case table (Table 2).

Size at recruitment

Snapper entering the stock assessment model have an associated mean size at the time of recruitment at age one. Our tank experiments (section 3) indicated that larval snapper exposed to higher

temperature have a faster growth rate, and therefore under a climate change scenario would likely have a larger mean size at age one. Some of the snapper from experiment 2 (those from the high temperature, ambient CO_2 and the low temperature, ambient CO_2 treatments) were retained and continued to be reared under high (22 °C) and ambient (18 °C) temperatures (one tank per treatment, both with ambient CO_2) until August 2018, or about 8 months post hatch. These fish were individually weighed six times over this period, and the weights converted to fork length (FL) using the length-weight relationship for snapper described by Taylor & Willis (1998). Overall the snapper reared under elevated temperature were 48% larger than the snapper reared at 18 °C. This increase in initial size was incorporated via a 48% increase to the size at recruitment parameter estimates generated by the base MCMC runs. Various scenarios were included to incorporate this change within the case table (Table 2).

Adult growth

Although the tank experiments did not assess the growth rate of adult snapper, there is good evidence to suggest that temperature does influence adult snapper growth (Fowler 2016, Martino et al. 2019, Wakefield et al. 2016, Peter Horn, NIWA, unpub. data). In many locations, snapper growth is positively influenced by temperature, however, a thermal optimum for growth will be reached at some temperature, after which growth will decline. This is most evident in Western Australia, where snapper growth is at its maximum at mid-latitudes, with the slowest growth at the extreme northern limit of the geographical range of snapper, where temperatures are at their highest (Wakefield et al. 2016). It seems unlikely, however, that the thermal optimum for growth of Western Australian snapper, or snapper from other regions, could simply be applied to snapper in New Zealand. Some degree of adaption to localised temperatures is more likely. As such, information on the response of New Zealand snapper to temperature is most relevant.

A recent New Zealand study (Morrongiello et al. 2021) assessed snapper growth by measuring annual otolith increments and relating this to sea surface temperature (SST) from the previous year. For Hauraki Gulf snapper, the relationship between snapper growth and the SST anomaly from the previous year was positive, but only encompassed +1 °C, at which point growth appeared to have plateaued. Conversely, snapper growth from the more southern (cooler) SNA 7 stock was still increasing at +1 °C. This would suggest that Hauraki Gulf snapper may reach a thermal optimum for growth at about +1 °C, but the effect of temperature on growth beyond this (a 2 to 3 °C change is expected by the end of century (Law et al. 2018b)) is less clear. As a result of this uncertainty, a sensitivity analysis was run to investigate the influence of adult growth on the modelled snapper population in the Hauraki Gulf. The analysis of Morrongiello et al. (2021) suggested the point at which the growth temperature relationship plateaued (+1 °C) equated to a c. 6% increase in snapper growth. This growth increase was simulated as a 6% increase in equilibrium biomass (yield) per-recruit under zero fishing mortality. Typical of most stock assessment models, growth in the length-based Hauraki Gulf snapper projection model was represented by a linear increment von Bertalanffy function where parameter k = the growth rate coefficient and L_∞ = the asymptotic length at infinite age. For fish generally, an increase in growth would largely occur via an increase in k (Audzijonyte et al. 2016); however, for snapper specifically, an increase in growth has been shown to occur via an increase in L_∞ (Fowler 2016, Wakefield et al. 2016). Thus, increasing growth related biomass per-recruit by 6% in these simulations was achieved by increasing L_∞ while holding k constant. The required adjustments were made to each of the 1000 base case L_∞ MCMC estimates to achieve effective ±6% change in biomass per-recruit. Although a concomitant and opposing change in k might also be expected to occur in reality as per Audzijonyte et al. (2016), omitting these changes in k would not have affected overall estimates of growth productivity in the simulations, just the method of how that change was achieved. Various scenarios were included to incorporate these changes within the case table (Table 2).

Modelling scenarios assessed

A number of different modelling scenarios were assessed which included the individual and combined effects of the various parameter adjustments described above on the Hauraki Gulf snapper population

(Table 2). Case 1 had no change to any parameters and represents a base case for comparison to cases 2 to 6, which each incorporated changes to individual parameters. Case 7 represents the most negative outlook for Hauraki Gulf snapper populations. It incorporated the negative sensitivity values for R_0 and adult growth, using the initial size adjustment that is anticipated to occur under a climate change scenario. Case 8 represents the most positive outlook for Hauraki Gulf snapper populations. It incorporated the positive sensitivity values for R_0 and adult growth, and also used the initial size adjustment that is anticipated to occur under a climate change scenario.

