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Exposure of an intertidal fish to simulated heatwaves and suspended sediment – a multistressor approach

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ABSTRACT

Extreme climatic events, such as marine heatwaves (MHW) and increased suspended sediment concentration (SSC), are increasing in frequency and intensity, resulting in sudden changes to coastal environments, especially intertidal zones. Intertidal animals experience conditions that substantially fluctuate over temporal and spatial scales and therefore require the ability to physiologically tolerate these fluctuations. Since multiple stressors often co-occur and natural populations tend to respond to local environmental fluctuations, we aimed to investigate individual and combined effects of MHW and increased suspended sedimentation in *Forsterygion lapillum* from two neighbouring coastal areas with distinct water temperatures and wave current regimes by assessing fish oxygen consumption rate, mortality and weight loss. Results showed that in both *F. lapillum* populations, oxygen consumption rate and survival probability were unaffected by any treatment. However, fish from both populations lost weight during heatwave and multistressor treatments (i.e. heatwave and sedimentation), while fish from the sedimentation treatment alone did not lose weight. Although a direct effect on fish respiration was not found, our results indicate that *F. lapillum* performance is reduced when exposed to heatwaves individually and in combination with increased sediment suspension. Weight loss indicates that fish experiencing these stressors were unable to meet their metabolic demands.

1. Introduction

Climate change is recognized as one of the most imminent global-scale threat to marine ecosystems (Hoegh-Guldberg and Bruno, 2010; Tittensor et al., 2021). Extreme weather and climatic events such as wind gusts, strong currents and heatwaves are expected to increase in frequency and magnitude, causing sudden changes to coastal environments (Guo et al., 2022; IPCC et al., 2023). Some of the changes to coastal environments include marine heatwaves (MHWs) and increased suspended sediment concentration (SSC) (Schiedek et al., 2007; Roberts, 2012; Zhou et al., 2017). MHWs are defined as prolonged extreme sea surface temperature (SST) exceeding the 90th-percentile temperature for at least five consecutive days (Hobday et al., 2016; Frölicher et al., 2018; Oliver et al. 2018, 2019). MHWs frequency has increased by 54 % globally over the past century and it is predicted to continue to increase not only in frequency but also in duration and intensity (Rahmstorf and Coumou, 2011; Schlegel et al., 2017; Fro;licher et al., 2018). Similarly, SSCs have become more frequent due to the combination of natural processes (i.e. waves and tides) and anthropogenic actions (i.e. vessel movement), which increases the vulnerability of sediments to being re-suspended by larger and repeated processes, possibly allowing for resuspended sediments to linger in the water column for longer (Schoellhamer, 1996; Roberts et al. 2012; Gabel et al., 2017).

Nearshore ecosystems, such as intertidal zones, are more at risk than those in the open ocean, since they are more affected by the intensity of wave actions and show highly variable temperatures (Fabiano et al., 2001; Stillman et al., 2025). Given the highly dynamic nature of shallow intertidal zones, where physical conditions can shift rapidly, MHWs and increases in SSC are likely to cause significant impacts on these environments (Gunderson et al., 2016; Blewett et al., 2022; Cook et al., 2022), resulting in greater susceptibility to biological impacts (Schlegel et al., 2017; Pietri et al., 2021). As a consequence, organisms living in the intertidal zone are better adapted to fluctuating environments and tend to exhibit phenotypic plasticity, adjusting their behavioural or

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physiological responses in response to environmental fluctuations (Barshis et al., 2011; Khan et al., 2014; McArley et al., 2018; Ziegler et al., 2023; Stillman et al., 2025). Hence, organisms of the intertidal zone, especially fish, have been used as models to assess responses to extreme events such as increases in temperature (Vinagre et al., 2018; Madeira et al., 2020; Willis et al., 2021; Paul et al., 2021) and increased sedimentation (Harris et al., 2016; Hess et al., 2017).

The effects of MHWs on fish are still being evaluated but are known to include changes in: food intake (Lowe et al., 2015; Hess et al., 2017), basic metabolism (Vinagre et al. 2005, 2018; Madeira et al., 2020; Almeida et al., 2022), and growth and weight (Wade et al., 2019; Barbeaux et al., 2020). Comparatively, suspended sediment can have knock-on consequences on intertidal fish, since it interferes with visual acuity through increased turbidity and light attenuation in the water column (Lowe et al., 2015; Hess et al., 2017; Wenger et al., 2017), which can lead to a reduced foraging efficiency and prey capture (Morrison et al., 2009; Lowe et al., 2015; Hess et al., 2017). Nonetheless, fish physiological processes may be impacted by the combination of increased temperature and sedimentation, which could lead to an increase in metabolic rate and compromise fish performance (Rosewarne et al., 2016; Hess et al., 2017; McArley et al., 2017).

While identifying the relative impact of individual stressors is of extreme importance, it might not be realistic for intertidal habitats, since multiple stressors often co-occur (Gunderson et al., 2016; Rogers-Bennett and Catton, 2019). Little is known about how marine fish will respond to combined stressors (Burleson et al. 2011; McBryan et al., 2013; Breitburg et al., 2018) and given that species respond physiologically and behaviorally to the characteristics of their local environment (Demello and Phillips, 2011; Glockner-Fagetti and Phillips, 2020), it is crucial to assess responses of natural populations in face of rapid climate change (Pecl et al., 2014; Camp et al., 2018).

The common triplefin, *Forsterygion lapillum* Hardy 1989 (Family: Tripterygiidae), is an endemic and abundant intertidal temperate fish found throughout New Zealand (McDermott and Shima, 2006). It inhabits a wide range of habitats, from sheltered harbors to exposed rocky reefs, and can withstand extreme high-temperature events (Caiger et al., 2021; McArley et al., 2018). This species is therefore a suitable model for studying thermal responses and the combined effects of multiple

