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Association between physiological performance and short temporal changes in habitat utilisation modulated by environmental factors

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ABSTRACT

Temporal environmental variability causes behavioural and physiological responses in organisms that can affect their spatial location in time, and ultimately drive changes in population and community dynamics. Linking ecological changes with underlying environmental drivers is a complex task that can however be facilitated through the integration of physiology. Our overarching aim was to investigate the association between physiological performance and habitat utilisation patterns modulated by short temporal fluctuations in environmental factors. We used *in situ* monitoring data from a system experiencing extreme environmental fluctuations over a few hours and we selected four fish species with different habitat utilisation patterns across dissolved oxygen (DO) fluctuations: two commonly observed species (*Siganus lineatus* and *Acanthopagrus pacificus*), including at low DO (40 and 50% saturation, respectively), and two reef species (*Heniochus acuminatus* and *Chaetodon vagabundus*) never recorded below 70% saturation. We hypothesised that these patterns were associated to species' physiological performance in hypoxia. Therefore, we measured different metabolic variables (O_{2crit}, incipient lethal oxygen (ILO), time to ILO, index of cumulative ambient oxygen deficit ($O_{2deficit}$), maximum oxygen supply capacity (α)) using respirometry. Physiological performance differed among species and was intrinsically associated to habitat use patterns. *S. lineatus* had a lower O_{2crit} than *H. acuminatus, A. pacificus* and *C. vagabundus* (13, 18.7, 20 and 20.2% saturation respectively). Additionally, *S. lineatus* and *A. pacificus* displayed better capacity for survival below O_{2crit} than *C. vagabundus* and *H. acuminatus* (lower ILO, higher $O_{2deficit}$ and longer time to ILO) and higher α. Field monitoring data revealed that DO temporarily falls below species' O_{2crit} and even ILO on most days, suggesting that short temporal variability in DO likely forces species to temporarily avoid harmful conditions, driving important changes in ecosystem structure over a few hours. Our results support the hypothesis that organismal physiology can provide insights into ecological changes occurring over a few hours as a result of environmental variability. Consequently, integrating physiology with ecological data at relevant temporal scales may help predict temporal shifts in ecosystems structure and functions to account for ecological patterns often overlooked and difficult to identify.

1. Introduction

1.1. The importance of understanding and predicting habitat utilisation

The occurrence of an organism in a specific habitat is intrinsically linked to its physiology and current external environmental conditions (Chown et al. 2004; Bozinovic et al. 2011). However, spatial location is not fixed, and through movement, it may be modified at any time based on individuals' needs and tolerances in order to maximise fitness (Nathan et al. 2008). For instance, the development of adverse environmental conditions triggering physiological changes can result in an avoidance response with relocation of individuals to a more favourable habitat (Helmuth 2009; Metcalfe et al. 2012). As the displacement of organisms plays a major role in ecosystem functioning by modifying the structure of communities, and fluxes of nutrients and energy (Bauer and Hoye 2014), it is of utmost importance to understand and predict

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changes in habitat utilisation in response to variations in environmental conditions. Linking habitat utilisation pattern of organisms with underlying environmental drivers is a complex task that can however be facilitated through the integration of knowledge on physiological traits (Lawton 1991; Spicer 2014; Jachowski and Singh 2015).

Movement is greatly influenced by environmental conditions as they cause physiological changes (Nathan et al. 2008; Jachowski and Singh 2015). As environmental conditions are not stable and fluctuate over space and time at a variety of scales that can range from centimetres to thousands of kilometres, and from minutes to decades (Boyd et al. 2016), respectively, they represent a continual challenge for organisms to maintain a stable physiological state. Spatial variation in environmental conditions has received considerable attention to which physiological measures have been successfully integrated to explain species distribution patterns and habitat partitioning (Chown et al. 2004; Deutsch et al. 2020). However, occupied niches can experience short temporal variations (over a few hours) which are often omitted despite growing recognition of short-term variability in key environmental factors that can equal and even exceed variations over large spatial scales in some locations (Bernhardt et al. 2020; Kroeker et al. 2020). Many valuable environments such as estuaries, coral reefs, intertidal zones and lakes are prone to short-term environmental variability (Mandic and Regan 2018; Bouyoucos et al. 2021), thereby exposing species to challenging conditions and forcing them to temporarily avoid these habitats (Bernhardt et al. 2020). Consequently, short temporal variability in environmental factors likely leads to substantial changes in ecological patterns that could only be discernible by investigating changes in habitat utilisation at appropriate temporal scales.

1.2. *Environmental hypoxia: a key driver of habitat utilisation*

Together with temperature, DO is a key limiting environmental factor in aerobic energy acquisition for marine organisms and consequently plays a crucial role in delimiting species ranges and habitat suitability (Portner and Knust 2007; Deutsch et al. 2015; Bouyoucos et al. 2021). Moreover, environmental hypoxia is increasing worldwide due to anthropogenic pressures and is expected to further exacerbate in the context of climate change, calling for a better understanding of its impact on marine species (Breitburg et al. 2018). Hereafter, we define environmental hypoxia as any level of DO that can challenge individuals and induce behavioural or physiological adjustments to meet energetic demands (Wu 2002; Farrell and Richards 2009). While the largest area of hypoxic habitats experiences persistent environmental hypoxia (oceanic oxygen minimum zones), most coastal habitats experience intermittent environmental hypoxia. In these habitats, DO can be extremely variable over a tidal and diel scale, as it is governed by many interacting factors, including temperature (D'Autilia et al. 2004; Dubuc et al. 2017). A common response to intermittent environmental hypoxia is behavioural avoidance of hypoxic areas, resulting in a temporary displacement of organisms (Chapman and McKenzie 2009; Tyler et al. 2009; Brady and Targett 2013). Through a wide range of physiological (Wu 2002) and behavioural adaptations (Chapman and McKenzie 2009) that vary among species, behavioural avoidance can be deferred. Consequently, based on the ability of individuals to cope with environmental hypoxia, a gradual modification of community composition across DO in a particular habitat is expected *in situ*. Therefore, determining species' ability to cope with environmental hypoxia can provide insight into understanding and predicting short temporal changes in habitat utilisation and ultimately in habitat functioning.

1.3. *Mangroves are a natural dynamic laboratory*

Mangroves are considered highly valuable habitats for coastal fish production (Nagelkerken et al. 2008). However, their fisheries value has been shown to vary spatially depending on numerous environmental factors (Dorenbosch et al. 2005; Reis-Filho et al. 2016; Sheaves et al. 2016; Dubuc et al. 2019b). Additionally, the fisheries value of mangroves has been shown to exhibit strong variability over short temporal scales (a few hours) (Ellis and Bell 2008; Krumme et al. 2015; Dubuc et al. 2019b). Low DO events are common in these environments, and it has been suggested that short temporal changes in fish composition could be linked to environmental hypoxia avoidance (Knight et al. 2013; Dubuc et al. 2017; Mattone and Sheaves 2017). Assigning ecological patterns to a single environmental factor is hazardous, especially if using only field observations, as fish rarely respond to a single stressor, but rather to a range of interacting stressors that can generate similar responses (Wu 2002; Vaquer-Sunyer and Duarte 2008). Their highly dynamic nature makes mangroves an ideal natural laboratory to further investigate the role of environmental hypoxia in driving short temporal scale changes in habitat utilisation while integrating information on species' physiological performance. As many other marine habitats experience short-term and severe DO fluctuations (Mandic and Regan 2018) this knowledge is relevant and essential to further understand ecological consequences of environmental hypoxia in these dynamic habitats that are often associated with high fisheries value.

We used previously published ecological data from a mangrove-coral reef system experiencing extreme diel and tidal DO fluctuations (Dubuc et al. 2019a) that induced distinct short temporal patterns of mangrove utilisation by fish. We integrated physiological measurements to these ecological data to provide additional insight into understanding short temporal changes in habitat utilisation modulated by environmental hypoxia. Four representative fish species that were recorded using mangrove habitats at varying DO ranges were selected, and ecologically relevant experiments were used to characterise their physiological performance in hypoxia. We expected the four species to display different physiological performance in hypoxia. Additionally, we hypothesised that species-specific physiological patterns would match ecological patterns of mangrove habitat use modulated by fluctuating DO *in situ*.