4.3 Results

The Hauraki Gulf snapper population model was used to project the snapper population forward under a range of scenarios that incorporated climate change adjustments to an equilibrium biomass of 40% B_0, which is the assumed management target for these scenarios. In all scenarios, the yield of snapper (total catch across all fishing methods) initially declined sharply, before rebuilding (Figure 14). This reflected the high levels of catch that the snapper population was experiencing as determined at the last assessment in 2013. After this initial decline the snapper population then recovered, under all scenarios, as it adjusted to the lower catch levels set by the model to achieve an equilibrium biomass of 40% of B_0. Ultimately all of the modelling scenarios considered achieved this equilibrium biomass within 70 years, with yield at equilibrium ranging from c. 2500 to 5000 t (Figures 14 and 15).

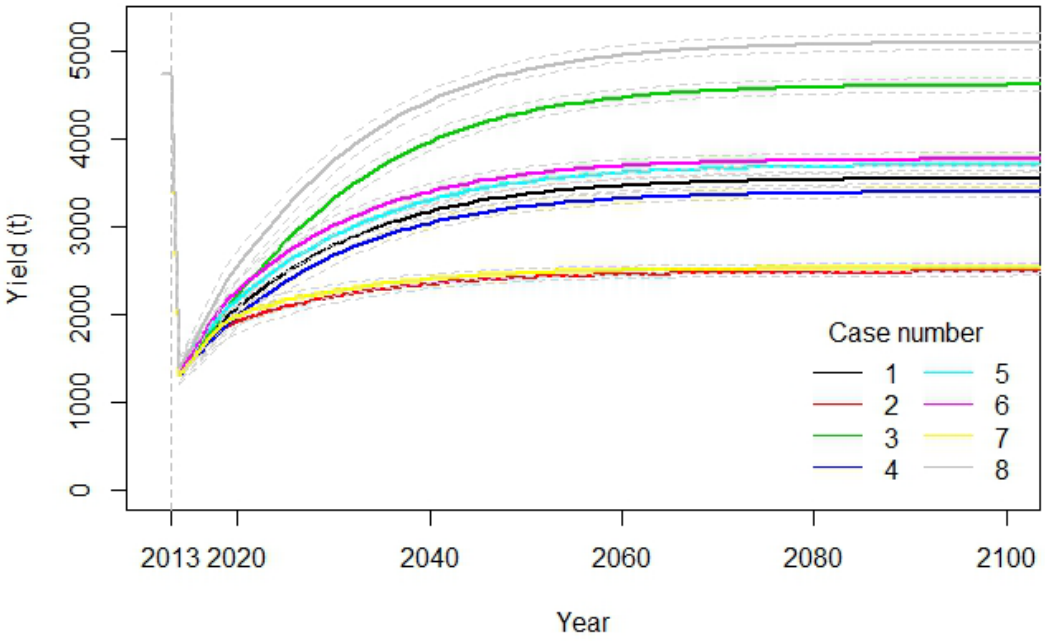

Figure 14: Yield (t) of Hauraki Gulf snapper (all fishing methods) through time for the various modelling scenarios (specified in Table 2). Vertical dashed line at 2013 represents the model's 'known' starting point at the last SNA 1 assessment. Dashed lines around yield projections represent 95% confidence intervals derived from 1000 MCMC estimates for each parameter of interest (but not considering variation associated with other parameters).

In terms of the effect of particular scenarios on yield and the time to achieve yield at equilibrium, the largest effect was associated with the sensitivity for R_0 (Cases 2 and 3). Specifically, a 30% change in R_0 resulted in a very similar overall percentage change in yield, and, for the positive R_0 sensitivity run (i.e., Case 3), a c. 68% reduction in the time taken to reach yield at equilibrium (Figure 15). Because changes made to adult growth rate (±6% change in biomass per recruit: Cases 4 and 5) were smaller, they resulted in smaller changes (c. 4%) to equilibrium yield at 40% B_0, and for the positive adult growth sensitivity run (i.e., Case 5), a c. 39% reduction in the time taken to reach the Case 1 40% B_0 equilibrium yield (Figure 15). The change made to size at age-one recruitment was the largest

proportional change made overall (a 48% increase), but this shift only resulted in a 6% increase in the 40% B_0 equilibrium yield, but it did have a c. 47% reduction in the time taken to attain the Case 1 40% B_0 equilibrium yield (Figure 15). Overall, the scenario predicting the most pessimistic outcome of climate change for Hauraki Gulf snapper (Case 7) predicted a 29% reduction in yield at equilibrium, and the most optimistic scenario (Case 8) predicted a 44% increase in yield at equilibrium and a 76% reduction in the time taken to achieve an equivalent Case 1 40% B_0 equilibrium yield (Figure 15). This suggests that the individual effects of each parameter adjustment were mostly additive, and largely driven by the large adjustment to R_0, which almost directly translated to the same change in yield at equilibrium.