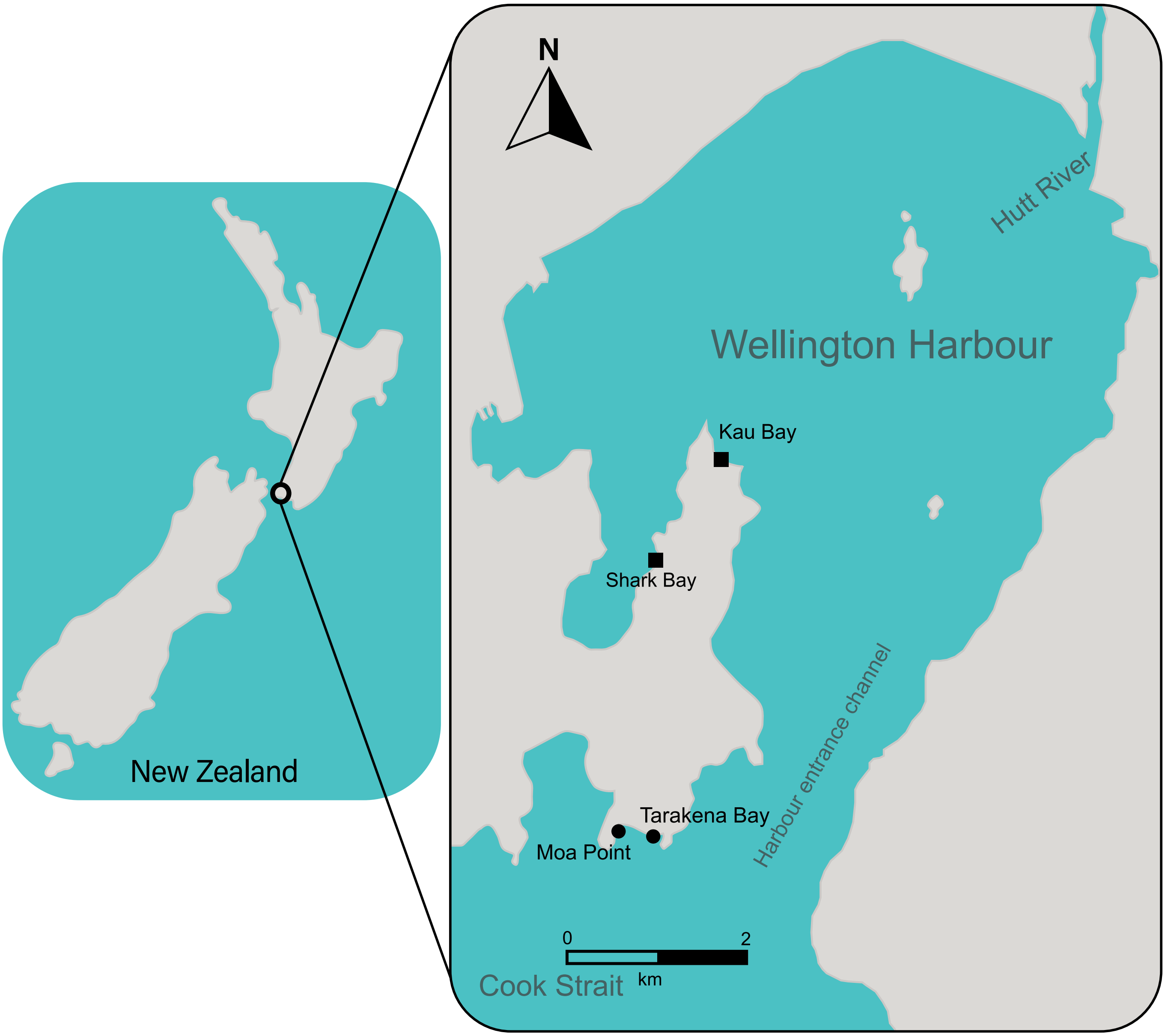

Fig. 1. Map showing sampling locations for each area. Wellington Harbour sites are marked with squares and Wellington South Coast sites marked with a full circle.

stressors. However, until now, no studies have assessed combined effects of heatwaves and increased sedimentation for *F. lapillum* physiology and survival. In this study we quantified oxygen consumption, mortality and weight change in response to individual *and* combined effects of a mimicked heatwave and increased sedimentation in *F. lapillum* from two neighbouring coastal areas.

2. Methods

2.1. Fish collection and maintenance

Forsterygion lapillum were collected using hand nets while snorkelling at about 1.5 m depth from rocky intertidal habitats, Shark Bay (41°18′7.46″S, 174°49′3.05″E) and Kau Bay (41°17′16.1″S, 174°49′48.8″E) in the Wellington Harbour during December 2023 and Tarakena Bay (41°20′38.6″S, 174°49′8.5″E) and Moa Point (41°20′26.6″S, 174°48′38.6″E) on the Wellington South Coast during March 2024 (Fig. 1).

The Wellington Harbour is partially isolated from oceanic waters, with an average depth of 20 m and experiences monthly mean temperatures ranging between 10.5 °C and 19.3 °C (Supplementary Material Fig. S1, Booth, 1975). The Wellington South Coast, located within the Cook Strait, is a highly exposed coastal environment characterized by large swells from southerly winds and high sedimentation, with monthly mean temperatures ranging between 10.9 °C and 17.6 °C (Supplementary Material Fig. S1, Glockner-Fagetti and Phillips, 2020). Only adult fish were used for both experiments. Average weight and length of fish collected were 1.10 ± 0.31 g and 4.36 ± 0.37 cm respectively for Harbour fish, and 2.18 ± 0.38 g and 5.55 ± 0.48 cm for South Coast fish, based on *F. lapillum* minimum adult size (Mensink and Shima, 2015).

After collection, fish (n = 48 per area) were transported to the Victoria University of Wellington Coastal Ecology Laboratory (VUCEL) in aerated cylindrical tanks containing water collected from the corresponding study sites and left to acclimate in a 100 L experimental tank. Fish were fed daily with frozen mysis shrimp (AquaOne). To allow fish acclimation in laboratory conditions, temperature was maintained at 15.8 ± 0.3 °C for fish from the Harbour and at 14.7 ± 0.3 °C for fish from the South Coast for at least seven days (Fig. 2), corresponding to the temperature conditions at the sampling site at the time of collection. After acclimation, fish were tagged using the tattoo method for visual reading and individual weight loss assessment, which consisted of injecting nanolitre quantities (~100 nL) of different Visible Implant Elastomer (VIE; Northwest Marine Technology) into the dorsal muscle using ultrafine syringes with an integrated needle (0.33 mm × 12.7 mm) (Shima et al., 2012). Thereafter, fish were randomly assigned to 20 L cylindrical tanks at an approximate density of 0.4 kg/m^3 per tank prior to starting the experimental conditions.

2.2. Experimental conditions

Fish were assigned to one of four treatments (4 fish per tank, n = 12 per treatment) and each treatment was replicated three times: (a) control temperature (same as acclimation) with no added sediments (b) increased temperature with no added sediments (c) control temperature with added sediment (d) increased temperature and added sediment (i.e. multistressor treatment) (Vieira et al., 2013; Lowe et al., 2015) (Supplementary Material Fig. S3).

Water temperature was controlled by an aquarium controller system (Apex Classic, Neptune Systems), connected to aquarium heaters (220–240 V, Eheims) and two chillers (HC-500A, Hailea) in water baths for each of the four treatments that held the three replicate cylindrical tanks, with a natural photoperiod of 11 h of light/13 h of darkness (Supplementary Material Fig. S3). Water temperature was also checked by a YSI Pro30 probe 3 times a day every day. After seven days of acclimation, water temperature was gradually increased at an average rate of 0.6 °C per day (modified from Strano et al., 2022), reaching the maximum temperature of 22.5 °C after 13 days for Harbour fish and 20.3 °C after 15 days for South Coast fish (Fig. 2).

