Marine Pollution Bulletin 205 (2024) 116599

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Coping with environmental degradation: Physiological and morphological adjustments of wild mangrove fish to decades of aquaculture-induced nutrient enrichment

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ARTICLE INFO

Keywords:
Coastal eutrophication
Hypoxia tolerance
Physiological plasticity
Conservation physiology
Oxygen uptake rates
Allometry mass scaling

ABSTRACT

The impact of eutrophication on wild fish individuals is rarely reported. We compared physiological and morphological traits of *Siganus lineatus* chronically exposed to aquaculture-induced eutrophication in the wild with individuals living at a control site. Eutrophication at the impacted site was confirmed by elevated organic matter (up to 150 % higher), phytoplankton (up to 7 times higher), and reduced oxygen (up to 60 % lower). Physiological and morphological traits of *S. lineatus* differed significantly between the two sites. Fish from the impacted site exhibited elevated hypoxia tolerance, increased gill surface area, shorter oxygen diffusion distances, and altered blood oxygen-carrying capacity. Elevated blood lactate and scope for anaerobic ATP production were observed, suggesting enhanced survival below critical oxygen levels. A significant 8.5 % increase in metabolic costs and altered allometric scaling, related to environmental degradation, were recorded. Our study underscores eutrophication's profound impact at the organism-level and the importance to mitigate it.

1. Introduction

The coastal ocean consists of productive and biodiverse ecosystems that provide vital services, including climate regulation, sediment and pollutant removal, food security, and nutrient cycling (Zhai et al., 2020). These values arise from the close interactions between land, atmosphere, and the open ocean and contribute to attract an important part of the world's population near coastal areas (Cohen et al., 1997). Thus, preserving healthy marine environments and resources (including fisheries) for human subsistence, well-being, and economic prosperity is critical. However, continued expansion of land-based anthropogenic activities including aquaculture, agriculture, urbanisation, and industry has resulted in substantial damage to coastal ecosystems (Dai et al., 2023; Dubuc et al., 2017; Zhai et al., 2020).

Eutrophication is one of the primary forms of aquatic habitat degradation, causing habitat loss and reduced biodiversity and ecosystem functions and services (Breitburg et al., 2018). Eutrophication is the direct consequence of excessive nutrient input, which leads to excessive growth of primary producers, followed by bloom die-off, and eventually decomposition by aerobic microorganisms that consume oxygen (Breitburg et al., 2018). The aquaculture industry is the sixth largest source of nutrient inputs, substantially contributing to coastal eutrophication (Malone and Newton, 2020). Reports of declining water quality have been documented on a global scale, particularly in tropical and sub-tropical areas close to aquaculture farming activities (*e.g.* Hossain et al., 2013; Quiñones et al., 2019). However, because aquaculture provides crucial socioeconomic benefits, the industry has been growing rapidly, with production tripling between 1997 and 2017 (Naylor et al., 2021). Unfortunately, poor planning and lack of management have resulted in unsustainable practices, which are thought responsible for declining water quality and coastal habitat degradation (Ahmed and Thompson, 2019). For example, water pollution from shrimp farming has been classified as a high level of concern following decades of extensive use of coastal systems as natural filters for nutrient-enriched effluents (Diana, 2009). The environmental concern associated with aquaculture activities and resulting eutrophication is now widespread and predicted to increase as activities intensify and with climate change (Ahmad et al., 2021; Rodgers, 2021).

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https://doi.org/10.1016/j.marpolbul.2024.116599
Received 15 November 2023; Received in revised form 10 June 2024; Accepted 11 June 2024

The process of eutrophication exposes organisms to multiple co-occurring environmental stressors, including hypoxia, acidification, increased turbidity, and harmful algal blooms (Rodgers, 2021). As eutrophication often occurs in productive coastal systems prone to natural environmental variability, it has the potential to add substantial pressure (Dubuc et al., 2019a; Nilsson and Ostlund-Nilsson, 2004). Organisms inhabiting these environments must adjust to compensate for additional stress. For many fish species, two pathways are possible to maintain homeostasis and performance as they can either 'persist in place' or 'shift in space' (Thurman et al., 2020). The 'shift in space' pathway involves fish temporarily or permanently relocating to alternative environments that provide more suitable conditions (Chapman and McKenzie, 2009; Dubuc et al., 2019a). However, this is not always possible, particularly for species with low mobility or those with specific resource requirements (Claireaux and Chabot, 2019). Alternatively, fish can 'persist in place' by adjusting their physiology and morphology in response to environmental changes through rapid and reversible phenotypic plasticity (Blewett et al., 2022; Donelson et al., 2023). For instance, fish exposed to environmental hypoxia may enhance oxygen transport and delivery to tissues by maximising oxygen uptake in the gills *via* reduction in oxygen diffusion distance across the lamellae and/or an increase in gill surface area (Bowden et al., 2014). Blood oxygen transport parameters may also be altered by increasing the number of erythrocytes, whole blood haemoglobin concentration, and haemoglobin oxygen binding affinity (Mandic and Regan, 2018). If strategies to sustain aerobic energy production are not sufficient, fish can reduce energetic demands by suppressing non-vital activities (Wu, 2002). Ultimately, fish can resort to anaerobic pathways to enhance energy production and maintain life-sustaining activities and survival (Blewett et al., 2022). These adjustments have limits and generate energetic costs, particularly increased standard metabolic rate (SMR) and altered maximum metabolic rate (MMR; Mandic and Regan, 2018). Any constraint to an individual metabolism can lead to trade-offs in key fitness metrics, such as reduced growth and reproduction, changes in behaviour, and increased disease susceptibility (Mandic and Regan, 2018; Zambonino-Infante et al., 2017).

Ecosystem functions and services are largely determined by organisms through their biological processing of energy and nutrients, with fish playing a pivotal role (Brandl et al., 2022; Brown et al., 2004; Munday et al., 2008). By altering the energetic demands of fish, environmental stressors can profoundly affect higher levels of biological organisation, ultimately influencing ecosystem functions and services (Brandl et al., 2022; Petitjean et al., 2019). Moreover, individuals' adjustments can result in cascading effects, such as reductions in species biomass, individual size, and genetic diversity, as well as changes in species composition, functional groups, predator-prey interactions, and food-web structure, eventually having impacts at the whole-ecosystem level (Breitburg et al., 1997; Steckbauer et al., 2011; Wu, 2002). In this context, investigating how wild organisms have adjusted to their environmental conditions is highly relevant to understand broader ecological implications with fewer limitations than controlled laboratory experiments that manipulate a single stressor (Todgham and Stillman, 2013). Such approaches enable more accurate predictions of responses to environmental degradation from individuals to communities and can aid in developing solutions to conserve, restore, and better manage biodiversity and ecosystems affected by anthropogenic activities (Illing and Rummer, 2017; Seebacher and Franklin, 2012).