2. Materials and methods

2.1. *Study species*

We previously conducted a field study in a mangrove-coral system in New Caledonia (21°56.971S, 165°59.481E) and tested the impact of key environmental variables on fish assemblage composition, namely water depth, lunar phase, temperature, DO, habitat type, tidal direction, and time of day (for additionnal information refer to Dubuc et al. 2019a). Findings identified DO as the third most important factor, after depth and lunar phase, for explaining variability in fish assemblage composition. Indeed, tidal fluctuations and time of day lead to extreme DO variations in this system, fluctuating from 13.7 to 114.4% saturation and reaching harmful values daily. We further explored species-specific responses to these extreme DO fluctuations and revealed three distinct short temporal patterns of mangrove utilisation across DO among the 36 common fish taxa identified (see Dubuc et al. 2019a for further details). These differences in short temporal patterns were driven by consistent apparent taxa's behavioural DO avoidance thresholds below which they were no longer observed (Fig. 1; Dubuc et al. 2019a). However, with only field data, it was difficult to attribute specific fish responses to DO. Therefore, to further explore the hypothesis of DO driving short temporal variability in fish assemblages, we selected four representative species among the 36 common taxa identified to determine metabolic responses to hypoxia and test for an association between habitat utilisation patterns and physiological performance. Golden-lined spinefoot, *Siganus lineatus*, was commonly observed in mangrove habitats and followed a *Pattern 1* (Dubuc et al. 2019a)—its occurrence was relatively constant across the entire range of DO recorded, including at low DO levels (up to 42.4% saturation; Fig. 1). Pacific seabream, *Acanthopagrus pacificus* (Iwatsuki et al. 2010), followed a *Pattern 2* (Dubuc et al. 2019a)—this species was not recorded at DO below 50.4% saturation, but occurred frequently at 50–60% saturation range (Fig. 1). Pennant

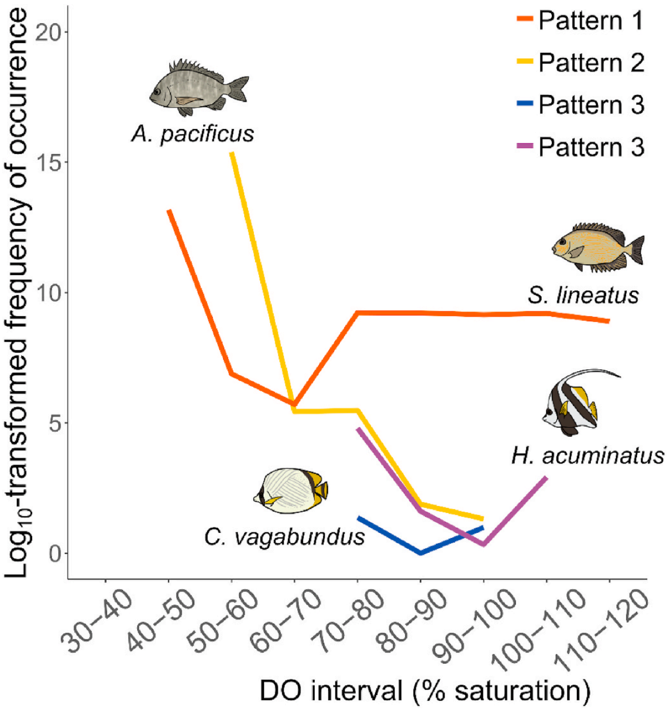

Fig. 1. Patterns of mangrove utilisation for the four study species in relation to short temporal DO fluctuations. Frequencies of occurrence were determined from a study conducted in a mangrove-coral system in New Caledonia where fish were observed with underwater video cameras coupled with DO loggers (Dubuc et al. 2019a). Frequencies of occurrence represent the percentage of time a species was recorded over the sampling period (over 118 h of video recording) at a specific DO interval and is used as a proxy for abundance.

coralfish, *Heniochus acuminatus* and vagabond butterflyfish, *Chaetodon vagabundus*, both followed a *Pattern 3* (Dubuc et al. 2019a)—both species were not recorded at DO below 70.2% saturation. These two species were occasionally observed in mangrove habitats although they are more commonly associated with coral reefs (Fig. 1).

A. pacificus (n = 20) and *S. lineatus* (n = 15) individuals were collected from the Ross River, Townsville, Australia (19°17′2.45"S, 146°48′53.80"E) using hook and line and cast net methods, respectively. Both *H. acuminatus* (n = 15) and *C. vagabundus* (n = 15) were professionally caught using hand-nets in the Coral Sea. Fish were caught in typical habitats in which they occur, providing a representative overview of performance in hypoxia among populations. Fish were maintained in multiple shaded outdoor 900 L flow-through tanks at James Cook University's Marine Aquarium Research Facilities Unit (MARFU). Tanks were continuously supplied with aerated, recirculating UV-filtered saltwater (salinity = 34 psμ). Fish were maintained for a minimum of 10 days post-capture to habituate to captivity and acclimate to the experimental temperature of 28 °C, which represents the average temperature recorded in mangrove habitats over summer months in New Caledonia and North Queensland, Australia (Dubuc et al. 2017, 2019a). Fish were fed twice daily, *ad libitum*, but were fasted 24 h prior to experimentation to ensure a post-absorptive state. We ensured that fish were feeding well and healthy in the days preceding the laboratory experiments.

2.2. Physiological performance measures

Metabolic rate, estimated by measuring oxygen uptake rates ($\dot{M}O_2$), is a powerful metric to characterise species' physiological performance (Chabot et al. 2016), and was adopted here. Five metabolic variables were calculated from the $\dot{M}O_2$ measurements to determine physiological performance in hypoxia that explored capacity to maintain aerobic metabolism, and capacity for survival once aerobic metabolism cannot be sustained. Additional information on the chosen metabolic variables is provided in the appendix.

2.2.1. Capacity to maintain aerobic metabolism (O_{2crit} and α)

Fish can upregulate oxygen extraction and transportation to sustain metabolic needs for aerobiosis as DO declines in the surrounding environment until the critical oxygen level (O_{2crit} or P_{crit}) is reached. At O_{2crit}, the maximum oxygen supply capacity (α) is reached, and aerobic metabolism becomes limited by ambient environmental O_2 availability. As a result, maximum metabolic rate (MMR) is equal to standard metabolic rate (SMR), leaving no excess energy for activities such as swimming or digestion (Claireaux and Chabot 2016). O_{2crit} indicates the DO limit below which metabolic rate is unsustainable and survival is compromised (Fry 1971; Claireaux and Chabot 2016), and is widely interpreted as a measure of hypoxia tolerance (Appendix).

2.2.2. Capacity for survival below O_{2crit} (ILO, time to ILO, $O_{2deficit}$)

O_{2crit} alone does not fully determine the ability of an individual to cope with hypoxia (Speers-Roesch et al. 2013); capacity for survival at DO below O_{2crit} is also a critical facet. As oxygen consumption decreases proportionally with environmental DO below O_{2crit}, the capacity of fish to maintain adenosine triphosphate (ATP) supply depends on a combination of anaerobic metabolism and metabolic rate depression (Richards 2009). However, accumulation of anaerobic end products and acid-base disturbances (Seibel 2011), eventually lead to acute signs of distress such as loss of equilibrium (LOE), indicating the limit to anaerobic capacity, and corresponding to the incipient lethal oxygen level (ILO) or 'near-death' threshold (Appendix 1; Claireaux and Chabot 2016). Capacity for survival below O_{2crit} is a function of hypoxic severity and time (Nilsson and Östlund-Nilsson 2008; Claireaux and Chabot 2016); therefore, the amount of time spent at DO levels below O_{2crit} (time to ILO) was also measured (Appendix). Finally, an index of cumulative ambient oxygen deficit ($O_{2deficit}$) corresponding to the amount of O_2 consumed below O_{2crit} until ILO was calculated to integrate simultaneously information on hypoxic severity and time spent in DO below O_{2crit} (Appendix).

2.2.3. Respirometry design

Oxygen uptake rates were measured with static, intermittent-flow respirometry, following best practices highlighted by Svendsen et al. (2015). As the four fish species were of different sizes and shapes (Table 1), three different models of acrylic, custom-made chambers were built and used (total volume: 10.5 L; 1.9 L; and 1.1 L). Two to six chambers were submerged in a thermoregulated (28.4 ± 0.2 °C) and aerated 300 L experimental tank. Each chamber was connected to two submersible pumps: a flush pump that intermittently replenished water in the chambers between oxygen measurements and a recirculation pump that continuously mixed water within the chamber. A timer was connected to the flush pumps to repeat an 8-min measurement cycle that consisted of a 3-min measurement period followed by a 5-min flush period. DO within the chambers was measured every 2 s using calibrated oxygen-sensitive REDFLASH® dye sensors on contactless spots fitted to the recirculation loop. Each oxygen sensor was connected to a four channel Firesting Optical Oxygen Meter (Pyro Science e. K, Aachen, Germany) via fibre-optic cables. Before each experiment, oxygen sensors were calibrated to 0% saturation (using a sodium sulphite solution) and 100% saturation (using aerated seawater). The experimental tank was surrounded by an opaque curtain and the individual chambers were fitted with dark covers to minimise visual stimuli.