To simulate a heatwave comparable to what is observed in real environments around the Wellington region, the experimental conditions were based on temperature anomalies and mean duration of MHW calculated for the greater Wellington region. Bunting et al., (2024) found that the mean duration of MHWs between 1982 and 2023 was 16 days, with a mean intensity of 1.27 °C, as well as an average of 3.2 MHW events per year. For the experiment with fish from the Wellington Harbour, a MHW was simulated according to the mean duration (16 days) and exceeded the mean intensity, at 6.5 °C higher than the mean environment temperature found in the month of collection (16 °C). For the experiment with fish from the Wellington South Coast, a MHW was simulated with a duration of 14 days and the mean intensity found in the real environment at an intensity of 5.5 °C higher than the mean environment temperature found in the month of collection (14.8 °C). The intensity of simulated MHWs reached temperatures that have not yet occurred in these coastal areas (22.5 °C for the Wellington Harbour and 20.3 °C for the Wellington South Coast), however, as showed by Behrens et al., (2022), these are plausible under the SSP 7.0 scenario predicted for 2080–2099. After the thermal maximum was reached, temperature was decreased at a 1 °C daily rate (based on Cook et al., 2022) for 6 days until all treatments were back to acclimation temperature.

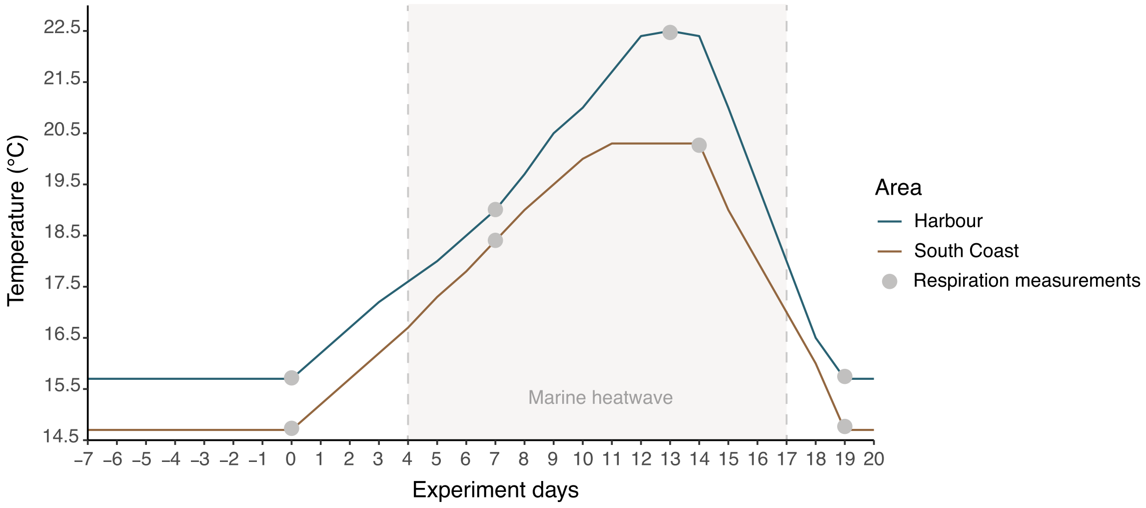

Fig. 2. Model of thermal conditions during each experiment. Dots represent time-points at which respiration measurements were performed.

The procedure for sediment input and resuspension was performed differently for each experiment. For the experiment with fish from the Wellington Harbour, sediments were kept suspended in an external round 100 L header tank by circulating the water with 2 pumps (Aquapro AP1050 Waterfeature/Pond, Max Flow 1400 L/h) with the help of a belt feeder (Belt Feeder Standard 24 h, FIAP) that delivered ~10 g sediment to the tank every hour for 24 h. For the experiment with fish from the Wellington South Coast, sediments were kept suspended in an external round 100 L header tank by circulating the water with 2 pumps (Aquapro AP1050 Waterfeature/Pond, Max Flow 1400 L/h), where 30g of sediment was manually delivered twice a day and sediment was manually resuspended every hour from 9 a.m. until 5 p.m. For both experiments, sedimented sea-water was then delivered from the header tank into tipping scoops that were positioned above each individual experimental sedimentation treatment via adjustable flow nozzles. The scoops were built with small weights attached slightly backwards of their geometric centre of gravity so that they were able to tip when full and then return to an upright position (modified from Lowe et al., 2015).

Since it is unlikely that the same amount of g/L of sediment will be transferred from the header tank into each individual buckets, turbidity in nephelometric turbidity unit (NTU) was used as a measure of suspended sediment (Kitchener et al., 2017; Bright et al., 2018). To accurately measure how much sediment was suspended in each individual bucket, turbidity was measured daily in each treatment with a *RBRconcerto*^{3} CTD equipped with a turbidity sensor. The turbidity levels in the control group for both experiments were maintained at < 5 NTU. The turbidity level for the experiment with fish from the Harbour peaked at ~180 NTU at the moment of sediment input, dropping in the first 3 h and subsequently maintained at ~20 NTU until the following sediment disposal. The turbidity level for the experiment with fish from the South Coast peaked at ~120 NTU at the moment of sediment input, dropping in the first 3 h, with hourly peaks at 20–45 NTU and lowest level found of ~8 NTU until the following sediment disposal (Fig. 3).

Kaolin clay (Northland, New Zealand), with a small particle size range (25–35 μm) was used for sedimentation treatments. This was chosen because it is chemically inert and hence does not add confounding effects to our study of chemicals or particles in natural sediment that could be variable, and could affect fish respiration (Yahaya et al., 2017). The selected suspended sediment concentrations and turbidity levels were based on average maximum turbidity values typically observed in Wellington bays during natural resuspension events (e.g., waves and currents), which peak between 70 and 200 NTU in both areas (Supplementary Material Fig. S2). The length of exposure at a higher turbidity (>18 NTU) in the experiment with fish from the Wellington Harbour was exacerbated, given that it is a partially closed embayment with constant small boat and ferry traffic and discharges from the Hutt river (Booth, 1975), which can corroborate with sediment staying suspended for longer. In contrast, for the experiment with fish from the Wellington South Coast, sediment was resuspended periodically simulating regular resuspension driven by tides, wind, gusts and currents forcing on circulation (Walters et al., 2010). Following the completion of both experiments, all fish that survived were released back at their original sites.

2.3. Oxygen consumption

Oxygen consumption (MO_2) of individuals and routine metabolic rate (RMR) (n = 12 per treatment) was determined at different time-points during each experiment (refer back to Fig. 1) using intermittent-flow respirometry in two subsequent rounds of measurements (Steffensen et al., 1984; Chabot et al., 2016; Svendsen et al., 2016). Seven custom-built respirometry chambers (152 mL volume) were maintained in a thermally controlled water bath, with temperatures and turbidity corresponding to experimental conditions (Strano et al., 2022) (Fig. 4A and B).