This study provides the first comprehensive assessment of key physiological and morphological compensatory mechanisms and fitness consequences that wild fish undergo in response to habitat degradation resulting from aquaculture-induced eutrophication in a tropical ecosystem. To achieve this, we first quantified temporal and spatial changes in key water quality parameters on two mangrove sites, one with no known anthropogenic inputs (control site) and one receiving aquaculture effluents (impacted site). Secondly, we investigated whether environmental degradation associated with aquaculture activities could be linked to adjustment mechanisms and fitness trade-offs in a representative fish species (*Siganus lineatus*) by comparing individuals living in these two sites.

2. Materials and methods

2.1. Study site

The two study sites are located 7.5 km apart in the Chambeyron Bay, South Province, New Caledonia (−21.826439° 165.804354°) and similarly exposed to tidal currents and trade winds, with mangrove forests at both sites exposed at low tide (Fig. 1). The first site (impacted; −21.850961° 165.834058°) is a mangrove-lined bay receiving effluents from an aquaculture farm producing the blue shrimp, *Litopenaeus stylirostris* since April 1995. Water in the eight shrimp ponds (covering ~30 ha) is partly renewed daily by pumping water from the adjacent mangrove bay while effluents are continuously discharged (~70,000 m^3 per day) throughout the mangrove forest (~30 ha) during the entire production period (September to June; Thomas et al., 2010). This site was chosen as a previous study had already established a clear impact of aquaculture activities on environmental conditions (Thomas et al., 2010). The second site was also a mangrove-lined bay of about 55 ha (control; −21.797632° 165.783376°) with comparable depth and sediment, not influenced by aquaculture activity or any other anthropogenic inputs or catchment.

2.2. Environmental conditions characterisation

Six sampling campaigns were conducted between March and September 2022 to characterise water quality at both sites while accounting for temporal variability in aquaculture activities (Fig. 1). Sampling was done consistently during the new moon, at slack high tide and early morning (~7 am) on the same day for both sites. A multiparameter probe (YSI) was used to measure *in situ* dissolved oxygen (DO), pH, temperature, turbidity, and salinity. To account for spatial variability, the probe was attached at the back of the boat to continuously record for ~90 min while the boat was driven slowly along the mangrove forest following a transect of about 500 m (Fig. 1). Additionally, water was collected at three different locations along the transect to subsequently measure phytoplankton biomass (total chlorophyll *a* (chl*a*)), total suspended solid (TSS), and chromophoric dissolved organic matter (cDOM). Parameters were measured following established protocols (*e.g.* Thomas et al., 2010; see Appendix A. supplemental materials and methods for details).

2.3. Fish collection

We focused on one representative fish species, the golden-lined spinefoot (*Siganus lineatus*), which is a diurnal herbivore acknowledged for its importance to ecosystem function, and a commercial and recreational species of interest. *S. lineatus* has a small home range and is commonly found in mangrove habitats (Dubuc et al., 2019b; Fox and Bellwood, 2011). Individuals were collected from both sites using gillnets (mesh 45 mm). About 10–20 individuals were collected at each trip to avoid having fish acclimated to laboratory settings for too long. About 10 collection trips occurred between April and June 2022 to collect a total of 108 individuals ($N = 53$ for control, $N = 55$ for impacted). Fish were maintained for a minimum of 5 days and a maximum of 10 days in multiple indoor flow-through 500 l tanks maintained at 28 °C, which represents the average temperature recorded in mangrove habitats over the summer months in New Caledonia (Dubuc et al., 2019a). Fish were fed twice daily, *ad libitum*, but were fasted 24 h prior to experimentation to ensure a post-absorptive state (Chabot et al., 2016). All collections were carried out under authorisation from the South Province of New Caledonia (permits: F16014.18) and all experimentations were approved by the animal ethics committee of Languedoc Roussillon n°36

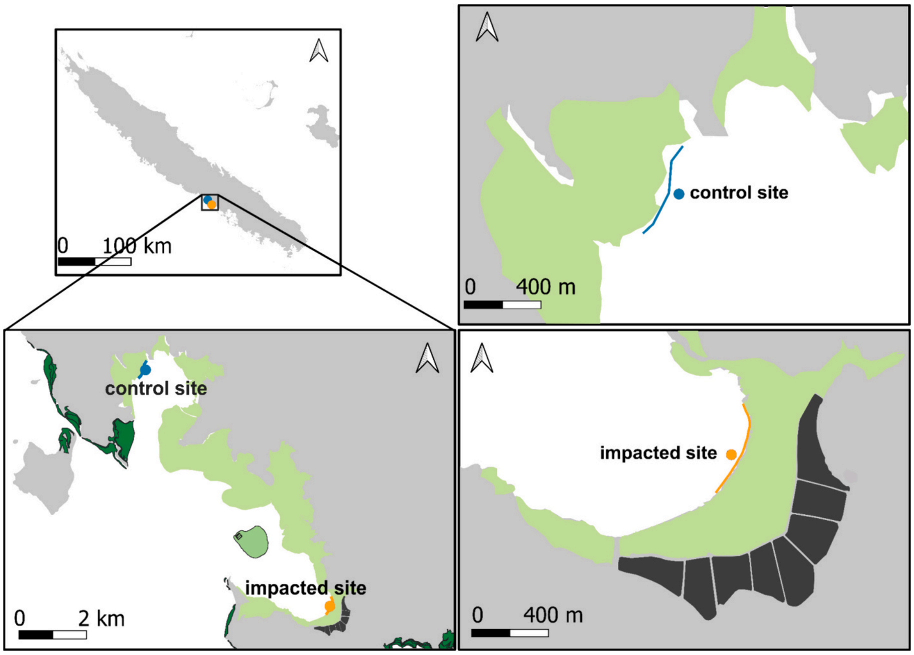

Fig. 1. Location of the two study sites on the west coast of New Caledonia (South Pacific). The coloured lines represent the 500 m transects followed during each sampling campaign at each corresponding site to account for spatial variability in environmental conditions. Black areas represent the 8 aquaculture ponds of the shrimp farm, light green areas are mangrove-lined bay and dark green areas are coastal mangroves following classification from Virly (2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(application reference: 2022092309258210 v3) and conducted according to the European and French animal ethics directive (2010/63/UE).

2.4. Respirometry

Oxygen uptake rates ($\dot{M}O_2$) were measured using automated intermittent-flow respirometry, following best practices highlighted by Svendsen et al. (2015). To meet guidelines recommended by Killen et al. (2021), an extended materials and methods is provided in Appendix A. Briefly, each fish was manually chased for 5 min and exposed to air for 1 min to reach exhaustion. It was then immediately transferred to a respirometry chamber housed either in the control (maintained at normoxia (> 80 % sat.) during the entire experiment) or the hypoxia tank. Fish were then left undisturbed for ~48 h to record SMR. On the morning of the third day, DO was gradually decreased during the last 8 h of the experiment by bubbling nitrogen in the hypoxia tank until individuals reached the incipient lethal oxygen level (ILO). The decreasing rate simulated the natural DO fluctuations recorded in mangrove habitats (Dubuc et al., 2021). At this point, DO and time were recorded and the fish was removed from the chamber to collect blood.