Fish were individually transferred to the chambers using scoop nets and plastic bags to limit stress induced by air exposure. Fish were left undisturbed for around 70 h at normoxia (>80% saturation) to acclimate to the chamber environment and for subsequent determination of SMR. After this period, DO was slowly decreased for about 6 h, from

Table 1

Summary of metabolic variables determined for the four species. Standard metabolic rate (SMR, mg O_2 kg^{-1} min^{-1}); critical oxygen level (O_{2crit}, % sat.); critical oxygen pressure (P_{crit}, kpa); index of cumulative ambient oxygen deficit ($O_{2deficit}$, mg O_2 kg^{-1}); incipient lethal oxygen level (ILO, % saturation); time to incipient lethal oxygen level (Time to ILO, hh:mm); maximum oxygen supply capacity (α, mg O_2 kg^{-1} min^{-1} kpa^{-1}). For each variable, the mean and standard error (±SE) are provided.

Species	n	Mass (g)	SMR	O_{2crit}	P_{crit}	$O_{2deficit}$	ILO	Time to ILO	α
S. lineatus 	15	96 (±10)	1.72 (±0.11)	13.0 (±0.7)	2.3	85.8 (±15.6)	7.0 (±0.5)	02:04 (±00:14)	0.76 (±0.04)
A. pacificus 	20	62 (±6)	2.59 (±0.13)	20.0 (±0.8)	3.5	103.1 (±11.9)	9.8 (±0.5)	01:44 (±00:09)	0.75 (±0.04)
C. vagabundus 	15	51 (±3)	1.97 (±0.11)	20.2 (±0.7)	3.5	39.8 (±7.0)	13.1 (±0.6)	01:03 (±00:07)	0.57 (±0.03)
H. acuminatus 	15	223 (±6)	1.52 (±0.08)	18.7 (±0.8)	3.3	33.1 (±4.7)	11.7 (±0.4)	01:05 (±00:06)	0.48 (±0.03)

100% saturation until fish lost equilibrium (decreasing rate of around 15% saturation per hour) using nitrogen gas connected to a degassing column. This decreasing rate simulated the natural DO fluctuations recorded in mangrove areas harbouring the four tested species (Fig. 2; Dubuc et al. 2019a). ILO was recorded as the DO level at which the individual was no longer able to elicit a righting response (LOE). The time at ILO was recorded and the fish was then removed from the chamber, wet weighed, measured, and transferred to a recovery tank with 100% saturated water. DO was measured in all chambers for 30 min before and after introduction of fish for subsequent determination of background respiration. To limit bacterial growth, all respirometry equipment (experimental tank, degassing column, chambers, connecting pipes and pumps) was bleached following the completion of each trial and the experimental tank was continuously supplied with UV-filtered seawater until the beginning of the hypoxia challenge.

2.3. Calculations and statistical analyses

All oxygen uptake rate measurements (MO_2 in mg O_2 kg^{-1} min^{-1}) were calculated from the slope of the decline in oxygen concentration according to the following formula (Steffensen 1989; Collins et al. 2013) using the commercial software LabChart v. 8.1.10 (ADInstruments, Sydney, NSW, Australia):

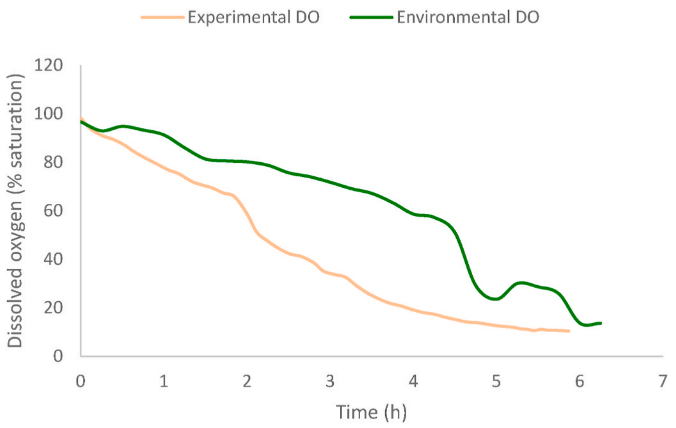

Fig. 2. Rates of DO decline in the natural environment and during the experiments. The green curve represents a typical DO profile obtained from a study conducted in Bouraké, New Caledonia (Dubuc et al. 2019a) and the orange curve represents a typical DO decline during the respirometry trials. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$$\dot{M}O_2 = \frac{\Delta O_2}{\Delta t} \times V \times \frac{1}{M}$$

where ΔO_2 is the variation in oxygen concentration corrected from the background respiration (mg L^{-1}), Δt is the duration of the measurement period (min), V is the volume of the chamber (L) and M is fish body mass (kg). Background respiration was modelled by an exponential function when correcting fish MO_2 (Zwietering et al. 1990).

The SMR was estimated by removing MO_2 measurements from the first 10 h (estimated chamber acclimation period) and from the hypoxia challenge using the calcSMR function in fishMO2 R package (Claireaux and Chabot 2016). The quantile method ($p = 0.2$) was deemed the most appropriate to calculate SMR on the remaining MO_2 measurements as coefficients of variation of the mean of the lowest normal distribution (MLND) were >5.4 in most cases (Claireaux and Chabot 2016). Then, after adding back the MO_2 measurements from the hypoxia challenge, two functions from the R package fishMO2 were used to calculate and visualise the O_{2crit}: calcO2crit and plotO2crit. The O_{2crit} was determined as the intersection of the horizontal line determining SMR and the linear regression between DO and MO_2 once MO_2 became proportional to DO (Claireaux and Chabot 2016). A recent study suggests that α is a more accurate and relevant measure than O_{2crit} to determine when aerobic metabolism becomes oxygen limited, therefore it was calculated here (Seibel et al. 2021). We used the measured α-method and averaged the three highest α_0 values ($\alpha_0 = MO_2/DO$) to obtain a more conservative α (Seibel et al. 2021). $O_{2deficit}$ was determined by plotting MO_2 across time and then by calculating the area between the horizontal line representing SMR and the MO_2 curve between O_{2crit} and ILO. A pseudo-integration was conducted to calculate the area, as described in Claireaux and Chabot (2016):

$$O_{2deficit} = \sum_{n=0}^{n=end} (\dot{M}O_2 - SMR) \times *(t_{n+1} - t_n)$$

Results were analysed using a one-way ANOVA and Tukey HSD post hoc test to identify significant differences between species' physiological performance in hypoxia. When normality and/or homoscedasticity were not met, a Kruskal Wallis test was used in combination with a Dunn's post-hoc test. Body mass was explored as a potential covariate within species, but no significant relationships were detected. Non-significant Pearson correlations were however observed between O_{2crit} and body mass for *H. acuminatus* (Pearson: $R^2 = 0.21$, $P = 0.09$) and between ILO and body mass for *C. vagabundus* (Pearson: $R^2 = 0.22$, $P = 0.08$) and *H. acuminatus* (Pearson: $R^2 = 0.21$, $P = 0.08$). All statistical analyses were conducted in R v.3.1.3 (R Core Team 2014).

2.4. Ecological insights

2.4.1. Metabolic index

Metabolic index (MI) is an insightful metric to determine metabolically suitable habitats and can be calculated using O_{2crit} (Deutsch et al. 2015). MI is defined as the ratio of environmental oxygen supply to organism metabolic needs and incorporate the effect of both temperature and oxygen availability (Seibel and Deutsch 2020). MI has proven to be an informative measure of habitat suitability with an average critical value of 3.3 delimiting geographical range limits for numerous marine species (Deutsch et al. 2015). Therefore, a MI value below 3.3 may indicate a critical threshold for species below which physiological limits are reached, and habitat becomes metabolically unsuitable. We calculated the MI for the minimum DO value at which species were respectively observed in their natural environment at Bouraké at the prevailing temperature (Fig. 1; Dubuc et al. 2019a). As MI and P_{crit} were determined at the same experimental temperature of 28.4 °C, the following equation was used (Deutsch et al. 2015, 2020):

$$MI = PO_2/P_{crit}$$

2.4.2. In situ exposure to DO levels below O_{2crit}

To determine to what extent mangrove habitats can become unsuitable, we also estimated how much time each species would have been exposed to DO below their O_{2crit}, i.e. DO levels compromising survival, in their natural environment. We plotted cumulative frequency curves of DO recordings from Annandale wetland, connected to the Ross River in Townsville, Australia (Dubuc et al. 2017) where *S. lineatus* and *A. pacificus* were both observed, and at Bouraké, New Caledonia, where all four species were observed (Dubuc et al. 2019a). The average O_{2crit} values determined for each species were plotted on the cumulative DO frequency plots to estimate the percentage of time these species would have been exposed to DO below their O_{2crit} if remaining at these sites.