Fish were fasted for at least 14 h prior to measurements and were subsequently placed into a respirometry chamber, where they were left to acclimate for 20 min in the dark (which was a sufficient period to acclimate fish in the respirometry chambers according to preliminary trials, Supplementary Material Tables S1–S2). In open-flow states, flush pumps supplied each chamber with aerated, UV-filtered seawater from the surrounding water bath every 15 min for 5 min, thus preventing oxygen levels from falling below 90 % air saturation. In closed states, the mixing of water inside each chamber occurred only by fish movement and oxygen concentration (mg O_2 kg^{-1} h^{-1}) inside the chambers was measured every 5 min using a Fibox 4 oxygen probe for a total of 1-h periods per fish. To record possible bacterial respiration in seawater, one empty chamber used as a blank measurement was included for each trial (Hess et al., 2017; Strano et al., 2022). MO_{2raw} (mg O_2 kg^{-1} h^{-1}) was calculated using the following equation (Grimmelpont et al., 2023):

$$MO_{2raw} = \left[\left(\frac{\Delta[O_2]}{\Delta t}\right) - \left(\frac{\Delta[O_2]_{bact}}{\Delta t}\right)\right] \times \frac{V_{resp}}{m} \tag{A}$$

where $\Delta[O_2]/\Delta t$ (mg O_2 L^{-1} h$-^1$) is the oxygen concentration decrease in the respirometer over time during each MO_2 measurement period and $\Delta[O_2]_{bact}/\Delta t$ (mg O_2 L^{-1} h$-^1$) is the oxygen concentration decrease in the blank respirometer. Slopes were obtained through a linear regression and only slopes with a regression coefficient above 0.95 were considered for further data analysis. V_{resp} is the respirometry chamber water volume (0.152 L) minus the volume of the fish (considered equivalent to their weight in kg), and m (kg) is the fish body mass.

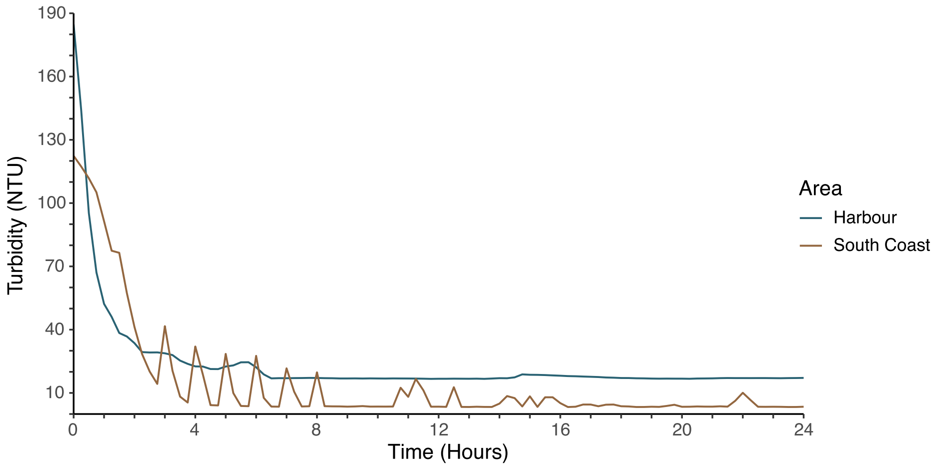

Fig. 3. Line plot of measured turbidity during both experiments period. Turbidity variation is displayed over a 24 h period for treatments with added sediment.

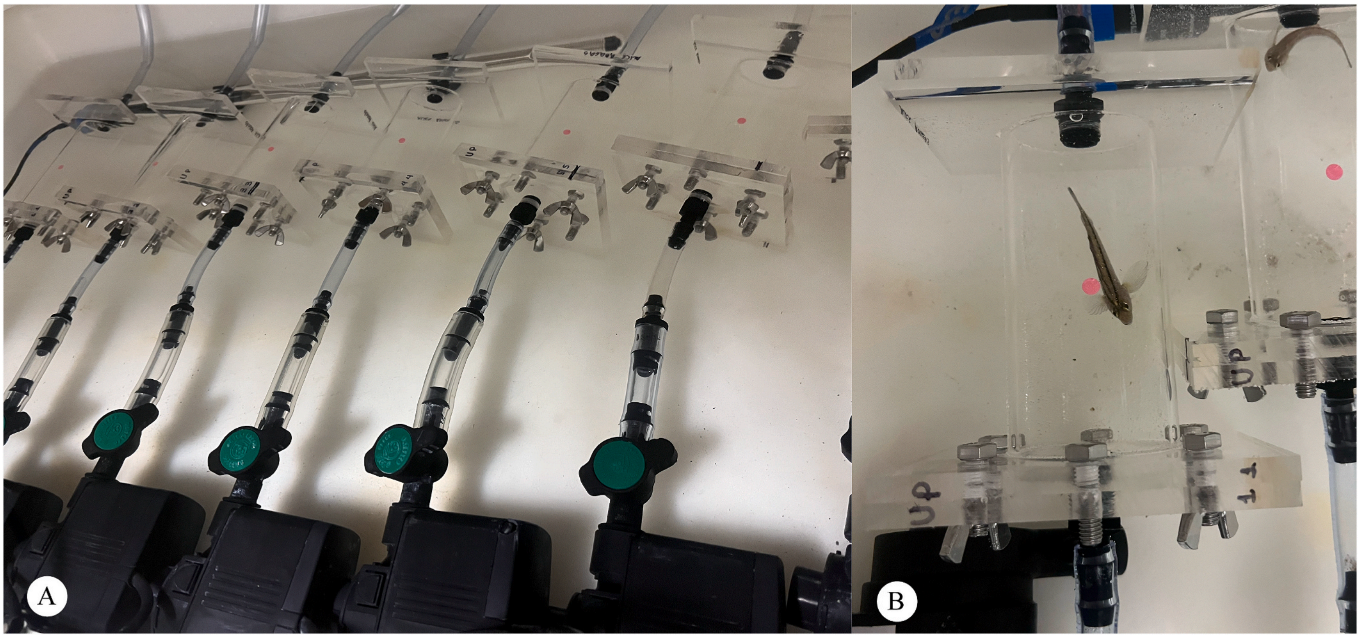

Fig. 4. Photos of the experimental set up of intermittent-flow respirometry chambers during O_2 measurement days. (A) Photo of the water bath with all respirometry chambers. (B) Close-up photo of one of the respirometry chambers used during the experiment.

Since fish respiration is nearly proportional to fish body mass, an allometric correction was done to assess MO_2 for a 1 g standard fish:

$$MO_2 = MO_{2raw} \times \left(\frac{m}{m_{corr}}\right)^{1-A} \tag{B}$$

where MO_{2raw} (mg O_2 kg^{-1} h^{-1}) is the calculated oxygen consumption with Eq. (A), for a fish with mass m (kg) and A is the allometric exponent of 0.89, an universal scaling relationship for fish and metabolic rate suggested by Jerde et al., (2019), resulting in MO_2 (mg O_2 kg^{-1} h^{-1}) as the oxygen consumption for a fish with a standard mass, mcorr = 0.001 kg.

F. lapillum from both areas were weighed (wet) on day 0 (initial weight) and again immediately after the experiments ended (final weight) using a high precision scale (Mettler AJ150). To assess weight loss during the experimental period, the final weight of each fish was subtracted from its initial weight.