The highest $\dot{M}O_2$ post-chase recovery was taken as MMR. SMR was estimated from the 20 % quantile method using the calcSMR function in fishMO2 R package (Claireaux and Chabot, 2016). Critical oxygen levels (O_{2crit}) were calculated using the limiting oxygen level (LOL) curve method with the calcO2crit and plotO2crit functions in fishMO2 R package (Claireaux and Chabot, 2016). In a recent study by Seibel et al. (2021), the α-method is proposed as an alternative approach to determine O_{2crit}. While the α-method is justified by some valid points, it has also received some constructive feedback and criticism (Farrell et al., 2021), and therefore, would benefit from further validation from additional studies (Molina et al., 2023). Therefore, in this study, we used both methods to provide an applied comparison. We used the measured α-method and averaged the three highest rates of oxygen supply (α_0) ($\alpha_0 = \dot{M}O_2/DO$) to obtain a more conservative oxygen supply capacity (α) that was then used to calculate O_{2crit} at SMR ($O_{2crit\text{-}smr} = SMR/\alpha$; Seibel et al., 2021). We also used α to calculate O_{2crit} at MMR ($O_{2crit\text{-}mmr} = MMR/\alpha$), as it has been suggested to be a more relevant proxy for hypoxia tolerance and could confirm whether a species has specifically evolved to better tolerate environmental hypoxia (Seibel and Deutsch, 2020). For both $O_{2crit\text{-}smr}$ and $O_{2crit\text{-}mmr}$, we used mass-adjusted $\dot{M}O_2$. Finally, an index of cumulative ambient oxygen deficit ($O_{2deficit}$) was calculated to integrate simultaneously information on hypoxic severity and time spent in DO below O_{2crit} (for more details see Dubuc et al., 2021).

2.5. Haematological, anatomical, and morphological variables

Immediately following the end of respirometry trial (< 2 min; Lawrence et al., 2018), approximately 0.3 ml of blood was drawn from the caudal vein of each individual using 5 ml heparinised syringes. Whole blood haemoglobin concentration [Hb] (reported as grams per 100 ml using a calibration curve corrected for tropical reef species (Clark et al., 2008; Rummer et al., 2013)) was determined using a HemoCue (Hb 201 System, Australia Pty Ltd.). Whole blood glucose ([Glu], in mg dl^{-1}) and lactate concentrations ([Lac], in mmol l^{-1}) were measured with a Taidoc hand-reader (Natech, France). Haematocrit (Hct) was determined by centrifuging 40 μl of whole blood in heparinised micro-capillary tubes for 3 min at 12,000 rpm (ZipCombo Centrifuge, LW Scientific) and calculated as the ratio of packed red blood cells to total blood volume (%). [Hb] and Hct were used to calculate the mean corpuscular haemoglobin concentration (MCHC).

Fish were then sacrificed by cranial concussion, weighed and measured to calculate Fulton's K condition factor, then dissected to collect the spleen, heart, and gills. The spleen and heart were weighted to calculate the spleen somatic index (SSI) and the cardio somatic index (CSI) as the ratio of the organ weight to body mass. Lamellar width, lamellar perimeter, oxygen diffusion distance and epithelial thickness were estimated according to methods described in detail in Bowden et al. (2014) and Johansen et al. (2021) (for more details see Appendix A supplemental materials and methods).

2.6. Statistical analyses

All statistical analyses were performed in R, version 4.2.1 (R Core Team, 2023). Before conducting any parametric test, assumptions of univariate and multivariate normality (if applicable) were visually inspected using QQplots and satisfied unless otherwise specified. Assumptions of homogeneity of variance were verified using Levene's test and verified unless otherwise specified. Homogeneity of covariances assumptions were verified using Box's M-test and verified unless otherwise specified.

2.6.1. Environmental conditions

Two-way ANOVAs were performed on each of the 6 environmental quality variables (a_{350}, chl*a*, DO, temperature, pH, salinity) with site, month, and their interaction as factors. Significant relationships were followed up by pairwise comparisons using Tukey adjustment.

2.6.2. Metabolic variables

To account for body mass differences, $\dot{M}O_2$ values were allometrically scaled to an average mass of 130 g. The mass scaling exponent was determined by plotting the raw $\dot{M}O_2$ values (mg h^{-1}) as a function of mass (g) on log-scaled transformed axis (Rosewarne et al., 2016). Fish from the two different sites were treated separately as a significant difference in allometry scaling was found (Homogeneity of slopes: ANOVA: Site*Mass $F_{1,98} = 12.77$, $p < 0.001$). The two mass scaling exponents for SMR were 0.6656 and 1.0748 for control and impacted site, respectively (Fig. S1). The two mass scaling exponents for MMR were 0.9329 and 0.813 for control and impacted site, respectively (Fig. S1). The different metabolic variables were then allometrically mass-adjusted (Rosewarne et al., 2016):

$$MO_{2\text{scaled}} = MO_{2\text{measured}}{}^{*}(M_{\text{measured}}/M_{\text{standard}})^{(1-b)} \quad (1)$$

where $\dot{M}O_{2\text{scaled}}$ is the $\dot{M}O_2$ allometrically mass-adjusted to a mass of 130 g, $\dot{M}O_{2\text{measured}}$ is the mass-adjusted $\dot{M}O_2$ calculated in Eq. 1, M_{measured} is the measured mass of the individual, M_{standard} is the average mass of 130 g, b is the mass-scaling exponent (Fig. S1).

Factorial aerobic scope (FAS) was calculated using the allometrically mass-adjusted $\dot{M}O_2$.

A MANOVA was conducted to determine whether SMR, MMR and FAS differed between sites. The homogeneity of covariances assumption (Box's M-test) was violated ($p < 0.001$). The Pillai's Trace test statistic is therefore reported as it is robust to violations of variance-covariance matrix when sample sizes are >30 and balanced (Tabachnick and Fidell, 2007). One-way ANOVAs were conducted to further identify statistically significant variables.

2.6.3. Hypoxia tolerance response

Preliminary data exploration using Pearson correlations found mass to be a significant covariate for all five hypoxia tolerance variables, but only for individuals at the impacted site (Fig. S2). To address this issue, five separate multiple linear regression models were fitted to analyse each of the variables ($O_{2\text{crit}}$, $O_{2\text{crit-smr}}$, $O_{2\text{crit-mmr}}$, α, $O_{2\text{deficit}}$) and test the effect of site while accounting for mass and the two-way interaction between mass and site. To account for the interaction between mass and site, we calculated the estimated marginal means (EMMs) from the fitted multiple linear regression models across three mass values (the average mass value, and ± 1 standard deviation of the average value). Pairwise comparisons were then performed on all significant variables between the two sites at each corresponding mass value using Tukey adjustment for multiple comparisons.