3. Results

All raw data are freely available online on Mendeley Data repository: https://doi.org/10.17632/hkjpmb9gsd.1 (Dubuc, 2021). They comprise raw MO_2 data, figures showing SMR and O_{2crit} determination, as well as the value of each metabolic variable for each individual tested.

3.1. Physiological performance

SMR significantly differed between species (one-way ANOVA: $F = 18.04$, $P < 0.0005$), with *A. pacificus* having higher basal metabolic costs than the other species. *H. acuminatus* on the other hand had the lowest SMR, followed by *S. lineatus* then by *C. vagabundus,* even though non-significant differences were recorded between *S. lineatus* and the two reef species. The four study species displayed marked differences in physiological performance in hypoxia characterised by O_{2crit} (one-way ANOVA: $F = 17.49$, $P < 0.0001$), $O_{2deficit}$ (Kruskal Wallis: $\chi^2 = 20.744$, $P < 0.0005$), ILO (Kruskal Wallis: $\chi^2 = 38.493$, $P < 0.0001$), time to ILO (Kruskal Wallis: $\chi^2 = 18.346$, $P < 0.0001$) and α (one-way ANOVA: $F = 13.68$, $P < 0.0001$) (Table 1; Fig. 3).

3.1.1. Critical oxygen level (O_{2crit})

S. lineatus had a significantly lower O_{2crit} (13% saturation) than *A. pacificus*, *C. vagabundus* and *H. acuminatus* (20, 20.2 and 18.7% saturation respectively; Tukey HSD: $P < 0.0001$ for all significant comparisons); however, O_{2crit} was not significantly different among *A. pacificus*, *C. vagabundus* and *H. acuminatus*.

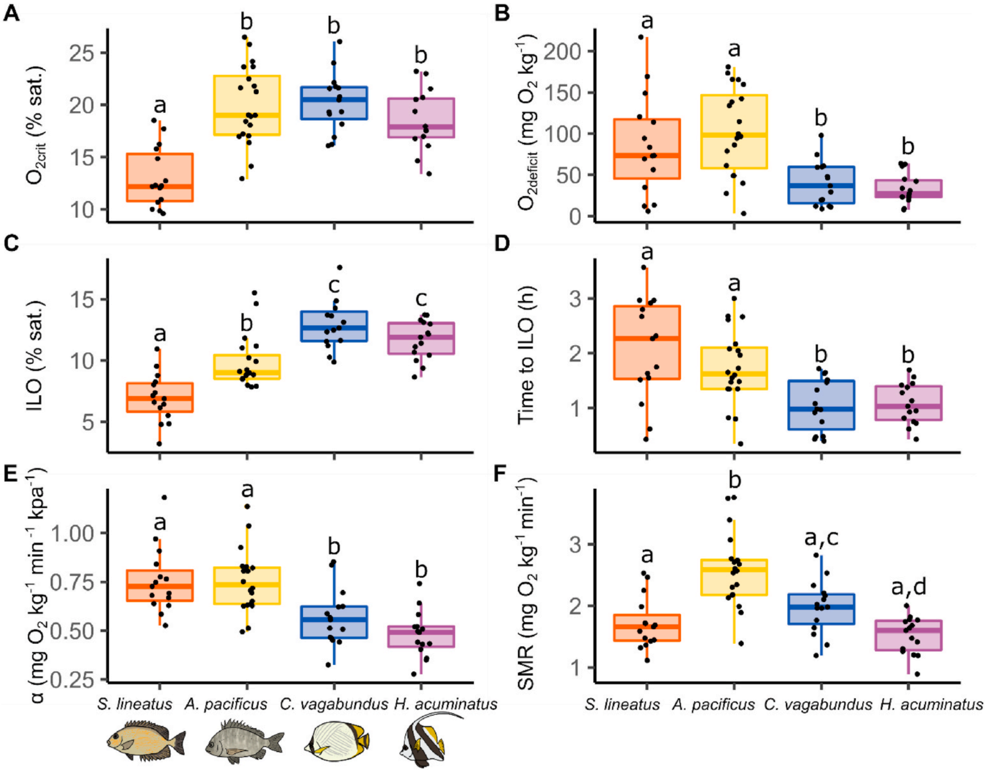

Fig. 3. Variations in hypoxia tolerance among four fish species utilising mangrove habitats characterised by different facets: A) O_{2crit} (% saturation); B) $O_{2deficit}$ (mg O_2 kg^{-1}); C) ILO (% saturation); D) Time to ILO (hour); E) α (mg O_2 kg^{-1} min^{-1} kpa^{-1}); F) SMR (mg O_2 kg^{-1} min^{-1}) Differential letters above boxes denote statistically different values among species ($P < 0.05$). Boxes represent the 25th and 75th percentiles and the median.

3.1.1.1. Index of cumulative ambient oxygen deficit ($O_{2deficit}$). *S. lineatus* showed a greater $O_{2deficit}$ than *H. acuminatus* and *C. vagabundus* (Dunn's test: $P < 0.01$ and $P < 0.05$ respectively). Likewise, *A. pacificus* displayed a greater $O_{2deficit}$ than *H. acuminatus* and *C. vagabundus* (Dunn's test: $P < 0.0001$ and $P < 0.0005$ respectively). No significant differences in $O_{2deficit}$ were found among the two estuarine species (*S. lineatus* and *A. pacificus*) or the two reef species (*H. acuminatus* and *C. vagabundus*).

3.1.2. Incipient lethal oxygen level (ILO)

Differences in ILO were observed among the species, with *S. lineatus* losing equilibrium at lower DO levels than *A. pacificus* (7 and 9.8% saturation respectively; Dunn's test: $P < 0.005$), *H. acuminatus* (11.7% saturation; Dunn's test: $P < 0.0001$) and *C. vagabundus* (13.1% saturation; Dunn's test: $P < 0.0001$). *A. pacificus* also lost equilibrium at lower DO levels than *H. acuminatus* and *C. vagabundus* (Dunn's test: $P < 0.05$ and $P < 0.0005$ respectively). However, ILO was not significantly different between the two reef fish species.

3.1.3. Time to incipient lethal oxygen level (Time to ILO)

Time to ILO also differed among the four species; *S. lineatus* took longer to lose equilibrium compared to *H. acuminatus* and *C. vagabundus* (02:04, 01:05 and 01:03, respectively; Dunn's test: $P < 0.0005$ for both comparisons). Similarly, time to ILO for *A. pacificus* (01:44) was longer than *H. acuminatus* and *C. vagabundus* (Dunn's test: $P < 0.005$ for both comparisons). However, time to ILO did not differ between the two estuarine species or between the two reef species.

3.1.4. Maximum oxygen supply capacity (α)

S. lineatus had a higher α than *C. vagabundus* and *H. acuminatus* (Dunn's test: $P < 0.005$ and $P < 0.0005$ respectively). Likewise, *A. pacificus* had a higher α than *C. vagabundus* and *H. acuminatus* (Dunn's test: $P < 0.005$ and $P < 0.0005$ respectively). However, there was no significant difference between the two estuarine species or between the two reef species.

3.2. Ecological insights

To investigate the potential impact of environmental hypoxia on habitat value in mangrove systems, we used our MI and O_{2crit} values to determine habitat suitability at sites where our study species are known to inhabit. MI values revealed that for the minimum DO at which species were observed *in situ* in Bouraké (70.2% saturation, 50.4% saturation and 42.4% saturation for *C. vagabundus* and *H. acuminatus*, *A. pacifcus*, *S. lineatus*, respectively) their respective MI were close to the 3.3 average reported as the physiological limits for many species (Deutsch et al. 2015). Indeed, MI was equal to 3.5 for *C. vagabundus*, 3.7 for *H. acuminatus*, 2.5 for *A. pacificus* and 3.2 for *S. lineatus*. As DO levels below O_{2crit} compromise survival, we also determined for each species the potential time spent below O_{2crit} in two different mangrove systems where they inhabit. Cumulative DO frequency curves obtained for the two sites where the study species were observed revealed species-specific differences in exposure time to DO below O_{2crit} (Fig. 4). In Annandale wetland, DO declined to levels equal to or below the O_{2crit} of *A. pacificus* and *S. lineatus* for about 4% of the recorded time (a total of 24h over 25 days of recordings), with hypoxic episodes lasting from several minutes up to 7h (Fig. 4; Dubuc et al. 2017). In Bouraké, DO declined to levels equal to or below the O_{2crit} of *A. pacificus*, *C. vagabundus* and *H. acuminatus* on four occasions lasting up to 45 min (a total of 1h30 over 8 days of recordings), while DO was never below the O_{2crit} determined for *S. lineatus* (Fig. 4; Dubuc et al. 2019a).

