

Increased energy expenditure is an indirect effect of habitat structural complexity loss

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Abstract

1. The deterioration of coastal habitats cascades to the decline of associated fauna by reducing trophic resource availability, shelter from predators and nursery grounds. The decline of biogenic habitat structure, such as in kelp forests, coral reefs, mangroves or seagrass beds, often causes a local increase in water flow velocity and wave exposure. The impact of this change in hydrodynamics on the energy expenditure of animals is largely unknown.
2. Here we demonstrate that loss of seagrass beds increases water current velocity, which impacts associated pipefishes through increased energy expenditure. We correlated ventilation frequency with metabolic rate in four pipefish species, to be able to estimate metabolic rates in free-swimming fish. Using a hydrodynamic flume, we then experimentally tested the effect of current velocity and substrate (seagrass or sand) on ventilation frequency and behaviour.
3. Ventilation frequency was consistently higher when they swam on sand substratum compared to seagrass substratum for all species, and this was especially noticeable for the species with prehensile tails (i.e. *Nerophis ophidion*). Seagrass canopies reduced flow velocities by 7%–44%, which increased the overall current exposure that pipefish tolerated. *N. ophidion*, *Syngnathus rostellatus* and *Syngnathus typhle* showed two behavioural responses to currents: holding on to the seagrass canopy, and moving to areas where the current was lower (i.e. bottom) in trials without seagrass. Most of the individuals of all species were unable to maintain position in velocities of 15–18 cm/s on sand substratum.
4. In this work, we demonstrate the reliance on seagrass hydrodynamic shelter of four species of pipefish. Among them, *N. ophidion* showed the highest seagrass shelter dependence and vulnerability, while *S. rostellatus* and *S. typhle* are potentially more resilient to vegetation changes. Increased energy expenditure is thus another impact on fishes as seagrass beds and other structural habitats continue to decline in coastal areas.

KEYWORDS

Entelurus, habitat degradation, metabolic rate, *Nerophis*, oxygen consumption, syngnathid conservation, *Syngnathus*, ventilation rates

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1 | INTRODUCTION

Global change, the cumulative anthropogenic effects of local and global activities, is a multifaceted process that poses major risks to species and ecosystems. Climate change, eutrophication, hypoxia or habitat destruction are some of the ongoing processes that result in biodiversity loss and the impairment of ecosystem functioning. Organisms may be directly affected by changing environmental conditions (i.e. heat waves that surpass the maximum temperature tolerated by a population; Freitas et al., 2010; Smale et al., 2019) but they have physiological and behavioural mechanisms to attenuate the effects of the changes (Helmuth et al., 2005; Kearney et al., 2009). Indirect effects of environmental change on organisms may stem from the reduction of prey availability, increased competition or predation pressure, or the destruction of their habitat. In addition to direct mortality, these changes in the biotic environment of organisms may have consequences on individual energy budgets if organisms are required to allocate more energy to movement (i.e. in search for prey) or to face stressful situations (i.e. interaction with competitors and predators, or presence in sub-optimal habitat). This could be critical in species with small body sizes and/or higher mass-specific metabolic rates (Kooijman, 2010; Peters, 1983) such as small-sized fishes (Brandl et al., 2018, 2020).

Habitat loss and fragmentation are major threats to biodiversity maintenance in marine ecosystems (Fahrig, 2003; Hoekstra et al., 2005; Mantyka-Pringle et al., 2012). Habitat loss or degradation alters the living conditions for populations associated with the habitat (Ellison et al., 2005; Hughes et al., 2009). Mechanisms controlling the persistence of the original species in the new conditions can operate at several organisational levels: individual (i.e. survival rates during different life stages), population (i.e. the rate at which individuals survive or are replaced by recruits) and metapopulation levels (i.e. if local population extinctions are balanced by establishment of new populations; Hylander & Ehrlén, 2013). Species that show high habitat specificity, those structured in small populations and/or with limited dispersal capability are especially vulnerable to habitat degradation or loss at population and metapopulation levels (Hylander & Ehrlén, 2013; Purvis et al., 2000). At the level of individuals, loss or degradation of habitat can be correlated with lower body condition and survival rate in fish (i.e. *Oncorhynchus* spp.; Magnusson & Hilborn, 2003) and birds (*Tringa* spp. & *Haematopus* spp.; Burton et al., 2006; Lambeck, 1990). Reduced body condition (i.e. slimmer individuals) is suggestive of an energy intake and expenditure mismatch (Atkinson et al., 2003; Camphuysen et al., 1996).