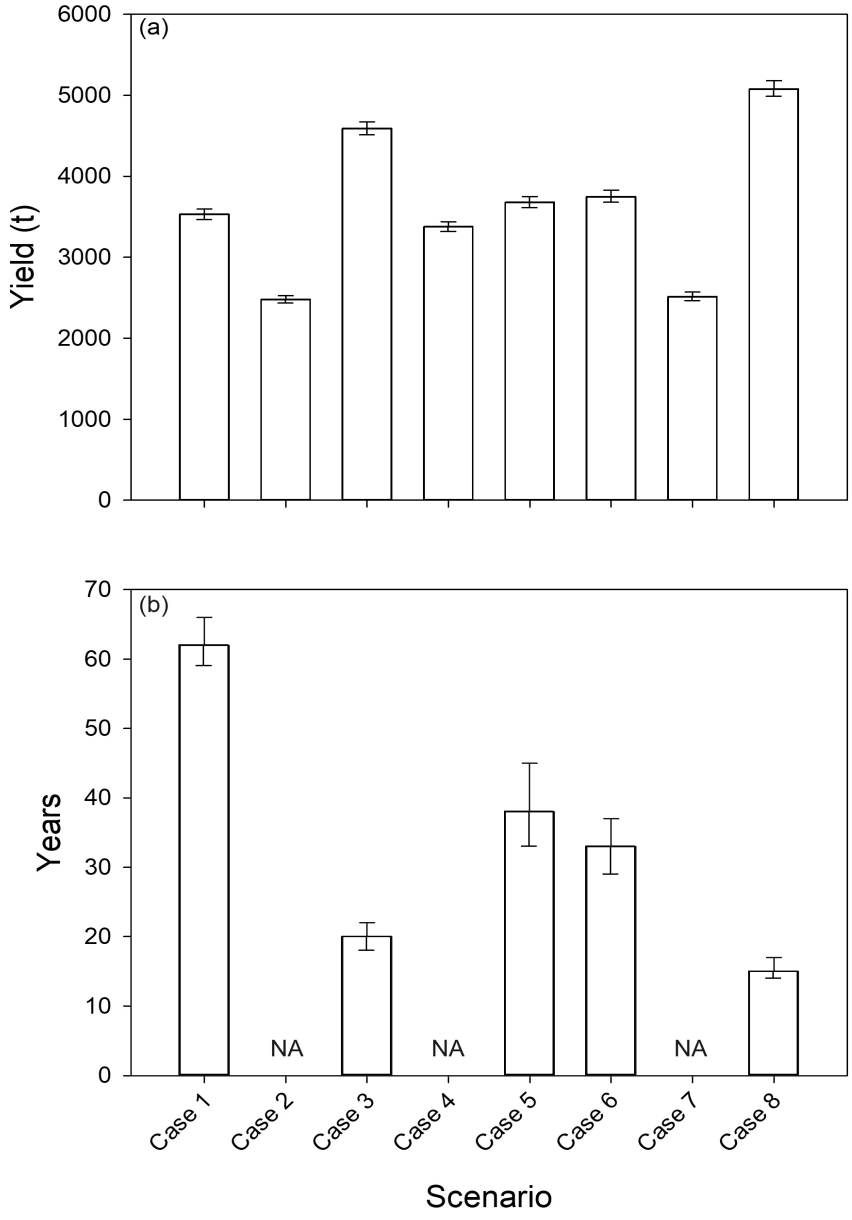

Figure 15: Model results depicting (a) total yield (t) (across all fishing methods) of Hauraki Gulf snapper at an equilibrium biomass of 40% B_0 (b) the number of years it took for each modelling scenario to achieve > 99% of Case 1 40% B_0 equilibrium yield. Scenarios that never reached the equilibrium yield achieved under Case 1 are denoted with 'NA'. Error bars denote 95% confidence intervals derived from 1000 MCMC estimates for each parameter of interest (but not considering variation associated with other parameters).