4. Discussion

Our overarching aim was to integrate physiological measures with ecological data to test for an association between physiological performance, and habitat use patterns modulated by extreme environmental variability. Our results in fact support the use of a collective assessment of ecologically relevant metabolic variables to help link ecological patterns with underlying environmental drivers such as hypoxia. This study has shown that individuals using dynamic habitats are dealing with environmental conditions that have the potential to impair their physiological functions daily. We stress the importance to consider short temporal variability in dynamic environments that can represent a great challenge for individuals, comparable to variations over large spatial scales. As environmental variability is forecasted to intensify as a consequence of anthropogenic actions, it is crucial to focus on the drivers and mechanisms underlying short temporal patterns if we are to accurately determine and predict its ecological effects on dynamic ecosystems.

4.1. Differential physiological performance in hypoxia and habitat use strategies among species

The four fish species displayed differential physiological performance in hypoxia, which closely matched their ecological patterns of mangrove habitats utilisation *in situ*. *S. lineatus* was remarkably performant in hypoxia, and data collected *in situ* (Dubuc et al. 2019a) showed that it was also the most frequently recorded species including at

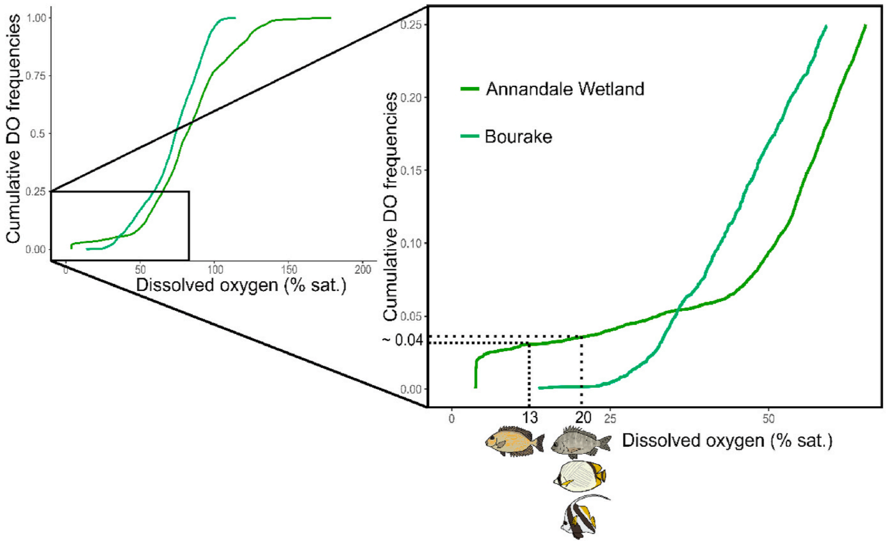

Fig. 4. Exposure to DO levels below species-specific O_{2crit} in the natural environment. Species-specific O_{2crit} is plotted on the x-axis. The intersection of a species' O_{2crit} with the cumulative DO frequency curve was used to estimate the percentage of recorded time that DO was equal to, or below, a species' O_{2crit} at a specific location. The two curves represent the cumulative DO frequencies recorded at two mangrove systems over several days: Annandale Wetland, Australia (25 days of recordings) where *S. lineatus* and *A. pacificus* have been observed (Dubuc et al. 2017), and Bouraké, New Caledonia (8 days of recordings) where the four study species have been observed (Dubuc et al. 2019a).

the lowest DO levels. The O_{2crit} of *S. lineatus* (13% saturation) was even lower than that of barramundi, *Lates calcarifer,* another iconic fish species associated with mangrove habitats in the tropical Indo-Pacific (16–20% saturation; Collins et al. 2016). Moreover, the O_{2crit} of *S. lineatus* was equal to the lowest value recorded among other fish species primarily associated with coral reefs (13–34% saturation; Nilsson and Ostlund-Nilsson 2004; Wong et al. 2018). In contrast, the two reef fish species examined here were indistinctly the least performant in hypoxia but also the least commonly observed species with the highest apparent behavioural avoidance threshold *in situ* (Dubuc et al. 2019a).

The evidence suggesting that species commonly found in mangrove habitats can cope with low DO indicates that they likely have specific physiological mechanisms allowing them to prosper in these hypoxic environments (Wells 2009; Borowiec et al. 2015). For instance, mechanisms conferring a higher capacity for oxygen extraction and tissue delivery (Childress and Seibel 1998), could explain the higher O_{2crit} found for *S. lineatus,* indicating that it is able to maintain metabolic rates at lower DO, and consequently, delay its behavioural avoidance response to environmental hypoxia *in situ* (Mandic et al. 2009). This hypothesis is further supported by the higher maximum oxygen supply capacity recorded for *S. lineatus*, as well as for *A. pacificus* indicating they both have a better capacity for oxygen extraction and transportation in support of metabolic demand (Seibel and Deutsch 2020). Other mechanisms can increase survival below O_{2crit}, which is achieved by utilising anaerobic pathways and metabolic depression (Richards 2009). Fish can, for instance, develop physiological mechanisms increasing tissue glycogen and causing changes in enzyme and protein expression patterns to improve anaerobiosis (Richards 2009; Speers-Roesch et al. 2013). The higher $O_{2deficit}$ recorded for *S. lineatus* and *A. pacificus* indicates that they can remain longer and at lower DO levels below O_{2crit}. At this stage, species mainly rely on anaerobiosis to meet metabolic demands, or must perform metabolic depression (Richards 2009). Therefore, this result suggests that these species may have a better ability to shift toward anaerobiosis and metabolic depression, thus making them more capable of spending time in hypoxic environments before eliciting behavioural avoidance responses. Mechanisms enhancing capacity to maintain aerobic metabolism, and mechanisms increasing survival below O_{2crit} may be synergistic, but they may also be discrete (McArley et al. 2019) which could explain why *A. pacificus* was able to access and remain in mangrove habitats at lower DO than the two reef fish species despite not having a lower O_{2crit}.

While O_{2crit} is often used as a species-specific threshold for hypoxia tolerance and provides useful information, it did not correspond to the DO levels at which species seemingly displayed behavioural avoidance *in situ*. Most of the recorded time, DO levels were above the O_{2crit} of the two reef fish species, and were comparable to values of O_{2crit} for other reef fish species (Nilsson and Ostlund-Nilsson 2004; Wong et al. 2018). These values indicate that, similarly to *S. lineatus* and *A. pacificus*, reef fish species could potentially use mangrove habitats even at the lowest DO values recorded (up to 30% saturation) without being exposed to lethal values. However, the two reef fish species, as well as most other reef fish species observed in Bouraké's mangrove system, were never recorded at DO below 70–80% saturation (Dubuc et al. 2019a), much before their O_{2crit}. Interestingly, this threshold is often considered as the limit for normoxia while conducting experiments, below which stress can occur and lead to long-term effects such as reductions in growth or reproduction (Wu 2002; Chabot and Claireaux 2008; Svendsen et al. 2015). At 70.2% saturation, which was the lowest DO at which *C. vagabundus* and *H. acuminatus* were recorded, their MI was close to the average 3.3 determined as a limit for habitat suitability for many marine species (Deutsch et al. 2015). This suggests that species have relatively limited scope for sustained activity at DO below 70% saturation for an average temperature of 28.4 °C and could explain why they were not observed below this threshold *in situ* (Duncan et al. 2020). Indeed, fish in the environment engage in many physiological functions, usually supressed during experiments, such as digestion, swimming, foraging and avoiding predators. These activities increase the metabolic demand above SMR and concurrently diminish the metabolic scope available to respond to hypoxia (Wang et al. 2009; Jourdan-Pineau et al. 2010; Zambonino-Infante et al. 2017). Additionally, when environmental hypoxia occurs, it can be accompanied by other stressors such as high temperature, low pH, or high concentration of toxins that can reduce their ability to cope with hypoxia (Wu 2002), and consequently lead to fish responding to environmental hypoxia much before it reaches their O_{2crit}. Furthermore, O_{2crit} depends on temperature, and variation around its value for each species is expected *in situ* (Nilsson et al. 2010; Slesinger et al. 2019) which could add to the disparity observed between O_{2crit} and apparent behavioural avoidance thresholds. Therefore, O_{2crit} is probably underestimating the risk that environmental hypoxia poses in these systems and MI could be a more relevant measure.