2.6.4. Gill morphometry

Homogeneity of slopes between sites and mass was verified ($F_{1,103} = 0.39$, $p = 0.533$ and $F_{1,103} = 0.57$, $p = 0.446$, respectively), therefore a MANCOVA was performed with lamellar perimeter, epithelial thickness, oxygen diffusion distance, and lamellar width as the dependent variables, the interaction between site (control (C) or impacted (I)) and treatment (control (C) or hypoxia (H)) as the predictors, and mass as a covariate. The results of the MANCOVA were further examined using one-way ANCOVAs. Statistically significant ANCOVAs were followed up by post-hoc planned comparisons according to combinations of site and treatment (CC-CH, CC-IC, CH-IH, IC-IH) on EMMs calculated for the average mass value (133.1 g).

2.6.5. Haematology, anatomy, and morphology

A MANCOVA was performed with all 8 variables as dependent variables ([Glu], [Lac], [Hb], Hct, MCHC, SSI, CSI, Fulton's K) and site and the interaction between site and treatment as the predictors, and mass as a covariate. One-way ANCOVAs were then performed on each variable. Mass was found to be a significant covariate only for CSI. For this variable, the EMMs calculated for the average mass value (133.1 g) were used for pairwise comparisons. For the other variables, statistically significant ANCOVAs were followed up by multiple pairwise comparisons while controlling for type I error.

3. Results

3.1. Environmental conditions

Environmental condition analyses revealed that the mangrove system receiving aquaculture effluent shows signs of eutrophication. Indeed, when compared to the control site, the impacted site exhibited significantly higher levels of dissolved organic matter (a_{350}) and phytoplankton biomass (chl*a*) associated with significantly lower DO and pH (Fig. 2; Table S1). A significant temporal variability in environmental conditions was also observed at the impacted site with, for instance, the highest a_{350} and chl*a* values obtained in March and the lowest DO and pH values obtained in May (Fig. 2; Table S1). Conversely, environmental parameters were relatively more constant at the control site. No consistent differences in temperature and salinity that could be attributed to aquaculture activities were detected between the two sites. Instead, differences were more likely associated with temporal variability in tidal regime and time of day.

3.2. Metabolic variables

The MANOVA outcome highlighted that site significantly influenced metabolic variables (Pillai's trace 0.10, $F_{1,95} = 3.38$, $P = 0.021$). One-way ANOVAs revealed that only SMR was affected, with fish from the impacted site displaying higher standard metabolic costs than fish from the control site ($F_{1,95} = 9.61$, $P = 0.003$, $\eta^2 = 0.09$; Fig. 3, Table S2). Following DO probe malfunction, data from 5 individuals at the control site and 6 individuals at the impacted site were excluded from the analyses.

3.3. Hypoxia tolerance

About 51 %, 40 %, 24 %, 27 % and 28 % of the variance associated with $O_{2\text{crit}}$, $O_{2\text{crit-smr}}$, $O_{2\text{crit-mmr}}$, α, and $O_{2\text{deficit}}$, respectively, was significantly explained *via* multiple linear regression models (Table S3). Site was a significant factor for all the variables, highlighting that the individuals displayed different hypoxia tolerance between the two sites (Fig. 4; Table S3). Mass had an influence on all the variables, but it was especially noted for fish from the impacted site. Indeed, the EMMs of each variable varied significantly across mass at the impacted site but remained relatively constant at the control site (Fig. 4). Examining the variables across a range of body masses revealed that, at an early stage of life (lowest mass value tested, 87.5 g), individuals from the impacted site had lower $O_{2\text{crit}}$ (and $O_{2\text{crit-smr}}$) and $O_{2\text{crit-mmr}}$ and higher α, when compared to their control site counterparts (Fig. 4, Table S4). However, as individuals from both the impacted and control site grew larger, there

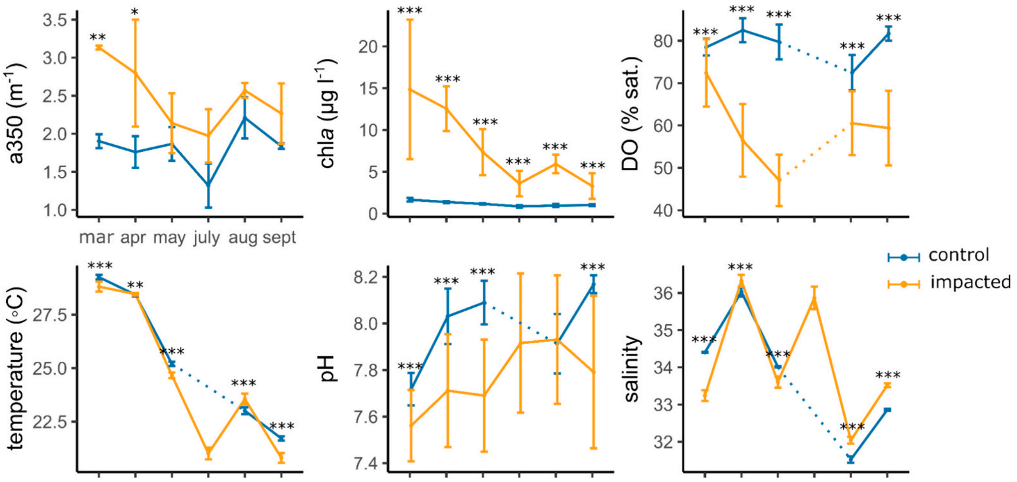

Fig. 2. Comparison of key environmental quality parameters between the control and impacted site. In July, no data were available for DO at both sites and for temperature, pH, and salinity at the control site. Asterisks denote significant differences between sites at the corresponding month following *post hoc* tests at significance levels: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. Error bars are ± sd.

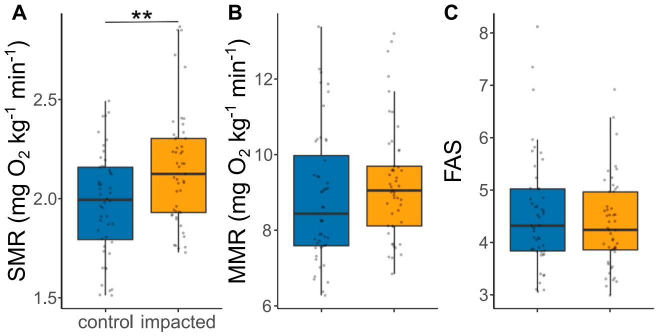

Fig. 3. Effect of site on three metabolic variables. Dots represent individual data points of allometrically mass-adjusted $\dot{M}O_2$ values. Asterisks denote significant differences between sites following *post hoc* tests at significance levels: * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

was a convergence in hypoxia tolerance variables between the two groups, leading to non-significant differences at higher mass. The only exception was the higher $O_{2deficit}$ exhibited by fish from the impacted site at the highest mass value tested (178.6 g; Fig. 4E).