5. DISCUSSION AND OVERALL CONCLUSIONS

The population modelling conducted in section 4 represents the culmination of all four years of this project. It has brought together the combined knowledge of climate change and snapper researchers, a review of the international literature describing the effect of OA on fish, as well as the results from a comprehensive experimental assessment of the effects of elevated temperature and CO_2 on snapper larvae and placed all this knowledge within a stock assessment modelling framework. As such, it represents the first attempt at modelling the population level consequences of the direct effects of climate change for a New Zealand fish population. Overall, all the modelling scenarios considered achieved an equilibrium biomass within 70 years, and a yield at equilibrium ranging from c. 2500 to 5000 t.

Because fishery models largely describe sub-adult and adult life stages, and many climate change impacts on fish occur during larval life stages, much of the likely direct effects of climate change were essentially encapsulated within an adjustment to a single stock-recruit parameter, R_0. This is undoubtedly an oversimplification of how climate change will actually operate. This demonstrates the difficulty in translating physiological effects into population level impacts, but the level of resolution this approach provides is probably a good match to the current level of understanding for how fish will respond to climate change. Others have also successfully adopted a similar approach when assessing climate change impacts on individual fish populations (Atlantic cod, Stiasny et al. 2016; Baltic sprat, Voss et al. 2011; jackass morwong, Wayte 2013).

In the experiments conducted in section 3, opposing effects on larval snapper were observed (e.g., positive larval growth and swimming performance effects observed under elevated temperature and positive survival effects observed under elevated CO_2 vs. negative metabolic and swimming performance effects observed under elevated CO_2). As such, it was not possible to specify the overall direction of the direct effect of climate change on snapper. Through sensitivity analysis, however, the most pessimistic scenario is one where the direct effects of climate change are unlikely to reduce the yield of the snapper fishery by more than 30%, and potentially by less. This is because this negative scenario was largely based on a 30% reduction in metabolic and swimming performance, which will not necessarily translate into a 30% reduction in larval survival (which is what was effectively modelled here). The most optimistic scenario could potentially result in a 30% or more increase in yield. In summary, the direct effects of climate change on snapper are: (1) likely to be largely determined by impacts on the larval life stage (here modelled by adjusting R_0), (2) that either positive or negative effects are possible, and (3) that the magnitude of the effect on these larval life stages (i.e., the specific survival rate that larval stages experience) should more or less translate into a similar magnitude effect at the population level. Although in an ideal scenario, it would have been possible to make precise predictions about both the direction and magnitude of the direct effects of climate change on snapper, these results still represent important advances in what is known. Furthermore, the last point may be particularly important, because others have found that climate change effects observed on the larval life stage can increase in magnitude (due to the specific stock-recruit relationship modelled) when considered at the population level (e.g., Stiasny et al. (2016).

The other parameter with the potential to be influential at the population level is adult growth (here defined as growth of any fish recruited to the model at age one, although sexual maturity will be later than this). Although changes in adult growth implemented in this study only resulted in a c. 4% change in yield, it must be noted that the magnitude of this change was based on growth observations occurring at a temperature anomaly of only +1 °C (Morrongiello et al. 2021). Considering the much larger percentage changes in larval/juvenile growth observed in response to elevated temperature (section 3), the size of this change seems quite small. Given the potential importance of growth responses to elevated temperature, conducting a tank experiment to provide a firmer understanding in this regard might be prudent.

One of the main findings of this modelling exercise, was the lack of certainty with which the effect of climate change on parameters could be specified within the model. Given that snapper is New Zealand's most well studied species, and the species-specific nature of how fish respond to climate change (Ferrari et al. 2011a), it seems likely that models which predict how whole ecosystems will respond to climate change (Fulton 2011, Griffith et al. 2012, Kaplan et al. 2010) will have even higher levels of uncertainty. Further to this, it is also important to note that the snapper population model presented here incorporated only direct effects of climate change. Indirect effects of climate change (e.g., juvenile habitat modification, disruptions to predator-prey relationships) could be even more influential than the direct effects (Branch et al. 2013, Le Quesne & Pinnegar 2012, Nagelkerken et al. 2016). This is potentially best illustrated by the strong correlation between snapper recruitment and SST (Francis 1993). This relationship could potentially be mediated via the strong positive effect of elevated temperature on growth and the reduced time spent at smaller life stages that are more vulnerable to predators (Ware 1975). Understanding how whole ecosystems, and all their interconnections, will respond to climate change is therefore likely an important consideration. Some potential options include: (1) conducting finer scale climate projections relevant to coastal ecosystems to provide a better understanding of how physical parameters such as wind and mixing patterns will alter nutrient dynamics and the productivity of coastal fish species, (2) conducting climate change experiments on key ecosystem components (i.e., not just species with fishery value, but the species they interact with, including their food sources), (3) conducting climate change experiments with multiple species to address how key ecosystem processes (e.g., predation) may be altered. Iterative data collection such as this, paired with ecosystem model development, may be able to provide more realistic and better-informed predictions of the effect of climate change on coastal ecosystems and their fisheries.