Our results support the idea that O_{2crit} does not fully represent species hypoxia tolerance (Wood 2018; Regan et al. 2019; Seibel et al. 2021), and therefore, cannot correctly predict behavioural avoidance. The corresponding α that was calculated allowed to identify *A. pacificus* has being more performant in hypoxia than the two reef fish species, which is more in adequation with our field observations. However, it did not allow to differentiate between *S. lineatus* and *A. pacificus,* so we could not conclude that the alpha-method was a better method to estimate the limitation for aerobic metabolism in our case (Seibel et al. 2021). However, our collective assessment of five metabolic variables, provided complementary information to characterise physiological performance in hypoxia and establish an association between species' physiological performance and their patterns of habitat utilisation. These results suggest that, together, these metabolic variables can provide valuable information to understand and predict short temporal variability in ecological patterns. Even if further analyses are necessary to confirm this trend, our results suggest that fish species frequently observed in temporarily hypoxic environments may have evolved physiological strategies that increase their ability to cope with intermittent environmental hypoxia (Borowiec et al. 2015), explaining why they are able to use more often and more abundantly these habitats (Dubuc et al. 2019a). Consequently, DO fluctuations and species-specific ability to cope with hypoxia are likely critical drivers of ecological changes at short temporal scales in dynamic environments.

Recently it has been suggested that O_{2crit} should be determined at maximum metabolic rate (MMR) using the alpha-method (Seibel and Deutsch 2020; Seibel et al. 2021), which could confirm whether a species has specifically evolved to better tolerate environmental hypoxia and could also have a greater predictive power for avoidance thresholds. It would be interesting to implement this technique and fully explore these hypotheses with ecological data in the future. Another interesting avenue will be to determine sublethal indicators following diel-cycling hypoxia exposure such as changes in haemoglobin-O_2 saturation curve, gill ventilation rate or cardiac output that could provide an estimate of when physiological functions start to become impaired and therefore aid in accurately predicting behavioural avoidance thresholds *in situ* (Richards 2009; Rummer and Brauner 2015).

4.2. Ecological implications of short temporal variability in DO for dynamic environments

Environmental hypoxia most likely temporarily reduces habitat value of dynamic environments and drives important short temporal ecological changes. *In situ* measurements conducted in areas commonly utilised by the four study species showed that DO temporarily reached levels below their O_{2crit} (Dubuc et al. 2017, 2019a). Being able to perform well in hypoxia could reduce metabolic costs associated with environmental hypoxia and concurrent stressors and allow species to remain in mangrove habitats for longer periods of time and thus more efficiently utilise them. There are several potential benefits to remaining in adverse conditions when most other taxa must leave, including opportunistic feeding with limited competition and reduced predation—this has been referred to as the 'hypoxic refuge' theory (Chapman et al. 2002; Chapman 2015; Hedges and Abrahams 2015). Both *S. lineatus* and *A. pacificus* are known to feed on mangrove roots and mangrove-associated sesarmid crabs, respectively (Sheaves and Molony 2000; Fox and Bellwood 2011), therefore, their relatively high performance in hypoxia may allow them to benefit from a safe and high-value feeding ground. The extreme pattern of utilisation recorded for *A. pacificus* strongly supports the hypoxic refuge theory—this species was most frequently observed at the lowest limits of its behavioural avoidance threshold (50.4% saturation) and then gradually became scarcer as DO increased (Fig. 1).

The constraint that environmental hypoxia poses—favouring species able to withstand challenging conditions and temporarily or permanently excluding sensitive species—may help explain the relatively low fish diversity found in some intertidal mangrove systems (Thollot 1992; Reis-Filho et al. 2016; Sheaves et al. 2016). Indeed, species not able to cope with low DO are probably not venturing into mangrove habitats experiencing hypoxia as the physiological and ecological costs associated would be too high. The constraint of environmental hypoxia can also help explain the low contribution of coral reef fishes to mangrove fish assemblages in some areas (Thollot 1992; Dorenbosch et al. 2005; Barnes et al. 2012; Dubuc et al. 2019b). Coral reef species usually live in environments with relatively high and stable DO (Wong et al. 2018; Nelson and Altieri 2019), even though some species may experience intermittent hypoxia at night in branching coals (Nilsson and Ostlund-Nilsson 2004; Nelson and Altieri 2019). Therefore, the challenging conditions of mangrove habitats may act as a strong selective factor in determining fish communities, allowing only a few species to temporarily utilise these environments.

Individuals repeatedly exposed to challenging conditions can develop acclimation and adaptation mechanisms that may allow them to use and persist in these environments. As this study used reef fish individuals inhabiting coral reef systems, it did not account for potential mechanisms that could have been developed by individuals living in suboptimal conditions, like the ones recorded in Bouraké, that could confer them additional performance in hypoxia. Our results suggest that reef fish species avoid DO conditions below 70% saturation and that they are therefore not, or rarely, exposed to stressful conditions in Bouraké. Consequently, we believe it is unlikely they have developed acclimation or adaptation mechanisms different to the individuals living in coral reef habitats that were tested here, and we would not expect performance traits to be different. It would however be interesting to test this hypothesis by selecting and comparing performance traits among reef fish subpopulations living in habitats experiencing more hypoxic, acidic and warm conditions like in Bouraké with subpopulations living in typical coral reef systems. Such comparison may constitute an interesting avenue of research and help understand traits and mechanisms that may promote resilience and persistence in a changing world (Chapman 2015).

Previous studies have established that physiological performance in hypoxia is a key determinant in setting species distribution (e.g. McKinsey and Chapman 1998; Hilton et al. 2008; Mandic et al. 2009). However, short temporal variability (over a few hours) in habitat quality within an occupied niche has been overlooked, although accounting for temporal variability in species responses to environmental conditions is key to understand and predict changes in ecosystem processes (Kroeker et al. 2020). This study is the first to test for an association between short temporal variations in habitat use as a response to changing environmental hypoxia and species' physiological performance. The results support the hypothesis that DO is a crucial environmental variable driving drastic changes in fish communities, and consequently in predator-prey interactions, productivity and transfer of energy, over short temporal scales. Therefore, species' hypoxia tolerance is likely to be a crucial physiological trait influencing temporal variations in ecosystem functions. Likewise, many valuable environments experience diel- and tidal-cycling hypoxia such as estuaries, coral reefs, intertidal zones and lakes (Mandic and Regan 2018), and temporal variability in fish communities responses is also likely to occur. Consequently, we suggest that integrating information on differential physiological performance and habitat use at relevant temporal scales in dynamic environments could reveal a temporal dimension in ecological patterns and consequences of hypoxia that has not been previously considered.

4.3. Outlook

Accounting for short temporal variability in environmental conditions is essential to accurately define ecological patterns. Organisms respond to temporal fluctuations by altering their physiology and behaviour which ultimately dictate their utilisation of habitats based on their needs and tolerance, affecting population and community dynamics and ultimately ecosystem functioning. Understanding the physiological coupling of habitat use and environmental change at relevant temporal scales is therefore key to comprehend the ecological consequences of temporal variability but is often complex to achieve. Integrating multiple measures of physiological traits with ecological data can provide valuable information to understand organisms' responses to changes in environmental conditions, and help predict the ecological consequences of temporal variability. Such approaches can also provide insights into the risks that expected increase in environmental variability poses by revealing how close organisms are to their physiological limits in a natural setting to predict what would be the ecological costs of future changes. Another interesting avenue of research is to identify the role of these temporally fluctuating environments in providing natural refuges into future climate changes with organisms being pre-conditioned to extreme environmental conditions.

Authors contributions

AD, GC and JR conceived the ideas and designed methodology;
AD and LC collected the data;
AD and LC analysed the data;
AD led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All raw data are freely available online on Mendeley Data repository: https://doi.org/10.17632/hkjpmb9gsd.1 (Dubuc, 2021). They comprise raw MO_2 data, figures showing SMR and O_{2crit} determination, as well as the value of each metabolic variable for each individual tested.