Many pipefish species (family Syngnathidae, subfamily Syngnathinae) exhibit strong preference for seagrass habitats (Scapin et al., 2018), strong habitat dependency (Mobley et al., 2011; Wilson et al., 2017), low densities (Foster & Vincent, 2004) and high levels of population differentiation in small geographical areas (Lourie et al., 2005; Teske et al., 2005). These characteristics indicate a limited dispersal capability and make pipefish particularly vulnerable to habitat loss or

degradation (Fagan et al., 2002). Impacts of local loss of seagrass habitat on pipefish populations have been well documented. For example, a 60% reduction in eelgrass *Zostera marina* cover drove dramatic declines in pipefish numbers, with abundances of *Syngnathid typhle* and *Nerophis ophidion* dropping by 71% and 87% respectively (Pihl et al., 2006). For the majority of pipefish species, habitat fragmentation is the main threat to their populations (IUCN, 2020).

The structural complexity underpinned by biogenic habitats reduces flow velocity within the habitat and increases turbulence (Ghisalberti, 2009; Narayan et al., 2016; van Rooijen et al., 2018). This interaction between flow and structural complexity affects the ecology of habitats over a range of spatial scales (Koch et al., 2006) and is a main driver of spatial patterns of species occurrence in marine habitats (Bejarano et al., 2017). Fish species distribution is partly explained by the adaptation of body shape to the hydrodynamics of the habitat (Bracciali et al., 2016; Cakić et al., 2002; Lauder & Drucker, 2004; Pakkasmaa & Piironen, 2000). Pipefish, with an elongated body shape and low fin surface, are adapted to low hydrodynamic energy habitats, and many of them are slow-moving, cryptic fishes with limited daily movements (Ahneshjö & Craig, 2011; Foster & Vincent, 2004). As vegetated bottoms, such as seagrass meadows, attenuate wave energy and flow velocities (Infantes et al., 2012; Koch & Gust, 1999; Luhar et al., 2013), it is likely that plant structural complexity reduces energy expenditure in resident fish species such as pipefish. The loss of structural complexity might increase the energy expenditure for associated fishes through higher exposure to hydrodynamic energy. There is evidence that energy expenditure increases in response to augmented wave intensity varies depending on swimming mode for coral reef fishes (Marcoux & Korsmeyer, 2019). However, tests of this question are still scarce/limited, pipefish are an appropriate model group for testing such effects because they are generally cryptic ambush predators and their lifestyle relies on habitat canopy protection rather than on swimming ability.

This study focuses on four species of pipefish found in European shallow coastal habitats: *Syngnathus typhle*, *S. rostellatus*, *Nerophis ophidion* and *Entelurus aequareus*. We hypothesized that the loss of hydrodynamic shelter provided by seagrass *Zostera marina* would force altered pipefish behaviour, increased swimming effort and increase energy expenditure. We tested how behaviour and energy expenditure are affected by current velocity and habitat structure (seagrass and sand) in the four species of pipefish.

2 | MATERIALS AND METHODS

Zostera marina shoots and pipefish specimens were collected in the west coast of Sweden during several fishing campaigns between August and September, at the bays of Bökevik (58°14'55.63"N, 11°26'53.37"E) and Gåsö (58°13'51.61"N, 11°24'3.72"E), in the Gullmar fjord. Shoots were collected by hand while snorkeling and fish were collected with a beach seine in a seagrass meadow with

sand patches. Adult fish of sizes between 9.8 and 34 cm were collected, transported to the laboratory in seawater containers and stored in aquaria under near natural temperature and salinity conditions using a seawater flow-through system, with water inlet located at 5 m depth. Once in the lab, the fish were placed in 500-L acclimation tanks during at least 48 hr before experimentation in the flume. Artificial seagrass mimics were placed in the tanks to provide shelter for the pipefish. The use of natural shoots in the acclimation tanks was discarded to facilitate cleaning tasks. The fish were fed live zooplankton and invertebrates caught from a boat three times per week in the fjord using a plankton net of 300 μm . Fish were maintained under daily conditions of 14 hr light and 10 hr dark to match natural conditions. The experiments were conducted during 4 months from July to September of 2017.