Aside from improving our understanding of the likely effect of climate change, it is also important to consider what can be done to mitigate any potential effects. This could involve reducing non-climate related stressors, such as fishery extraction, to account for the impact of climate. Other stressors such as land-based effects, including sedimentation and eutrophication, may also be able to be reduced, but would first require longer term adjustments to land use practice. Being aware of any change that is occurring, however, is potentially the most empowering management response. To this end, the frequency of assessments and, in particular, the monitoring of annual recruitment strengths, will be of increasing importance in times of increasing uncertainty.

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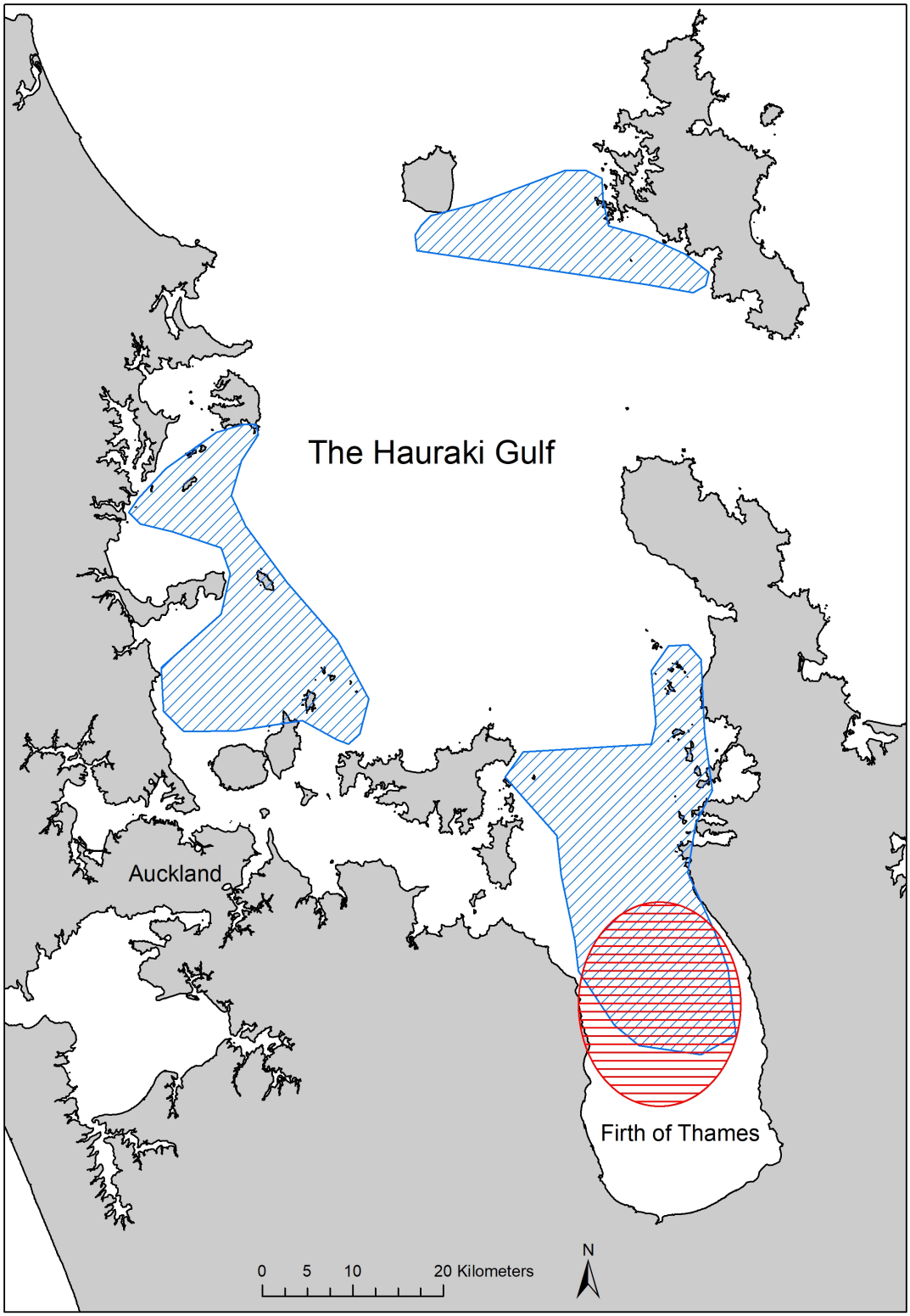
8. Appendix 1: Areas of snapper spawning and elevated pCO_2 in the Hauraki Gulf