3.4. Gill morphometry

The MANCOVA revealed a significant difference in the overall change in gill morphometry in response to site (Pillai's trace 0.44, $F_{1,102} = 19.37$, $P < 0.001$) and an interaction between site and treatment (Pillai's trace 0.42, $F_{2,102} = 6.58$, $P < 0.001$). Results from all ANCOVAs were significant (Table S5), confirming that fish from the impacted site displayed significantly longer lamellar perimeters, reduced oxygen diffusion distances, thicker epithelia, and thinner lamellae (Fig. 5). Gill morphometry variables also displayed modifications in response to hypoxia exposure that were significantly different between sites (except for epithelial thickness; Table S5). For example, in individuals from the impacted site, lamellar perimeter significantly increased in response to

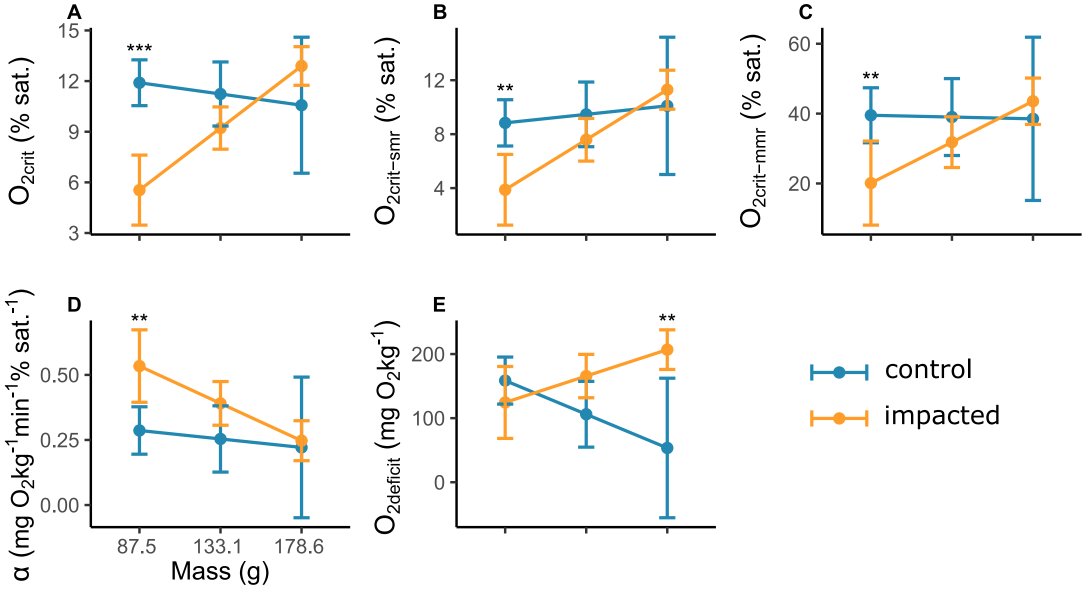

Fig. 4. Comparisons of hypoxia tolerance variables between sites and across fish body mass. EMMs were calculated for three different values of mass (87.5, 133.1, 178.6 g). EMMs are represented as circles with 95 % confidence intervals. Asterisks denote significant differences among sites at an equal mass value following *post hoc* tests at significance levels: * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

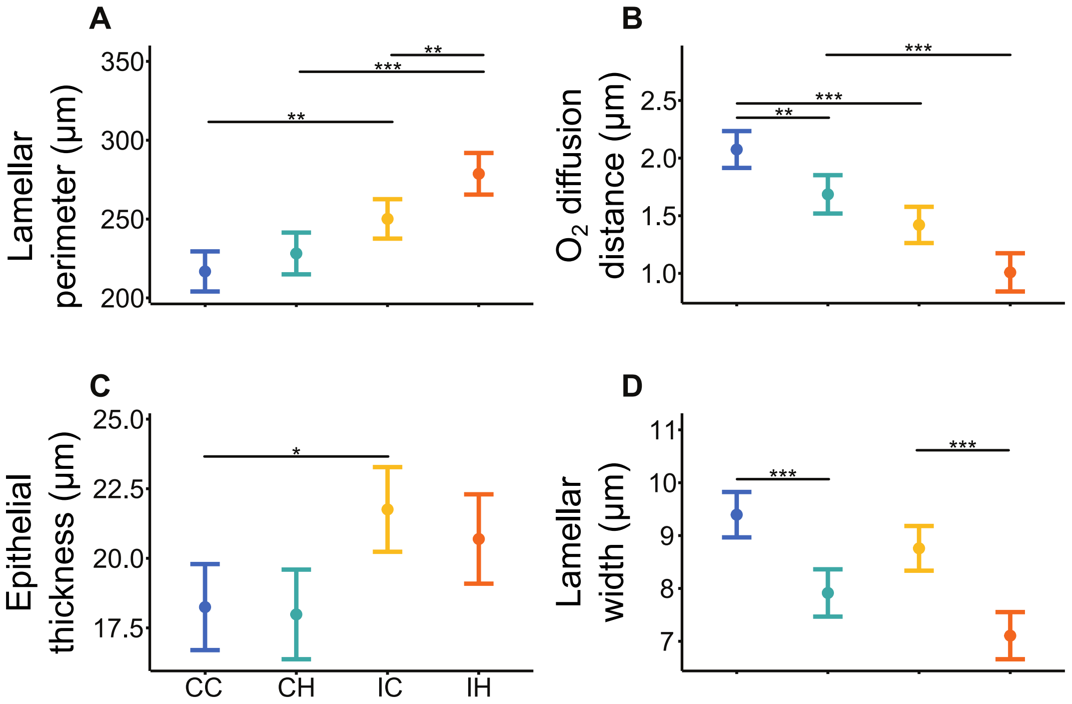

Fig. 5. Comparisons of gill morphometry variables between sites (control or impacted) and treatments (control or hypoxia). CC = control-control, CH = control-hypoxia, IC = impacted-control, IH = impacted-hypoxia. Circles represent EMMs with 95 % confidence intervals calculated at the average mass of 133.1 g. Asterisks denote significant differences following *post hoc* tests at significance levels: * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

hypoxia, but this was not the case for individuals from the control site (Fig. 5 A).