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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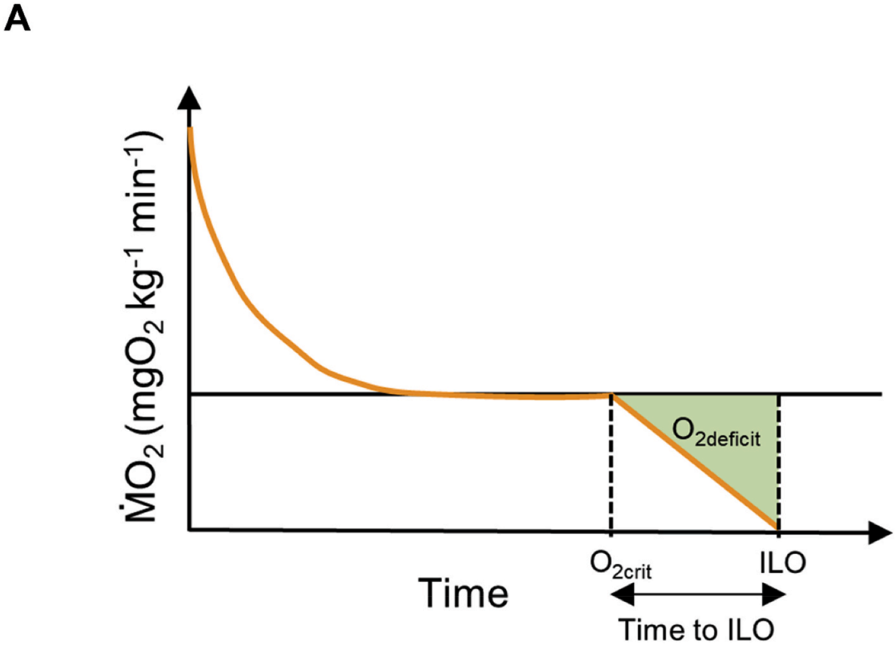
Appendix. Characteristics of the different metabolic variables measured in this study. (A) Schematic representation of the different metabolic variables measured using idealised fish oxygen uptake rates across time (orange line); (B) Definition and visual explanation for which direction was considered an increase in physiological performance for each metabolic variable



B

Metabolic variables	Critical oxygen level (O_{2crit}): O_2 level below which aerobic metabolism cannot be maintained	High	Low
	Incipient lethal oxygen level (ILO): O_2 level indicating the limit to anaerobic capacity	High	Low
	Time to ILO: amount of time spent at O_2 levels below O_{2crit} until ILO	Low	High
	Index of cumulative ambient oxygen deficit ($O_{2deficit}$): amount of O_2 consumed below O_{2crit} until ILO	Low	High
	Maximum oxygen supply capacity (α): constant indicating species' capacity to supply oxygen at O_{2crit}	Low	High

References

Barnes, L., Bellwood, D.R., Sheaves, M., Tanner, J.K., 2012. The use of clear-water non-estuarine mangroves by reef fishes on the Great Barrier Reef. Marine Biology 159, 211–220.

Bauer, S., Hoye, B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 344, 1242552.

Bernhardt, J.R., O'Connor, M.I., Sunday, J.M., Gonzalez, A., 2020. Life in fluctuating environments. Philos. Trans. R. Soc. Lond. B Biol. Sci. 375, 20190454.

Borowiec, B.G., Darcy, K.L., Gillette, D.M., Scott, G.R., 2015. Distinct physiological strategies are used to cope with constant hypoxia and intermittent hypoxia in killifish (*Fundulus heteroclitus*). J. Exp. Biol. 218, 1198–1211.

Bouyoucos, I.A., Trujillo, J.E., Weideli, O.C., Nakamura, N., Mourier, J., Planes, S., Simpfendorfer, C.A., Rummer, J.L., 2021. Investigating links between thermal tolerance and oxygen supply capacity in shark neonates from a hyperoxic tropical environment. Sci. Total Environ. 782, 146854.

Boyd, P.W., Cornwall, C.E., Davison, A., Doney, S.C., Fourquez, M., Hurd, C.L., Lima, I. D., McMinn, A., 2016. Biological responses to environmental heterogeneity under future ocean conditions. Global Change Biol. 22, 2633–2650.

Bozinovic, F., Calosi, P., Spicer, J.I., 2011. Physiological correlates of geographic range in animals. Annual Review of Ecology, Evolution, and Systematics 42, 155–179.

Brady, D.C., Targett, T.E., 2013. Movement of juvenile weakfish *Cynoscion regalis* and spot *Leiostomus xanthurus* in relation to diel-cycling hypoxia in an estuarine tidal tributary. Mar. Ecol. Prog. Ser. 491, 199–219.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. Science 359, eaam7240.

Chabot, D., Claireaux, G., 2008. Environmental hypoxia as a metabolic constraint on fish: the case of Atlantic cod, *Gadus morhua*. Mar. Pollut. Bull. 57, 287–294.

Chabot, D., McKenzie, D.J., Craig, J.F., 2016. Metabolic rate in fishes: definitions, methods and significance for conservation physiology. J. Fish. Biol. 88, 1–9.

Chapman, L.J., 2015. Low-oxygen lifestyles. In: Riesch, R., Tobler, M., Plath, M. (Eds.), Extremophile Fishes: Ecology, Evolution, and Physiology of Teleosts in Extreme Environments. Springer International Publishing, Cham, pp. 9–33.

Chapman, L.J., Chapman, C.A., Nordlie, F.G., Rosenberger, A.E., 2002. Physiological refugia: swamps, hypoxia tolerance and maintenance of fish diversity in the Lake Victoria region. Comp. Biochem. Physiol. Mol. Integr. Physiol. 133, 421–437.

Chapman, L.J., McKenzie, D.J., 2009. In: Richards, Jeffrey G., Farrell, A.P., Colin, J.B. (Eds.), Behavioral Responses and Ecological Consequences. Fish Physiology: Hypoxia. Academic Press, pp. 25–77.

Childress, J.J., Seibel, B.A., 1998. Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. J. Exp. Biol. 201, 1223.

Chown, S.L., Gaston, K.J., Robinson, D., 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. Funct. Ecol. 18, 159–167.

Claireaux, G., Chabot, D., 2016. Responses by fishes to environmental hypoxia: integration through Fry's concept of aerobic metabolic scope. J. Fish. Biol. 88, 232–251.

Collins, G.M., Clark, T.D., Carton, A.G., 2016. Physiological plasticity *v.* inter-population variability: understanding drivers of hypoxia tolerance in a tropical estuarine fish. Mar. Freshw. Res. 67, 1575–1582.

Collins, G.M., Clark, T.D., Rummer, J.L., Carton, A.G., 2013. Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). Conservation Physiology 1 cot029-cot029.

D'Autilia, R., Falcucci, M., Hull, V., Parrella, L., 2004. Short time dissolved oxygen dynamics in shallow water ecosystems. Ecol. Model. 179, 297–306.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., Huey, R.B., 2015. Climate change tightens a metabolic constraint on marine habitats. Science 348, 1132.

Deutsch, C., Penn, J.L., Seibel, B., 2020. Metabolic trait diversity shapes marine biogeography. Nature 585, 557–562.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I., van der Velde, G., 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density coral and diversity on adjacent reefs. Mar. Ecol. Prog. Ser. 302, 63–76.

Dubuc, A., 2021. Data from: Association between physiological performance and short temporal changes in habitat utilisation modulated by environmental factors. Mendeley Data V.1. https://doi.org/10.17632/hkjpmb9gsd.1.

Dubuc, A., Baker, R., Marchand, C., Waltham, N.J., Sheaves, M., 2019a. Hypoxia in mangroves: occurrence and impact on valuable tropical fish habitat. Biogeosciences 16, 3959–3976.

Dubuc, A., Waltham, N., Malerba, M., Sheaves, M., 2017. Extreme dissolved oxygen variability in urbanised tropical wetlands: the need for detailed monitoring to protect nursery ground values. Estuar. Coast Shelf Sci. 198, 163–171.

Dubuc, A., Waltham, N.J., Baker, R., Marchand, C., Sheaves, M., 2019b. Patterns of fish utilisation in a tropical Indo-Pacific mangrove-coral seascape, New Caledonia. PloS One 14, e0207168.

Duncan, M.I., James, N.C., Potts, W.M., Bates, A.E., 2020. Different drivers, common mechanism; the distribution of a reef fish is restricted by local-scale oxygen and temperature constraints on aerobic metabolism. Conservation Physiology 8.

Ellis, W.L., Bell, S.S., 2008. Tidal influence on a fringing mangrove intertidal fish community as observed by in situ video recording: implications for studies of tidally migrating nekton. Mar. Ecol. Prog. Ser. 370, 207–219.

Farrell, A., Richards, J., 2009. In: Richards, Jeffrey G., Farrell, A.P., Colin, J.B. (Eds.), Defining Hypoxia: an Integrative Synthesis of the Responses of Fish to Hypoxia. Fish Physiology: Hypoxia. Academic Press, pp. 487–503.

Fox, R.J., Bellwood, D.R., 2011. Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, Siganus lineatus. Funct. Ecol. 25, 1096–1105.

Fry, F.E.J., 1971. The Effect of Environmental Factors on the Physiology of Fish. University of Toronto Press, Toronto.

Hedges, K.J., Abrahams, M.V., 2015. Hypoxic refuges, predator-prey interactions and habitat selection by fishes. J. Fish. Biol. 86, 288–303.

Helmuth, B., 2009. From cells to coastlines: how can we use physiology to forecast the impacts of climate change? J. Exp. Biol. 212, 753.

Hilton, Z., Wellenreuther, M., Clements, K.D., 2008. Physiology underpins habitat partitioning in a sympatric sister-species pair of intertidal fishes. Funct. Ecol. 22, 1108–1117.