To calculate *F. lapillum* survival probability, fish mortality was assessed throughout the experiment period as the number of deceased individuals per day for both experiments.

2.4. Statistical analysis

All statistical analysis were performed in R version 4.4.1, 2024, The R Foundation for Statistical Computing (R Core Team, 2024). Significant changes in fish oxygen consumption were estimated by linear mixed models using the *lme4* package (Bates et al., 2015), using time and treatment as fixed factors and experimental buckets and fish ID as a random factor. Thereafter, the effects of fixed factors were tested using ANOVA and the effects of random factors were tested with RANOVA from the *lmerTest* package (Kuznetsova et al., 2017). For significant results, a post hoc pairwise test was performed with the *emmeans* package, using the Tukey method (Lenth, 2024). To test differences in mortality for both experiments, a Kaplan-Meier analysis was performed to calculate the probability of fish survival between different treatments, with p-values calculated using the *survival* package (Therneau, 2021). Fish initial *vs.* final weight were compared using a repeated measures ANOVA from the *rstatix* package (Kassambara, 2023).

3. Results

3.1. Harbour experiment

Oxygen consumption rate for *F. lapillum* from the harbour experiment changed significantly over the course of the experiment (i. e. individual effect of days) ($F_{(0.116)} = 7.33$, $p = 0.00017$), but no significant effect between treatments over time was found (i. e. interaction between the time and treatment variables) (Fig. 5, Supplementary Material Table S3). When comparing the initial and final weight of fish during this 19-day long experiment, individuals in the control group ($F_{(0.004)} = 47.84$, $p = <0.0001$), in the multiple stressor treatment ($F_{(0.004)} = 68.88$, $p = <0.0001$) and in the individual heatwave treatment ($F_{(0.004)} = 36.35$, $p = 0.002$) significantly lost weight (Fig. 6).

A total of 11 fish died during the course of this experiment. In the heatwave treatment, 1 fish died on day 11 during temperature increase, 3 fish died on day 15 at the maximum temperature and 1 fish died on day 19. In the multiple stressors treatment, 1 fish died on day 15 and 1 fish died on day 19. In the sedimentation treatment, 2 fish died on day 7 and 1 fish died on day 15. In the control group, 1 fish died on day 7 and 1 fish died on day 15. Despite the fact that more deaths were observed in heatwave treatments, the Kaplan-Meier analyses showed that the probability of fish survival did not significantly change in response to the treatments (Fig. 7).

3.2. South coast experiment

Oxygen consumption rate change over time was significantly different between treatments ($F_{(0.363)} = 4.360$, $p < 0.0001$) for *F. lapillum* from the south coast (Fig. 8). Pairwise comparisons between treatments showed significant differences in fish MO_2 on day 0 between the control group and the sedimentation treatment ($p = 0.001$) and between the multiple stressor treatment and sedimentation treatment ($p = 0.009$), with the highest MO_2 rate found in the control group. On days 7 and 15, no significant differences were found over time between treatments. On day 19, when temperature was decreased back to acclimating temperature, MO_2 rate was different between the control group and the multiple stressor treatment ($p = 0.0034$), the heatwave treatment and sedimentation treatment ($p = 0.0001$) and the multiple

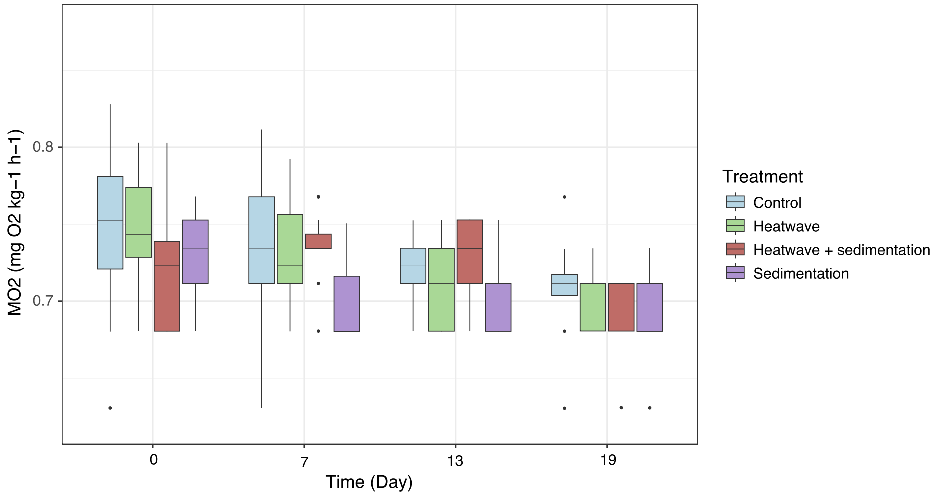

Fig. 5. Box plots representing changes in *F. lapillum* from the Wellington Harbour oxygen consumption rate in different treatments and at different time-points during the experiment. The mean temperature ±SD in temperature conditions for each day were: day 0, 15.8 ± 0.3 °C; day 7, 19.3 ± 0.3 °C; day 13, 22.5 ± 0.1 °C; day 19, 15.8 ± 0.3 °C.

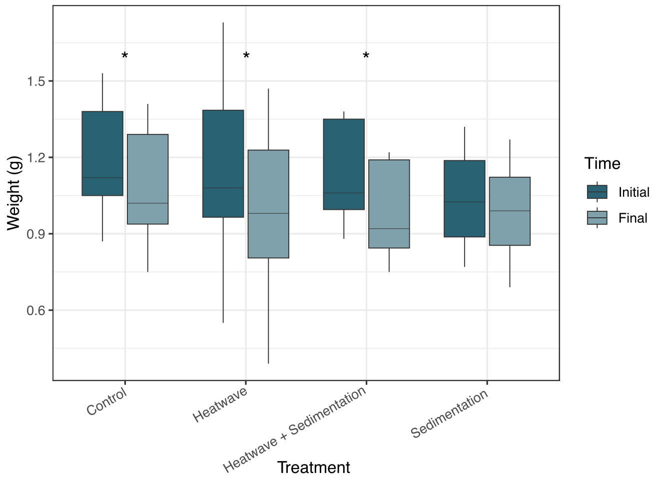

Fig. 6. A comparison across treatments of the average fish weight. Boxplots display initial and final weight for fish from the Wellington Harbour over the course of the experiment. Asterisks indicate significant differences between initial and final weight ($p < 0.05$).

stressor treatment and the sedimentation treatment ($p = 0.004$), with the highest MO_2 rate found in the sedimentation treatment. Variations in MO_2 rate at each treatment were also observed over the course of the experiment. The control group showed higher respiration rate on day 0 in comparison to days 7 ($p = 0.036$), 15 ($p = 0.049$) and 19 ($p = 0.003$). The heatwave treatment showed decreased respiration rate on day 19 in comparison to days 0 ($p = 0.005$), 7 ($p = 0.003$) and 15 ($p = 0.0012$). The multiple stressor treatment showed higher respiration rate on day 0 in comparison to day 7 ($p = 0.0021$) and 19 ($p = <0.0001$) and lower respiration rate on day 19 in comparison to day 7 ($p = 0.012$) and 15 ($p = 0.0002$). The sedimentation treatment showed increased respiration rate on day 19 in comparison to day 0 ($p = 0.03$) (Supplementary Material Table S4).