3.5. Haematology, anatomy, and morphology

The MANCOVA revealed that variability in haematological, anatomical, and morphological traits were significantly explained by site (Pillai's trace 0.24, $F_{1,71}$ = 2.57, *P* = 0.017) and the interaction between site and treatment (Pillai's trace 1.04, $F_{2,71}$ = 8.78, P < 0.001). Follow-up ANCOVAs indicated that every parameter measured significantly responded either to site, treatment, or both (Table S6). Haematological, anatomical, and morphological traits also displayed modifications in response to hypoxia exposure that were for all but one ([Hb]) similar between the two sites (Fig. 6). For instance, an increase in Hct was recorded at both sites when individuals were exposed to hypoxia (Fig. 6D). Overall, at both sites, we observed increases in [Glu], [Lac], and Hct, and decreases in MCHC and SSI when individuals were exposed to hypoxia. However, fish from the impacted site had

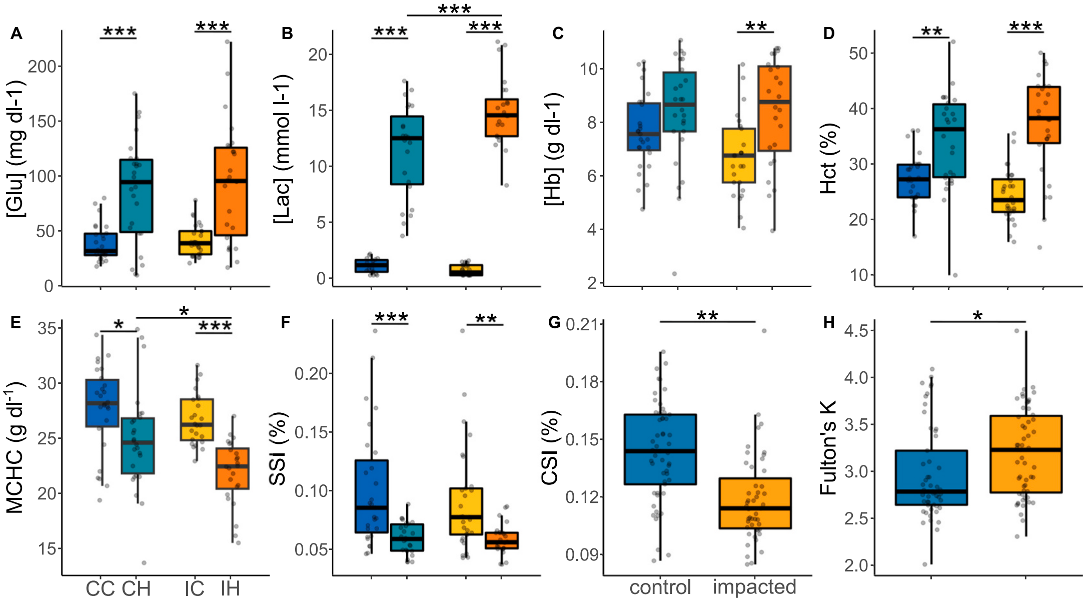

Fig. 6. Effect of site (control or impacted) and the interaction between treatment (control or hypoxia) and site on haematological, anatomical and morphological variables. CC = control-control, CH = control-hypoxia, IC = impacted-control, IH = impacted-hypoxia. Dots represent raw data. Raw data are presented for CSI but EMMs were used for statistical testing (Fig. S3). Asterisks denote significant differences following *post hoc* tests at significance levels: * P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

significantly higher [Hb] following hypoxia exposure, whereas no significant changes in [Hb] were recorded in fish from the control site. Additionally, following hypoxia exposure fish from the impacted site had a lower MCHC and a higher [Lac] compared to fish from the control site. We did not record differences in baseline haematological parameters between the two sites (comparison between CC and IC), but we recorded anatomical and morphological differences. Indeed, fish from the impacted site exhibited a lower CSI and a higher Fulton's K than fish from the control site (Fig. 6G and H).

4. Discussion

4.1. Environmental degradation

Nutrient discharge from anthropogenic activities has been intensifying over the past 50–100 years, resulting in widespread eutrophication (Dai et al., 2023). Despite being one of the most prominent issues marine coastal ecosystems face, our understanding of how wild organisms cope with associated environmental degradation is limited (Rodgers, 2021). Our findings confirmed eutrophication at the impacted site with notably higher levels of dissolved organic matter and phytoplankton biomass, and lower DO and pH. These changes were directly attributed to farm activities, as water quality improved after effluent discharge stopped early June. For instance, in March, during peak farming activity, chl*a* reached a high of 14.8 μg l^{-1} but dropped to 3.28 μg l^{-1} by September, four months after farming activities stopped for the year. For reference, 2 μg l^{-1} is typical for a mangrove-lined bay of New Caledonia, matching values recorded at the control site (Jacquet et al., 2006). Our results are consistent with a previous study conducted between 2004 and 2005 (Thomas et al., 2010). Consequently, organisms inhabiting this environment are chronically exposed to more turbid, hypoxic, and acidic waters, creating a multi-stressor environment; therefore, we expected fish, to exhibit coping mechanisms to prevail in these degraded conditions.

4.2. Metabolic rate changes

Metabolic rate provides a comprehensive understanding of an organism's physiological status and fitness, driving ecological patterns (Brandl et al., 2022; Deutsch et al., 2020). This study determined that *S. lineatus* inhabiting the impacted site exhibited higher SMR compared to *S. lineatus* from the control site, indicating higher energy requirements in degraded environments. SMR is a plastic trait influenced by various biotic and abiotic factors (Jutfelt et al., 2018). Typically stress, excluding temperature (Clarke, 2004), results in lower SMR, allowing individuals to conserve energy and optimise other fitness-related functions, particularly in environments where oxygen is limiting (Blewett et al., 2022; Mandic et al., 2009). Conversely, a higher SMR suggests increased maintenance costs due to environmental stress responses (Sokolova, 2021). For example, increased gill surface area improve oxygen supply capacity, which is commonly reported in response to hypoxic conditions (Mandic et al., 2009), and observed in this study, but leads to higher tissues maintenance and homeostatic mechanisms costs (Abdel-Tawwab et al., 2019).

A high SMR may provide a fitness advantage in food-abundant environments by promoting higher growth rates through faster and more efficient meal processing and digestion (Millidine et al., 2009). This “increased-intake hypothesis” strategy (Pettersen et al., 2018) may be an effective adaptation in enriched systems, such as the impacted site in this study, where food is likely abundant. However, this strategy can become maladaptive if food resources become limited, unpredictable, or exposure to stressors increases, thereby limiting energy available for digestion (Reid et al., 2012). While high SMR can be beneficial in some specific context, it can also cause adverse long-term effects, such as reduced longevity (Rosenfeld et al., 2015). Although it is unclear how observed changes in SMR translate into performance in the natural environment, as it is context-dependent, changes in SMR are known to influence behaviour, fitness, and survival (Burton et al., 2011; Killen et al., 2012). Consequently, our findings suggest that environmental degradation has altered *S. lineatus*' costs of living, likely affecting their behaviour, fitness, and possibly survival.