Iwatsuki, Y., Kume, M., Yoshino, T., 2010. A new species, *Acanthopagrus pacificus* from the Western pacific (Pisces, Sparidae). Bulletin of the National Museum of Nature and Science 36, 115–130.

Jachowski, D.S., Singh, N.J., 2015. Toward a mechanistic understanding of animal migration: incorporating physiological measurements in the study of animal movement. Conservation Physiology 3.

Jourdan-Pineau, H., Dupont-Prinet, A., Claireaux, G., McKenzie, David J., 2010. An investigation of metabolic prioritization in the european sea bass, *Dicentrarchus labrax*. Physiol. Biochem. Zool. 83, 68–77.

Knight, J.M., Griffin, L., Dale, P.E.R., Sheaves, M., 2013. Short-term dissolved oxygen patterns in sub-tropical mangroves. Estuar. Coast Shelf Sci. 131, 290–296.

Kroeker, K.J., Bell, L.E., Donham, E.M., Hoshijima, U., Lummis, S., Toy, J.A., Willis-Norton, E., 2020. Ecological change in dynamic environments: accounting for temporal environmental variability in studies of ocean change biology. Global Change Biol. 26, 54–67.

Krumme, U., Grinvalds, K., Zagars, M., Elferts, D., Ikejima, K., Tongnunui, P., 2015. Tidal, diel and lunar patterns in intertidal and subtidal mangrove creek fish assemblages from southwest Thailand. Environ. Biol. Fish. 98, 1671–1693.

Lawton, J.H., 1991. From physiology to population dynamics and communities. Funct. Ecol. 5, 155–161.

Mandic, M., Regan, M.D., 2018. Can variation among hypoxic environments explain why different fish species use different hypoxic survival strategies? J. Exp. Biol. 221, jeb161349.

Mandic, M., Todgham, A.E., Richards, J.G., 2009. Mechanisms and evolution of hypoxia tolerance in fish. Proceedings of the Royal Society B 276, 735–744.

Mattone, C., Sheaves, M., 2017. Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests. Estuar. Coast Shelf Sci. 197, 205–213.

McArley, T.J., Hickey, A.J.R., Wallace, L., Kunzmann, A., Herbert, N.A., 2019. Intertidal triplefin fishes have a lower critical oxygen tension (P_{crit}), higher maximal aerobic capacity, and higher tissue glycogen stores than their subtidal counterparts. J. Comp. Physiol. B 189, 399–411.

McKinsey, D.M., Chapman, L.J., 1998. Dissolved oxygen and fish distribution in a Florida spring. Environ. Biol. Fish. 53, 211–223.

Metcalfe, J.D., Le Quesne, W.J.F., Cheung, W.W.L., Righton, D.A., 2012. Conservation physiology for applied management of marine fish: an overview with perspectives on the role and value of telemetry. Phil. Trans. Biol. Sci. 367, 1746–1756.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat. Bot. 89, 155–185.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. Unit. States Am. 105, 19052–19059.

Nelson, H.R., Altieri, A.H., 2019. Oxygen: the universal currency on coral reefs. Coral Reefs 38, 177–198.

Nilsson, G.E., Ostlund-Nilsson, S., 2004. Hypoxia in paradise: widespread hypoxia tolerance in coral reef fishes. Proceedings of the Royal Society B 271, S30–33.

Nilsson, G.E., Ostlund-Nilsson, S., Munday, P.L., 2010. Effects of elevated temperature on coral reef fishes: loss of hypoxia tolerance and inability to acclimate. Comp. Biochem. Physiol. Mol. Integr. Physiol. 156, 389–393.

Nilsson, G.E., Östlund-Nilsson, S., 2008. Does size matter for hypoxia tolerance in fish? Biol. Rev. 83, 173–189.

Portner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315, 95–97.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria accessed May 2019). http://www.R-project.org/.

Regan, M.D., Mandic, M., Dhillon, R.S., Lau, G.Y., Farrell, A.P., Schulte, P.M., Seibel, B. A., Speers-Roesch, B., Ultsch, G.R., Richards, J.G., 2019. Don't throw the fish out with the respirometry water. J. Exp. Biol. 222, jeb200253.

Reis-Filho, J.A., Giarrizzo, T., Barros, F., 2016. Tidal migration and cross-habitat movements of fish assemblage within a mangrove ecotone. Marine Biology 163, 111.

Richards, J.G., 2009. In: Richards, J.G., Farrell, A.P., Brauner, C.J. (Eds.), Metabolic and Molecular Responses of Fish to Hypoxia. Fish Physiology: Hypoxia. Academic Press, pp. 443–485.

Rummer, J.L., Brauner, C.J., 2015. Root effect haemoglobins in fish may greatly enhance general oxygen delivery relative to other vertebrates. PloS One 10, e0139477.

Seibel, B.A., 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J. Exp. Biol. 214, 326.

Seibel, B.A., Andres, A., Birk, M.A., Burns, A.L., Shaw, C.T., Timpe, A.W., Welsh, C.J., 2021. Oxygen supply capacity breathes new life into the critical oxygen partial pressure (P_{crit}). J. Exp. Biol. 224 (8).

Seibel, B.A., Deutsch, C., 2020. Oxygen supply capacity in animals evolves to meet maximum demand at the current oxygen partial pressure regardless of size or temperature. J. Exp. Biol. 223.

Sheaves, M., Johnston, R., Baker, R., 2016. Use of mangroves by fish: new insights from in-forest videos. Mar. Ecol. Prog. Ser. 549, 167–182.

Sheaves, M., Molony, B., 2000. Short-circuit in the mangrove food chain. Mar. Ecol. Prog. Ser. 199, 97–109.

Slesinger, E., Andres, A., Young, R., Seibel, B., Saba, V., Phelan, B., Rosendale, J., Wieczorek, D., Saba, G., 2019. The effect of ocean warming on black sea bass (Centropristis striata) aerobic scope and hypoxia tolerance. PloS One 14, e0218390.

Speers-Roesch, B., Mandic, M., Groom, D.J.E., Richards, J.G., 2013. Critical oxygen tensions as predictors of hypoxia tolerance and tissue metabolic responses during hypoxia exposure in fishes. J. Exp. Mar. Biol. Ecol. 449, 239–249.

Spicer, J.I., 2014. What can an ecophysiological approach tell us about the physiological responses of marine invertebrates to hypoxia? J. Exp. Biol. 217, 46–56.

Steffensen, J.F., 1989. Some errors in respirometry of aquatic breathers: how to avoid and correct for them. Fish Physiol. Biochem. 6, 49–59.

Svendsen, M.B.S., Bushnell, P.G., Steffensen, J.F., 2015. Design and setup of intermittent-flow respirometry system for aquatic organisms. J. Fish. Biol. 88, 26–50.

Thollot, P., 1992. Importance des mangroves pour la faune ichtyologique des récifs coralliens de Nouvelle-Calédonie. Cybium 16, 331–344.

Tyler, R.M., Brady, D.C., Targett, T.E., 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. Estuar. Coast 32, 123–145.

Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences of the United States of America 105, 15452–15457.

Wang, T., Lefevre, S., Thanh Huong, D.T., Cong, N.v., Bayley, M., 2009. In: Richards, Jeffrey G., Farrell, A.P., Colin, J.B. (Eds.), The Effects of Hypoxia on Growth and Digestion. Fish Physiology: Hypoxia. Academic Press, pp. 361–396.

Wells, R.M.G., 2009. In: Richards, Jeffrey G., Farrell, A.P., Colin, J.B. (Eds.), Blood-gas Transport and Hemoglobin Function. Fish Physiology: Hypoxia. Academic Press, pp. 255–299.

Wong, C.C., Drazen, J.C., Callan, C.K., Korsmeyer, K.E., 2018. Hypoxia tolerance in coral-reef triggerfishes (Balistidae). Coral Reefs 37, 215–225.

Wood, C.M., 2018. The fallacy of the P_{crit} – are there more useful alternatives? J. Exp. Biol. 221, jeb163717.

Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. Mar. Pollut. Bull. 45, 35–45.

Zambonino-Infante, J.L., Mazurais, D., Dubuc, A., Quéau, P., Vanderplancke, G., Servili, A., Cahu, C., Le Bayon, N., Huelvan, C., Claireaux, G., 2017. An early life hypoxia event has a long-term impact on protein digestion and growth in juvenile European sea bass. J. Exp. Biol. 220, 1846–1851.

Zwietering, M.H., Jongenburger, I., Rombouts, F.M., van ’t Riet, K., 1990. Modeling of the bacterial growth curve. Appl. Environ. Microbiol. 56, 1875–1881.