Fish were found to have lost weight when comparing final and initial weight in fish from the heatwave ($F_{(0.004)} = 84.01$, $p < 0.0001$) and multiple stressors treatment ($F_{(0.004)} = 18.52$, $p < 0.001$) (Fig. 9).

Fish mortality was also observed over the course of this experiment, where 2 fish died, 1 in the heatwave treatment and 1 in the sedimentation treatment, both on day 7. The Kaplan-Meier analyses showed that the probability of fish survival did not significantly change in between treatments (Fig. 10).

4. Discussion

Intertidal fish are typically well adapted to fluctuating environments and often exhibit phenotypic plasticity, adjusting their physiological and behavioural responses to local conditions (Khan et al., 2014; Ziegler et al., 2023; Stillman et al., 2025). Similarly, although both assessed populations of *F. lapillum* showed weight loss under the multistressor and heatwave treatments, their MO_2 and survival probability was unaffected by these stressors, suggesting that the observed responses are more closely linked to local environmental variability.

This study shows that *F. lapillum* from the Wellington Harbour did not increase their MO_2 when exposed to the simulated marine heatwave even in combination with increased suspended sediment concentration, while *F. lapillum* from the Wellington South Coast only had a higher MO_2 at the start of the experiment for all treatments. The initial high values of MO_2 for all treatments in fish from the Wellington South Coast can be attributed to a possible chronic stress of being moved from the experimental tanks into the respirometer chambers for the first time, given that when there is a threat of change in housing condition some animals experience physiological adjustments (e.g. increased respiration rate) to the perceived threat (Morgan and Tromborg, 2007; Resende et al., 2022). Furthermore, we acknowledge that it would have been beneficial for fish to have had a longer acclimation time in the respirometry chambers before the first MO_2 measurement (Chabot et al., 2016; Killen et al., 2021).

MO_2 estimates for *F. lapillum* in the present study are comparable to those of different *F. lapillum* populations found in other studies (Khan et al. 2012; Khan et al., 2014; McArley et al., 2017; McArley et al., 2018). When assessing *F. lapillum* physiological performance (i.e. respiration) and thermal preference at different acclimating temperatures (15–21 °C), Khan et al. 2012 have found that fish exhibited similar oxygen consumption rates at all assessed temperatures and preferred temperatures around ~21 °C regardless of the acclimating temperature. Comparatively, in a thermal ramping study with *F. lapillum*, McArley et al., (2018) found that fish did not significantly change their oxygen consumption in temperature increases from 21 to 24 °C in normoxia, only showing an increase in MO_2 from 26 °C in the same condition. In a study to assess triplefins energy demands under thermal stress, Willis et al., (2021) found that although *F. lapillum* had an increase in respiratory capacity, less of the consumed oxygen was directed towards ATP production, meaning that fish might present a reduced performance

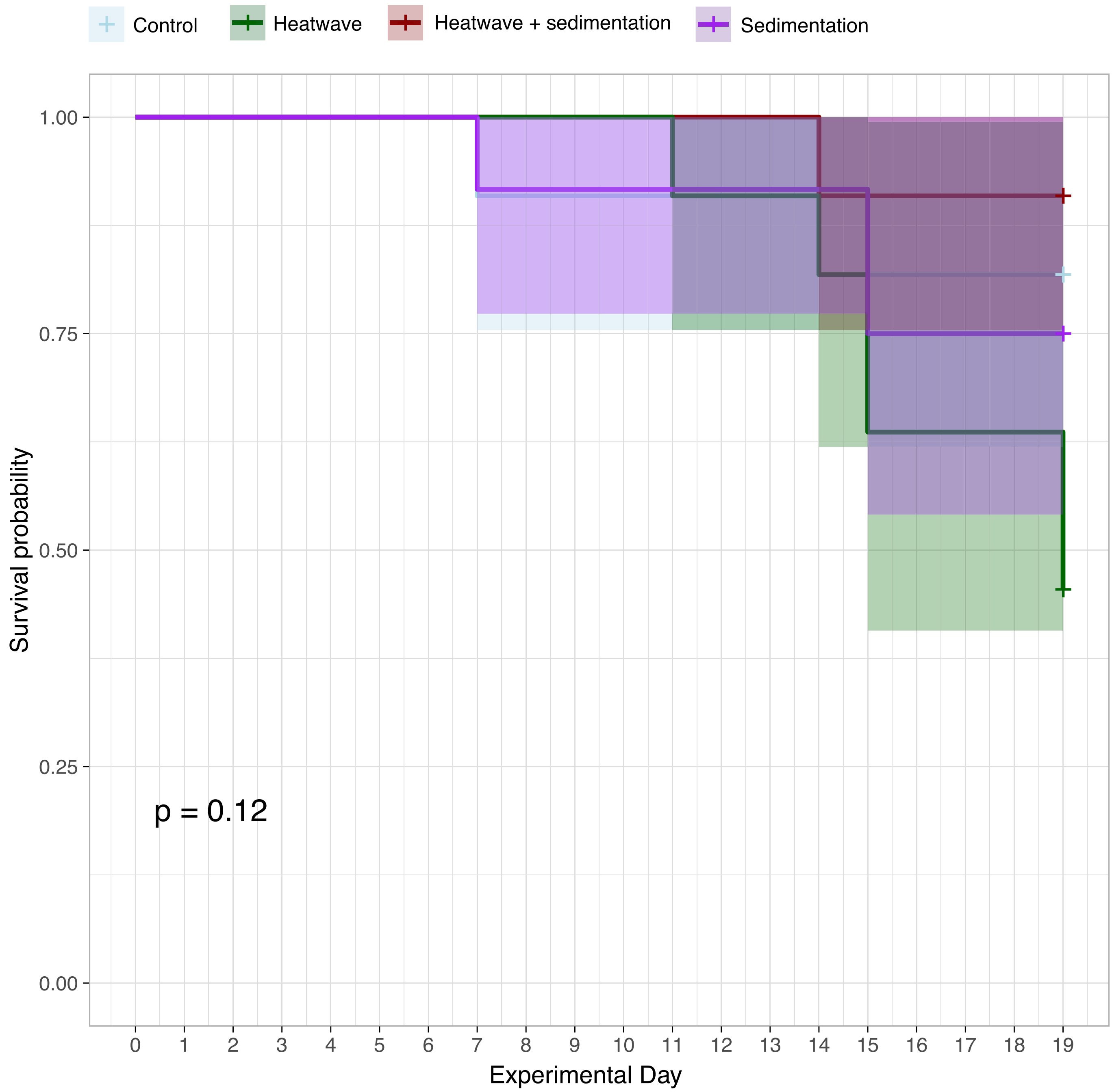

Fig. 7. Kaplan-Meier curves for fish survival at different time-points in each experimental condition. The mean temperature ±SD in temperature conditions for each day were: day 0, 15.8 ± 0.3 °C; day 7, 19.3 ± 0.3 °C; day 13, 22.5 ± 0.1 °C; day 19, 15.8 ± 0.3 °C.

under thermal stress. Since in other studies *F. lapillum* presented only a slight increases in oxygen consumption and reduced ATP production when facing increases in temperature (McArley et al., 2018; Willis et al., 2021) along with significant mortality found at 25 °C (Khan et al., 2014), we suggest that *F. lapillum* lack of increase in MO_2 as temperature increases in this study can result in a loss in performance or death, given that *F. lapillum* are already close to their upper thermal range and increases in oxygen consumption could help mitigate the constraints of energetic processes (Clark et al., 2013; McArley et al., 2017).