Key:
Blue hatching – spawning areas derived from egg distribution (Zeldis & Francis 1998);
Red hatching - an area where elevated autumnal pCO_2 has been observed (Green & Zeldis 2015).

9. Appendix 2: Workshop on ocean acidification effects on snapper

Introduction and Methods

In December 2015 a workshop introducing the concept of ocean acidification effects on fish in the New Zealand context was held at the NIWA Auckland office. Attendees included: Mary Livingston (Ministry for Primary Industries), Phil Munday (James Cook University, Townsville, Australia), Cliff Law, Vonda Cummings, John Zeldis, Kim Currie, Jeremy McKenzie, Darren Parsons, Steve Pether, Alvin Setiawan (all NIWA). Phil Munday gave a presentation reviewing the known effects of acidification on larval fish, with a focus on the sensory and behavioural experiments conducted on larval tropical reef fish by his lab in Townsville. John Zeldis spoke about the time series of oceanographic data he and others have collected from the Firth of Thames. Cliff Law spoke about the large Ministry for Business, Innovation, and Employment funded CARIM (Coastal Acidification: Rates, Impacts and Management) project and the different aspects it will be addressing. Jeremy McKenzie spoke about different modelling approaches relevant to snapper and gave a demonstration of a snapper Bayes Net model. These presentations stimulated a number of discussions that were largely focused on addressing the ensuing years' objectives (the literature review, the experiments, and modelling these results). The day after the workshop Steve Pether and Alvin Setiawan showed Phil Munday and Darren Parsons around NIWA's Northland Marine Research Centre (where experiments were conducted in year 3) and specific issues relating to experimental design and logistics were discussed.

Outcomes from the workshop

Literature review (to be conducted in 2016/17 under specific objective two):

Phil Munday identified a number of primary literature publications relevant to the project and Vonda Cummings identified a risk assessment project she is managing as having potential synergies with the literature review. A highly relevant link between the current project and present-day conditions within the Firth of Thames (an important snapper spawning area) was established by John Zeldis. Nutrient loading within the firth has led to low oxygen and low pH conditions occurring every summer/autumn. This is now well documented in a report that Dr Zeldis has co-authored (Green & Zeldis 2015) and could provide a useful case study to set the context for how ocean acidification, and environmental degradation in general, may be influencing larval snapper.

Tank experiments (to be conducted in 2017/18 under Specific Objective three):

A strong emphasis was placed on holding our own snapper brood stock at Bream Bay rather than sourcing eggs from a sub-contractor. By doing this we would reduce the risk that the sub-contractor cannot supply eggs, the eggs would be immersed in experimental conditions sooner, the pH history and selection history of the brood stock would be known, the brood stock would be sourced from northeastern New Zealand rather than a potentially ecologically different stock, and we could ensure a larger number of potential parents to facilitate genetic analysis. Holding brood stock, however, has an additional cost associated, so this also needs to be taken into consideration.

A number of experimental setup and logistics issues were also discussed including the availability of control systems to be used to manipulate CO_2 levels, the need to increase the number of header tanks available to avoid pseudoreplication, the timing of when fish larvae will be sampled, behavioural analyses that could be performed, and the availability of CO_2 monitoring data from the CARIM project that could be used to set treatment levels. Following on from the relevance of the Firth of Thames spawning area as a case study, the importance of understanding how the low oxygen conditions present there affect snapper larvae was also raised. A potential way of addressing this was to have a combined low O_2 and high CO_2 treatment. The practicality and cost of such an experimental design still needs to be assessed.