2.1 | Respirometry

Energy expenditure (i.e. metabolic rate) is normally measured in static respirometers for resting metabolic rate or in swim respirometers with laminar flow for measurements of active metabolic rate (Clark et al., 2013). However, estimating the energy expenditure of fish exhibiting normal behaviours in the complex hydrodynamics of seagrass meadows is more difficult. For this reason, we used individual correlations between metabolic rate and ventilation frequency to estimate the effect of hydrodynamic stress on energy expenditure.

In order to assess how the oxygen consumption of the fish and ventilation frequency correlate, both variables were simultaneously measured using intermittent flow respirometers during routine metabolic activity according to the best practice guidelines (Clark et al., 2013). The oxygen consumption and ventilation rate were measured repeatedly for each fish during daylight with normal activity in the lab room. Two slender cylindrical respirometers of 0.0228 L (29 cm length \times 1 cm inner diameter) each were set inside a 125 L (50 \times 50 \times 50 cm) temperature-controlled aquarium. The respirometers were closed and flushed using intermittent flow following (Clark et al., 2013). The aquarium had continuous air bubbling to keep the oxygen levels at 100% of air saturation, and seawater flow-through to maintain stable temperatures (17.3–19.0°C over the course of the experiment). The room was illuminated with natural light:dark cycle (14:10 hr). Water mixing inside the respirometers was achieved using a peristaltic pump on a closed loop. The water bath had plastic plants surrounding the respirometers to reduce stress in the fish. Pipefish length and mass were 16.3 ± 5.0 cm and 1.32 ± 0.68 g (mean \pm SD) respectively, and the respirometer volume was large enough to reduce confinement stress and minimize unwanted activity yet small enough to be able to reliably measure the oxygen consumption of the fish. In addition, vertical positioning is frequently observed in pipefish in the field where they remain inconspicuous to predators by mimicking seagrass leaves, so the vertical positioning of the respirometer may have helped to reduced stress (Chabot et al., 2016). Fish

were starved for 24 hr before respirometry measurements (Clark et al., 2013).

The respirometer oxygen concentration was measured with an optode oxygen meter (Piccolo2—PyroScience) in the respirometry chambers with 5 + 5 min intermittent flow and stop intervals (Svendsen et al., 2016). Ventilation frequency and routine oxygen consumption were recorded simultaneously during 1 min. During oxygen measurement, no new water entered the respirometer and the ventilation frequency was measured by direct observation and video recording. The Standard Metabolic Rate (MO_2 min) was assessed for 34 *S. typhle*, 11 *S. rostellatus*, 2 *N. ophidion* and 7 *E. aequareus* and was measured during night in darkness. Metabolic rate was expressed as $\text{mg O}_2/\text{kg hr}$ and was calculated following the equation:

$$\text{MO}_2 = [(V_r - V_f) \times \Delta\text{CwO}_2]/(\Delta t \times \text{Mf}), \quad (1)$$

where V_r is the respirometer volume (L), V_f is the fish volume (L) assumed to be linearly related with a coefficient of 1 to the fish mass (Mf, kg), ΔCwO_2 is the change in oxygen concentration in the respirometer water (mg), and Δt is the change in time during which ΔCwO_2 is measured (hr^{-1} ; Clark et al., 2013). $\Delta\text{CwO}_2/\Delta t$ in the respirometer was calculated using LabChart Reader Software ($\text{\textcircled{C}}$ ADInstruments).

The background respiration of the system (caused by the micro-organisms in the system) was measured at the end of each experiment and used for correcting the fish oxygen consumption. During the background consumption there was no fish in the respirometer, it lasted for 25 min without intermittent flow. Between each fish, the system (e.g. respirometers, caps, aquaria, peristaltic tubing) was cleaned with diluted bleach and rinsed with deionized water to remove micro-organisms.