Both assessed *F. lapillum* populations in the present study did not change their MO_2 when exposed to increased sedimentation. Increased suspended sediment concentration can limit oxygen delivery to tissues by reducing the gills capacity for oxygen uptake, which has been observed in some fish species under different sediment concentrations (Lowe et al., 2015; Hess et al., 2017). Conversely, like *F. lapillum*, some fish species show no significant increase in MO_2 as sedimentation concentration increases (e.g. Cumming and Herbert, 2016; Firth et al., 2024), which could be explained by either: (i) the fish energy demand does not change in face of increased sedimentation (Elliott, 1976; Cumming and Herbert, 2016; Hess et al., 2017; Firth et al., 2024) or (ii) a range of physiological adjustments occur to compensate for the maintained oxygen consumption and avoid a reduction in oxygen transference (Gold et al., 2015; Cumming and Herbert, 2016).

The combined effects of temperature and increased sedimentation have been found to either have positive (e.g. Pasparakis et al., 2023) or negative effect (e. g. Allibhai et al., 2023) on fish. In the present study, although *F. lapillum* did not change their MO_2 when subjected to multistressors (i.e. heatwave and increased sedimentation), fish from both

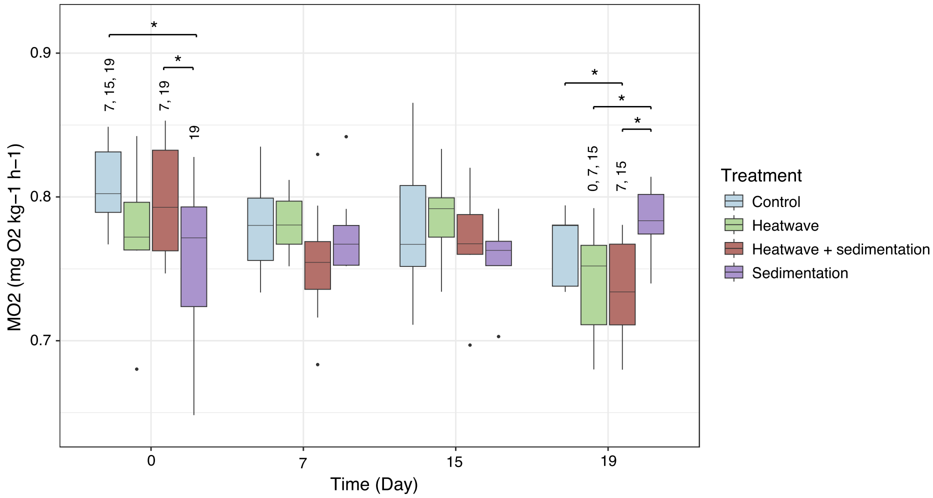

Fig. 8. Box plots representing changes in *F. lapillum* from the Wellington South Coast oxygen consumption rate in different treatments and at different time-points during the experiment. The mean temperature ±SD in temperature conditions for each day were: day 0, 14.7 ± 0.3 °C; day 7, 18.0 ± 0.3 °C; day 15, 20.3 ± 0.1 °C; day 19, 14.7 ± 0.3 °C. Asterisks indicate significant differences between treatments for that specific measurement day ($p < 0.05$). Numbers above the bars indicate significant differences between measurement days within the same treatment.

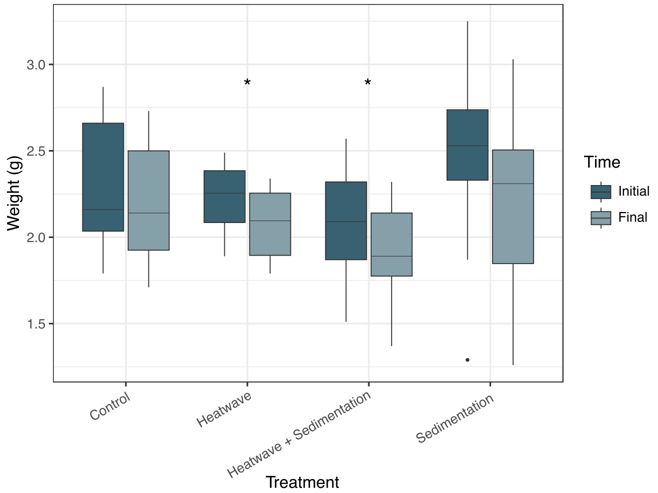

Fig. 9. A comparison across treatments of the average fish weight. Boxplots display initial and final weight for fish from the Wellington South Coast over the course of the experiment. Asterisks indicate significant differences between initial and final weight ($p < 0.05$).

the Wellington Harbour and Wellington South Coast exhibited weight loss in the heatwave and multistressor treatment, indicating that there can be a negative effect of these stressors on *F. lapillum* (Gunderson et al., 2016). The weight loss observed in the control group for the Wellington Harbour fish may be attributed to stress caused by the ambient temperature being the highest for summer during this trial and/or the stress of confinement and handling (Lowe et al., 2015). Additionally, because intertidal fish often exhibit local adaptations to the temperature conditions of their habitats (Stillman et al., 2025), it was expected that *F. lapillum* from the Wellington Harbour would be acclimatized to higher temperatures. However, this was not observed in the present study. For less active benthic fish, like *F. lapillum*, the oxygen capacity might have evolved to accommodate metabolic requirements during digestion rather than continuous swimming (Clark et al., 2013; Fu et al., 2022) and the relevance of increasing oxygen consumption would be to reduce digestion time in order for fish to strike again when new prey items appear. In this study, since *F. lapillum* from both populations did not increase their MO_2 but lost weight in the heatwave and the multistressor treatment, we suggest that the lack of metabolic adjustment in face of these physical stressors might have impacted fish predation or digestion, resulting in weight loss.