Modelling (to be conducted in 2018/19 under Specific Objective Four):

Given the existing knowledge of ocean acidification experiments on larval fish, it is possible that our tank experiments will not yield any differences in direct mortality. Rather, the influence of acidification is likely to be observed through the sub-lethal modification of aspects such as larval fish behaviour or morphology. These sub-lethal effects may indeed lead to indirect mortality when real world factors, such as predator presence and food limitation, are present. Discussion at the workshop suggested that where these sub-lethal effects are identified from tank experiments and the literature review, we should conduct sensitivity analyses to assess the impact of acidification effects on snapper populations. Modelling approaches discussed included Management Strategy Evaluation and Bayes Net models.

Conclusions

Some of the main points raised at the workshop were: (1) the environmental degradation of the Firth of Thames could be a very relevant case study to set the context for this project, (2) for the experimental component of this project it may be worthwhile considering holding our own brood stock and including a low O_2 manipulation treatment, (3) the modelling component of this project could potentially be viewed as an assessment of the sensitivity of snapper populations to ocean acidification because it is likely to be very difficult to fix early life stage parameters based on tank experiments.

10. Appendix 3: Summary of literature describing the direct effects of elevated CO2 on fish [continued on next three pages]

Species	Common name	Response variable(s) assessed	Response type	Reference
Pomacentrus amboinensis and *Pseudochromis fuscus*	Ambon damselfish and brown dottyback	Escape response and predation success	Predation success lower when predator and prey on mismatched CO_2 treatments	Allan et al. 2013
Amphiprion melanopus	Cinnamon anemonefish	Escape response	Reduced ability	Allan et al. 2014
Menidia beryllina	Inland silverside	Survival and growth	Reduced	Baumann et al. 2011
Rachycentron canadum and Coryphaena hippurus	Cobia and Mahimahi	Otolith growth and growth	Increased otolith growth, decreased growth for cobia, no growth effect for mahimahi	Bignami et al. 2013
Rachycentron canadum and Coryphaena hippurus	Cobia	Growth, survival, otolith growth	No effect on growth or survival, otoliths larger	Bignami et al. 2013b
Thunnus albacares	Yellowfin tuna	Hatch time, growth and survival	Negative effects, but very high pCO_2 treatments	Bromhead et al. 2015
Paralichthys dentatus	Summer flounder	Hatching, growth, development, deformities, survival	Negative effects	Chambers et al. 2013
Atractoscion nobilis	White sea bass	Otolith growth	Increased	Checkley et al. 2013
Acanthochromis polyacanthus	Spiny damselfish	Visual ability	Reduced flicker frequency	Chung et al. 2014
Pseudochromis fuscus	Brown dottyback	Olfactory ability	Preference behaviour reversed	Cripps et al. 2011
Paragobiodon xanthosomus and Gobiodon histrio	Yellow-green goby and broad-barred goby	Olfactory ability	Preference behaviour lost	Devine & Munday 2013
Amphiprion percula	Orange clownfish	Odour choice	Reversal	Dixson et al. 2010
Pomacentrus wardi	Ward's damselfish	Cognitive ability	Reversed behavioural lateralisation bias	Domenici et al. 2014

Species	Common name	Response variable(s) assessed	Response type	Reference
Pomacentrus moluccensis, *P. amboinensis*, *P. nagasakiensis* and *P. chrysurus*	Lemon damselfish, Ambon damselfish, Nagasaki damselfish and Whitetail damselfish	Anti-predator response and boldness	Reduced anti-predator response and increased boldness, but to different degrees for each species	Ferrari et al. 2011a
Pomacentrus amboinensis	Damselfish	Cognitive ability	Reduced learning capacity	Ferrari et al. 2012a
Pomacentrus amboinensis	Damselfish	Visual ability	Reduced anti-predator response	Ferrari et al. 2012b
Gobiusculus flavescens	Two-spotted goby	Spawning production, hatching, phototaxis	No effect on spawning production, but reduced hatching success and negative effects on phototaxis	Forsgren et al. 2013
Clupea harengus	Atlantic herring	Hatch rate, growth, otolith growth, RNA:DNA	No effect except reduced RNA:DNA	Franke & Clemmesen 2011
Gadus morhua	Atlantic cod	Tissue damage, survival	Increased tissue damage but no survival effect	Frommel et al. 2012
Thunnus albacares	Yellowfin tuna	Organ damage, growth, survival	Negative effects	Frommel et al. 2016
Hippoglossus hippoglossus	Atlantic halibut	Metabolic rate and swimming performance	Positive	Grans et al. 2014
Sebastes diploproa	Californian rockfish	Anxiety	Increased	Hamilton et al. 2014
Theragra chalcogramma	Walleye pollock	Growth, condition, otolith growth	Largely no effect or in some instances an increase on growth/condition. Increase in otolith growth	Hurst et al. 2012
Gasterosteus aculeatus	Stickleback	Boldness	Decreased	Jutfelt et al. 2013
Pomacentrus amboinensis	Damselfish	Visual ability	Reduced anti-predator response	Lönnstedt et al. 2013
Gadus morhua	Atlantic cod	Otolith growth	Increased	Maneja et al. 2013