A linear mixed-effects model was used to test the degree of influence of ventilation frequency on metabolic rate for each pipefish species, temperature treated as covariate. The model had a random intercept using fish as random factor since we performed several measures of oxygen consumption and ventilation rate in the same fish during the experimental day. This model revealed a negligible influence of the small experimental temperature fluctuations on metabolic rate (*S. typhle*: $z = -0.614$ $p = 0.539$, *S. rostellatus*: $z = -0.724$ $p = 0.469$, *E. aequareus*: $z = -1.068$ $p = 0.286$). For *N. ophidion*, the effect of temperature on metabolic rate cannot be separated from fish individual effect in the model since only two fishes were tested. Afterwards, the fit between metabolic rate and ventilation rate was done on a simpler linear mixed-effects model, ignoring temperature, with metabolic rate as dependent variable, ventilation rate as independent variable and random intercept for fish. We analysed all model data with the package GLMMTMB (Brooks et al., 2017). A complementary analysis was performed on the log-log scale, with random intercept, to explore linearity and proportionality of the relation between metabolic rate and ventilation (see Appendix S1). Linear analysis showed an adequate goodness of fit (Pearson coefficients *S. typhle* = 0.8109, *S. rostellatus* = 0.7874, *E. aequareus* = 0.7082, *N. ophidion* = 0.9336) and was finally conserved.

2.2 | Hydraulic flume and fish ventilation frequency

A unidirectional (current) flume located at Kristineberg Marine Station was used to: (a) assess the impact of the presence of seagrass on the hydrodynamic environment, (b) evaluate pipefish ventilation frequency under different current velocities with and without a seagrass substratum, substratum and (c) assess the effect of current velocity on pipefish behaviour, quantified as a combination of what they were doing (time spent either swimming or resting/holding) and where they were in the water column. The flume allowed modifying one variable (e.g. flow) while leaving others constant (e.g. substratum). Current velocities from 0 to 18 cm/s were applied in the flume. This range contains velocities representative from sheltered (0–8 cm/s) and exposed (6–20 cm/s) meadows (Widdows et al., 2008). The flume was 8 m long, 0.5 m wide and 0.5 m deep, and is described in detail in (Meysick et al., 2019). The test-section was 2 m long, 0.45 m wide and the water level was maintained at 0.2 m. Flume walls were covered with a black PVC layer to reduce fish stress. Current velocities were generated by a motor-run propeller at the far end of the flume controlled by an adjustable speed drive (Dayton Electronic, model 6K119). In all treatments with a sandy substratum, the test-section of the flume bottom was filled with natural fine sand that was previously cleaned from debris with a 2-mm sieve. For treatments with vegetated substratum, *Z. marina* shoots were cleaned from epiphytes and anchored in the flume test section at a density of 150 shoots per m² (shoot density in the natural meadows in the area: 100–380 shoots per m²; Pihl et al., 2006). Shoots were anchored in the test section using wood sticks of 3 × 0.5 cm (length × diameter) and fixed with a cable tie to each shoot rhizome. The water in the flume was temperature controlled (17.5–19.5°C) using a water chiller (Hailea, HC500A) to have similar conditions as in the respirometry experiment (see Clark et al., 2013).

To determine the effect of *Z. marina* on hydrodynamics, current velocities were measured with an acoustic Doppler velocimeter (ADV, Nortek, Vectrino) at a sampling rate of 25 Hz during 3 min.

Vertical profiles of flow velocity were measured in the presence of sand only and sand with seagrass, at six positions (0.5, 1, 2, 3, 5 and 7 cm above the bottom).

Fish were acclimatized in the 500 L holding tanks for at least 48 hr before experimentation in the flume. Each fish was acclimatized in the flume for 30 min before each trial. A total of 14 *S. typhle*, 12 *S. rostellatus*, 9 *N. ophidion* and 7 *E. aequareus* were trialled. The ventilation frequency was expected to recover from the handling stress during transfer to the flume after 15 min (Barreto & Volpato, 2004). After acclimatization, the trial lasted for 63 min during which each fish was exposed to seven current velocities (0, 3, 6, 9, 12, 15 and 18 cm/s) for 9 min each or ended when the fish was dragged by the current to the exit mesh. During each experiment, the fish was continuously observed, and ventilation frequency was measured by direct visual observation for one min, repeated twice for each velocity: first at 3 min (i.e. after 2 min of exposure to the new velocity) and then at 9 min (i.e. the last min of exposure before moving into the new current velocity conditions). Fish behaviour was also observed during minutes 3 and 9. We recorded whether the fish was swimming or resting/holding to a seagrass shoot with the body or the tail (Appendix S1, Figure 1c), whether the fish body was oriented with the head facing the current or in the opposite position (hereafter with or against current respectively, Appendix S1, Figure 1a) and whether the fish was located in the upper half or lower half of the water column (Appendix S1, Figure 1b). We also recorded how frequently each fish was positioned at the edge versus the centre of the flume. The assay was repeated twice for each fish. The substratum (i.e. sand or seagrass) that was tested first was randomly assigned. The assay was terminated when the fish either repeatedly touched the rear grid after being dragged by the current or failed to move off it after 5 s. The fish rested for at least 24 hr between experiments. After the experiments fish length and weight were measured. Ventilation response to flume engine noise at the different velocities was also evaluated in the fish in the resting tanks, close to the flume,