Unlike SMR, we found no changes in aerobic scope or MMR. Thus, despite a higher basic maintenance cost (SMR) and no apparent matched increase in MMR, fish from the impacted site do not appear to be aerobically constrained. However, if MMR does not change with SMR, organisms will eventually suffer from reduced aerobic scope (Sokolova, 2021). As the metabolic capacity of an individual is limited, a mandatory trade-off between basic maintenance costs, growth, reproduction, and other activities must exist (Burton et al., 2011). Consequently, an increase in maintenance costs without an increase in aerobic capacity leads to less energy being available for other activities, likely having fitness consequences (Sokolova, 2021). It is plausible that this physiological status is life-stage-specific (White et al., 2022). Given that the study individuals were sexually immature, fish from the impacted site could be prioritising growth during this developmental phase whilst taking advantage of this resource-rich environment, upregulating digestive machinery, and therefore inflating SMR (Burton et al., 2011; Rosenfeld et al., 2015), potentially altering proportions of organisms attributes (allometry).

4.3. Changes in allometry

Metabolic rate scaled allometrically with body mass in *S. lineatus*, as expected; however, the relationship differed significantly between the two sites. Fish at the impacted site had a higher mass scaling exponent for SMR (1.08) compared to control fish (0.67), exceeding the typical range reported for fishes (0.67–1.00; Glazier, 2005; Killen et al., 2010; Rosenfeld et al., 2015). Our study indicates that habitat degradation alters allometry, modifying the relative influence of surface area- (food assimilation, waste removal, heat dissipation) and volume-related (basal maintenance and other fitness-related activities such as growth or locomotor activities) metabolic processes (Glazier, 2005). Although mass scaling exponents are species-specific, intra-specific differences, beyond ontogeny are rarely considered (Glazier, 2005), even though environmental factors are known to impact metabolic rate and body mass in isolation (Killen et al., 2010).

A mass scaling exponent close to 1.00, like on the impacted site (*i.e.*, 1.08), indicates an isometric relationship, whereby metabolic rate increases linearly with body tissue mass, potentially due to increased growth rates (Glazier, 2005). This supports our hypothesis that individuals at the impacted site prioritise growth during early life stages, taking advantage of food abundance, leading to a high mass scaling exponent and elevated SMR. As the scaling exponent characterises the relationship between metabolic rate and body mass, it is, indeed, reasonable to expect that different growth rates may explain the dissimilarity between these two groups. Unfortunately, neither growth rates nor aging were investigated in this study so we cannot infer different growth rates to variability in mass scaling exponents.

4.4. Hypoxia tolerance

An organism's critical oxygen level (O_{2crit}) is often used as a proxy for hypoxia tolerance, representing the DO level below which basic maintenance costs can no longer be met. However, O_{2crit} only partially captures the metabolic response to hypoxia, and its accuracy at predicting hypoxia tolerance has been challenged (Wood, 2018). While O_{2crit} is insightful, its usefulness improves when combined with other parameters characterising other aspects of the hypoxia response (Dubuc et al., 2021; Zhang et al., 2021). In this study, we combined O_{2crit} with parameters related to the capacity to survive under O_{2crit} ($O_{2deficit}$), supply oxygen (α), and maintain aerobic scope ($O_{2crit\text{-}max}$). Significant differences in hypoxia response were found between the two groups of

S. lineatus, with individuals from the impacted site being more tolerant to hypoxia than individuals from the control site. However, this result was only valid in smaller individuals (*i.e.*, smaller body mass), and as fish grew, their hypoxia tolerance more closely matched that of the control fish.

Typically, body mass is not expected to directly impact aerobic hypoxia tolerance, due to the relative constant scaling of oxygen uptake rates with metabolic rate across size (Mandic et al., 2009; Nilsson and Östlund-Nilsson, 2008). This hypothesis holds for fish from the control site, as mass had no effect on hypoxia tolerance variables. However, in the impacted site, mass strongly influenced all hypoxia tolerance variables. Of particular interest, in the impacted site, larger fish exhibited a lower α than smaller fish, indicating a reduced capacity to extract and transport oxygen in support of aerobic activities. If body mass is observed to influence hypoxia tolerance, it is likely related to adaptations to different lifestyles or habitat preferences (Nilsson and Östlund-Nilsson, 2008). Small individuals of *S. lineatus* are highly associated with mangrove habitats and have limited migration capacity. Therefore, being more tolerant and able to 'persist in place' is likely to be a strong selective pressure for small individuals, especially in degraded habitats prone to extreme changes in environmental conditions. Larger individuals may rely less on compensatory mechanisms that are potentially costly as they can 'shift in space' and avoid stressful conditions by temporarily using adjacent habitats where environmental conditions may be more favourable. Indeed the impact of aquaculture effluents can be relatively localised (Thomas et al., 2010) and the existence of water quality gradient is expected, making adjacent habitats less affected.

Focussing on the smaller mean size (87.5 g), individuals from the impacted site displayed lower O_{2crit} and $O_{2crit\text{-}max}$ and higher α compared to individuals from the control site, indicating an enhanced capacity to extract and supply O_2 to meet aerobic metabolic needs. Specifically, $O_{2crit\text{-}max}$ has been proposed as a preferred measure of hypoxia tolerance, with a value lower than air saturation suggesting adaptation to environmental hypoxia (Seibel et al., 2021). In our case, $O_{2crit\text{-}max}$ was extremely low for small individuals from the impacted site (20.1 % sat.; Table S4), similar to species living in permanently hypoxic environments (Seibel et al., 2021), allowing them to maintain aerobic performance even at very low DO. Interestingly, the α-method yielded significantly and consistently lower values than the LOL method in determining O_{2crit}; yet, regardless of method, our conclusions remained (Table S4). Focussing on the larger mean size (178.6 g), $O_{2deficit}$ (*i.e.*, the scope for survival below O_{2crit}) was higher for individuals from the impacted site compared to fish from the control site, indicating longer survival at DO levels below O_{2crit}. Our findings suggests that individuals from the impacted site have optimised compensatory mechanisms to respond to more prolonged and severe hypoxia events caused by eutrophication, making them overall more tolerant to hypoxia, especially during early life stages when heavily reliant on mangrove habitats with limited capacity to 'shift in space'.

4.5. Haematological, anatomical, and morphological changes

Small individuals from the impacted site were able to sustain aerobic metabolism at lower DO likely through gill remodelling, exhibiting longer and thinner gill filaments to increase the surface area for gas exchange. This is a commonly observed mechanism by which fish cope with hypoxia, as gills are one of the first organs to respond to environmental change, and gills are critical in terms of oxygen supply and transport (Borowiec and Scott, 2021; Bowden et al., 2014). While this compensatory mechanism favours gas exchange, it challenges ion regulation that becomes challenging and costly (Nilsson, 2007). A thicker epithelium was recorded for fish from the impacted site, which could help reduce permeability and improve ion regulation but at the cost of gas exchange efficiency (Abdel-Tawwab et al., 2019). Epithelium thickness appeared to be plastic and was reduced with hypoxia exposure, highlighting an osmorespiratory compromise between ion regulation and gas transfer depending on environmental conditions (Borowiec et al., 2015).