Species	Common name	Response variable(s) assessed	Response type	Reference
Pomacentrus amboinensis and *Pomacentrus moluccensis*	Ambon damselfish and lemon damselfish	Aggression	Increased for *Pomacentrus amboinensis* and decreased for *Pomacentrus moluccensis*	McCormick et al. 2013
Gadus morhua	Atlantic cod	Metabolic rate and swimming performance	No change	Melzner et al. 2009
Amphiprion melanopus	Cinnamon anemonefish	Metabolic rate, growth, survival	Combined effect of elevated temperature and pCO_2 increased metabolism, reduced growth and survival, but mediated by parental exposure	Miller et al. 2012
Amphiprion melanopus	Cinnamon anemonefish	Reproduction	Increased	Miller et al. 2013
Ostorhinchus doederleini and *Ostorhinchus cyanosoma*	Cardinalfish	Metabolic rate and survival	Negative effect on metabolic rate, no effect on survival	Munday et al. 2009a
Amphiprion percula	Orange clownfish	Odour choice/homing	Disruption	Munday et al. 2009c
Amphiprion percula	Orange clownfish	Growth and hatching success	Smaller yolks, but larger larvae, no difference in hatching success	Munday et al. 2009d
Pomacentrus wardi	Ward's damselfish	Boldness and predation mortality	Increased	Munday et al. 2010
Amphiprion percula	Orange clownfish	Otolith growth	Increased	Munday et al. 2011a
Acanthochromis polyacanthus	Spiny damselfish	Growth, survival, morphometry, otolith growth	No effect	Munday et al. 2011b
Pomacentrus wardi	Ward's damselfish	Olfactory ability, activity, boldness, predation	Reduced olfactory discrimination, increased activity, boldness and predation	Munday et al. 2012
Seriola lalandi	Yellowtail kingfish	Activity and escape response	No effect	Munday et al. 2015
Amphiprion percula and *Pomacentrus amboinensis*	Orange clownfish and Ambon damselfish	Escape response	Reduced ability	Munday et al. 2016

Species	Common name	Response variable(s) assessed	Response type	Reference
Menidia menidia	Atlantic silverside	Survival	Reduced, but mediated by parental exposure	Murray et al. 2014
Argyrosomus regius	Croaker	Hatching, growth, survival, activity	Largely negative (under combined temperature and pCO_2 treatment), although increased growth	Pimental et al. 2016
Sparus aurata	Gilthead seabream	Hatching, growth, survival, activity, deformities	Negative effects (under combined temperature and pCO2 treatment)	Pimental et al. 2016
Solea senegalensis	Senegalese sole	Hatching, growth, metabolic rate, deformities, survival	Negative effects	Pimentel et al. 2014b
Dicentrarchus labrax	Eurpoean sea bass	Metabolic rate	Negative	Pope et al. 2014
Lates calcarifer	Barrumundi	Auditory ability	Preference reversed	Rossi et al. 2015
Acanthochromis polyacanthus	Spiny damselfish	Metabolic rate	Positive	Rummer et al. 2013
Atherina presbyter	Sand smelt	Swimming ability and morphology	No effect on swimming ability, larger larvae in high CO_2 treatment	Silva et al. 2016
Amphiprion percula	Orange clownfish	Auditory ability	Preference reversed	Simpson et al. 2011
Gadus morhua	Atlantic cod	Survival	Decrease	Stiasny et al. 2016
Notothenia rossii	Marbled rockfish	Metabolic rate	Mo effect	Strobel et al. 2012
Syngnathus typhle	Broad-nosed pipefish	Reproduction	No effect on mating propensity	Sundin et al. 2013
Amphiprion percula and *Acanthochromis polyacanthus*	Orange clownfish and spiny damselfish	Reproduction	Reproductive output increased for orange clownfish, but decreased for spiny damselfish	Welch and Munday 2016
Acanthochromis polyacanthus	Spiny damselfish	Olfactory ability	Avoidance behaviour lost	Welch et al. 2014