Although some *F. lapillum* died over the course of both experiments of this study, mortality does not seem to be related to the treatment fish were in, given that fish died both in the control and the experimental treatments. Nonetheless, more deaths were observed in the experiment with fish from the Wellington Harbour then in the experiment with fish from the Wellington South Coast. As a cautionary note, we acknowledge that the experiment set up for Harbour fish and South Coast fish were different, therefore, the discussion below is taking into consideration *F. lapillum* probability of survival in regard to changes in housing and environmental conditions in general. When studying *F. lapillum* larvae quality and development in both the Wellington Harbour and the Wellington South Coast, Shima and Swearer 2009 found that larvae developing in the Wellington Harbor appeared to be of higher quality. However, since in this study adult *F. lapillum* from the Wellington South Coast exhibited a higher survival rate, we suggest that ontogeny and acclimatization responses to the highly dynamic system that is the Wellington South Coast might shape the survival of these fish when facing changes in environmental conditions (Komoroske et al., 2014; Barbeaux and Hollowed, 2018). Similarly, distinctive patterns of behaviour and recruitment have been previously recognized between these two areas in other organisms, which were found to be related to differences in water flow patterns and food availability (Helson and Gardner, 2004; Demello and Phillips, 2011; Glockner-Fagetti and Phillips, 2020).

5. Conclusion

Overall, our results indicate that even though the individual and combined effects of heatwaves and increased sediment concentration did not directly affect *F. lapillum* physiology, increases in temperature alone and in combination with increased sedimentation can still have a negative impact on fish performance and well-being, as seen by fish weight loss in heatwave and multistressor treatments. In addition, *F. lapillum* in this study were not affected by increased sediment concentration alone. Nonetheless, extreme thermal events are becoming more frequent and intense (Frölicher et al., 2018) and will greatly impact intertidal species behaviour and survival. The present study is the first to assess the sedimentation effects and combined effects of sedimentation and temperature on *F. lapillum* physiology and survival,

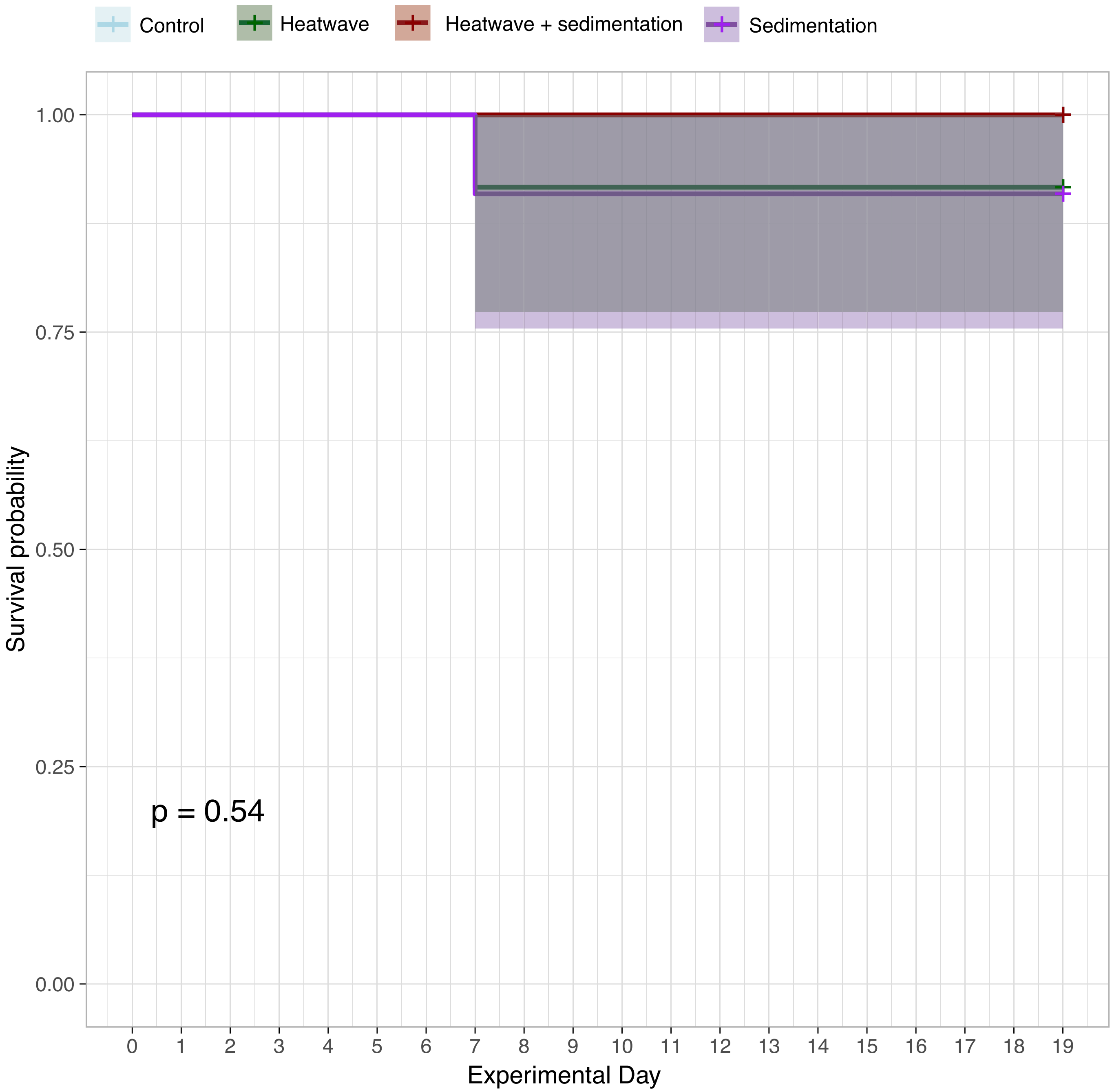

Fig. 10. Kaplan-Meier curves for fish survival at different time-points in each experimental condition. The mean temperature ±SD in temperature conditions for each day were: day 0, 15.8 ± 0.3 °C; day 7, 19.3 ± 0.3 °C; day 15, 22.5 ± 0.1 °C; day 19, 15.8 ± 0.3 °C.

therefore, other possible physiological and behavioural adjustments for this species when facing increased sedimentation alone or in combination with other stressors remain unknown. Further studies considering multistressors impacts on fish behaviour, physiology and interspecific interactions are recommended. Future research on the impacts of multiple stressors should also incorporate tissue-level responses, such as gill damage, enzymatic activity, and the expression of stress-related proteins.

CRediT authorship contribution statement

Anna Carolina Resende: Writing – original draft, Visualization, Formal analysis, Conceptualization. **Catarina Vinagre:** Writing – review & editing, Supervision, Methodology. **Alice Rogers:** Writing – review & editing, Supervision, Conceptualization.

Ethical approval

We state that all fish collections and experimental designs were made in compliance with the special permit 711-4 issued by the Ministry for Primary Industries of New Zealand and the project was approved by the Animal Ethics Committee of Victoria Wellington University, application number 0000030063.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2025.104260.

Data availability

I have made my data available on Figshare: at the following DOI https://doi.org/10.6084/m9.figshare.28811915.

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