Another likely mechanism to explain the sustained aerobic metabolism at low DO is changes in haemoglobin's affinity and carrying capacity for oxygen (Mandic et al., 2009). When exposed to hypoxia, we observed an increase in Hct in all individuals and an increase in [Hb] for fish from the impacted site. This is likely related to splenic release of red blood cells into circulation, as highlighted by changes in SSI between control and hypoxia treatments (Borowiec and Scott, 2021). Alongside this, a decrease in MCHC was also observed, suggesting swelling of erythrocytes *via* Na^+/H^+ exchange to protect intracellular pH and O_2 uptake at the gill (Randall et al., 2014). This is another known mechanism in response to generalised acidosis, caused here by O_2 limitations, responsible for haemoconcentration and increased affinity of Hb to oxygen, overall increasing oxygen carrying capacity and delivery to tissues *via* Bohr/Root shifts (Rummer and Brauner, 2011). Our results suggest that individuals from the impacted site have enhanced oxygen supply and carrying capacity *via* optimised blood-gas transport mechanisms to efficiently respond to O_2 limitations.

Fish from the impacted site exhibited a decrease in CSI, suggesting anatomical changes in the heart. Reduction in heart mass has previously been observed in *Oncorhynchus mykiss* chronically exposed to hypoxia (Magnoni et al., 2019). This modification could be a developmental alteration caused by chronic exposure to hypoxia. Alternatively, it could be an adaptation to hypoxia optimising cardiac performance, or a strategy to decrease energy investment in maintenance costs (Rosenfeld et al., 2015).

Fish from the impacted site were more aerobically tolerant to hypoxia, their survival below O_{2crit}, survival is dictated by their ability to maintain ATP supply using anaerobic metabolism. Larger individuals from the impacted site were more resistant to hypoxia (higher $O_{2deficit}$) due to enhanced capacity for anaerobic ATP production, indicated by higher [Lac] (Mandic and Regan, 2018). Furthermore, higher Fulton's K values for these individuals suggest increased anaerobic fuel stores improving hypoxia resistance (Nilsson and Östlund-Nilsson, 2008).

In conclusion, our findings show that aquaculture-induced eutrophication results in physiological and morphological adjustments in fish to cope with low O_2 availability, thus allowing fish to withstand more prolonged and severe hypoxia events. Although identified coping mechanisms are related to phenotypic plasticity responses and are therefore reversible, we have also recorded long-term impacts on morphology and allometry indicating non-reversible consequences likely having adverse fitness consequences and ecological implications.

4.6. Ecological implications

Dynamic environments, such as mangroves, present some of the most physiologically challenging contexts for marine organisms (Blewett et al., 2022). As such, organisms inhabiting these habitats have evolved specific mechanisms to efficiently use these environments and withstand extreme environmental variability they may encounter (Dubuc et al., 2021; Molina et al., 2023). However, anthropogenic activities can seriously compromise these trade-offs by exacerbating these challenging environmental conditions (Breitburg et al., 2018). We show that *S. lineatus*, a relatively tolerant species that relies on mangrove habitats (Dubuc et al., 2021), exhibits physiological and morphological adjustments to cope with environmental degradation from aquaculture activities. Using O_{2crit}, we estimated that *S. lineatus* has physiologically adjusted to maintain a metabolic index of 3.3 at oxygen levels as low as 13 % air saturation, particularly in smaller individuals. This is a critical threshold for most aquatic organisms beyond which physiological limits are surpassed, rendering the habitat metabolically unsuitable (Deutsch et al., 2015). The lowest DO value recorded at the impacted site was 31 % air saturation; however, it is likely that DO plummets at nighttime, a period for which we lack data, which would pose a serious threat to organisms. Although *S. lineatus* appears to have mechanisms in place to cope with environmental degradation, the capacity for physiological and phenotypic plasticity and eventually adaptation through genetic changes is species specific (Hofmann and Todgham, 2009). Therefore, some species may experience fitness declines, or be unable to cope with additional anthropogenic stressors, leading to their temporary or permanent exclusion from impacted habitats, altering community composition, food-web dynamics, energy and nutrients fluxes and ultimately ecosystem functioning (Brandl et al., 2022; Petitjean et al., 2019). Further research is needed to expand on these findings by investigating other sites, changes in community composition and subsequent impacts on ecosystem functioning in relation to aquaculture activities.

5. Conclusion

Physiological responses of natural populations to environmental disturbances *in situ* represents a profound knowledge gap (Blewett et al., 2022). Understanding these responses at the individual level provides insight into acclimation and adaptation capacities, essential to predict ecological consequences and inform effective conservation and management strategies (Illing and Rummer, 2017). This is particularly relevant for challenging, yet productive, coastal ecosystems, where many organisms appear to be living at the edge of their environmental tolerance limits (Dubuc et al., 2021). Coastal ecosystems are especially vulnerable to deteriorating environmental conditions from increasing anthropogenic activities, to which aquaculture contributes substantially. Our study shows that even semi-intensive systems likely impact ecosystems at different levels of biological organisation. Thus, the rapidly growing aquaculture industry is likely causing severe ecological disruptions (Naylor et al., 2021). Mitigating the impact of eutrophication is achievable locally by reducing organic matter loading into adjacent coastal ecosystems (Ahmed and Thompson, 2019). Consequently, there is urgent need to monitor environmental impacts, and prioritise sustainable management practices that implement solutions to reduce organic matter loads to preserve these ecosystems and the critical ecological services they provide.

Funding

This research was funded by a Pacific Fund grant provided by the France Ministry of Europe and Foreign Affairs. AD was awarded a IFREMER postdoctoral fellowship.

CRediT authorship contribution statement

A. Dubuc: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft. **J.L. Rummer:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. **L. Vigliola:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. **H. Lemonnier:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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.

Data availability

The dataset generated and analysed during the study is available from Mendeley data repository (doi: 10.17632/48z94txmpk.1).

Acknowledgements

We are grateful to: L. Wantiez and N. Wabete for early discussions and guidance; R. Wamalo, R. Perrot, and G. Fogliani for laboratory and field assistance; the staff at IFREMER LEAD NC, especially F. Antypass and T. Haize, and the staff at ADECAL for technical support throughout the project; the staff at IRD, especially J. Giraud, for field support; the staff at the Laboratoire de la Nouvelle-Calédonie, especially R. Perrot. and A. Desoutter; and the staff at IMAGO-LAMA.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.116599.

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