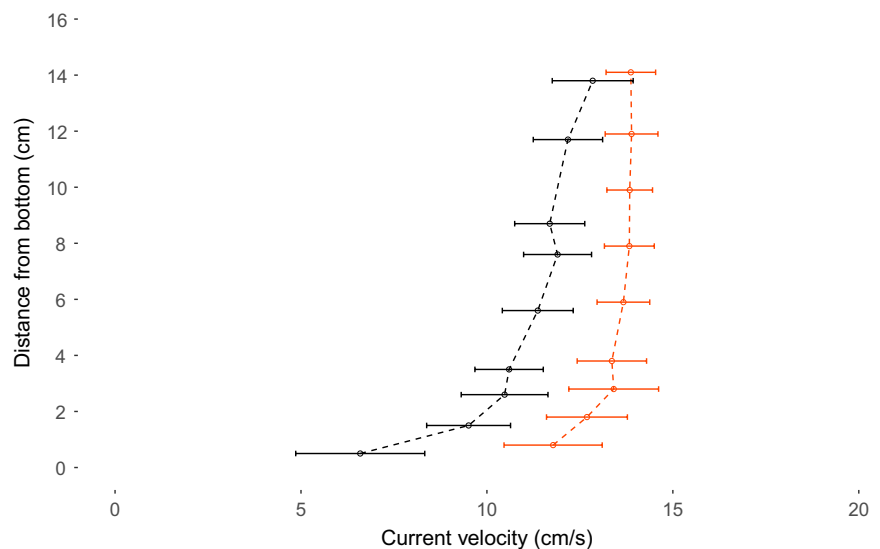


FIGURE 1 Mean and SE of flow velocity in the hydrodynamic flume at increasing distance from the bottom with the two tested substrata: seagrass (black) and sand (orange)

but no evidence for an effect of noise independently from flow was found (Estim = -0.599 , $SE = 1.072$, $t\text{-val} = -0.559$, $p = 0.578$).

A generalized linear mixed effect model, family Poisson (package GLMMTMB, Brooks et al., 2017), was used to evaluate the response of ventilation frequency to current velocity and substratum type. Each species was analysed separately. Substratum and velocity were treated as discrete and continuous fixed factors respectively. Fish mass was treated as covariates. Fish ventilation frequency at the beginning (i.e. intercept) for each fish were treated as random for all the species. Linear regression, with ventilation frequency as response variable and velocity as a continuous factor was used to check whether engine noise caused changes of fish ventilation.

Logistic regression with velocity as a continuous factor was used to analyse the frequency of observed fish behaviour (i.e. swim or hold), the vertical position on the flume (i.e. top or bottom) and fish orientation to the current (i.e. with or against). The substratum factor was excluded from behaviour analysis because, in sand substratum, fish need to continuously swim to avoid being dragged.

Finally, a linear mixed effect model with two fixed factors (i.e. current velocity and substratum) and estimated metabolic rate as response variable (fitted values based on ventilation frequency) was run to explore the response of oxygen consumption to the flume experimental conditions. Fish mass was treated as covariates. R software (R Core Team, 2014) was used for all the statistical analysis.

3 | RESULTS

Flow velocities were reduced on average 20% by the presence of seagrass along the water column (Figure 1). Flow reduction was

higher (44%) near the bottom and lowest (7%) at the top of the water column.

There was a positive relationship between oxygen consumption and ventilation frequency for all the species (Figure 2, Table 1). This allowed to indirectly estimate the effect of current velocity on fish oxygen consumption (Figure 3). Ventilation frequency and estimated metabolic rate increased with velocity of current for all the species studied (Figure 3, Table 2).

Both ventilation frequency and estimated oxygen consumption increased faster in sandy substrate than in seagrass substrate for *N. ophidion* (Ventilation rate (GLM): Slope sand = 0.057; Slope seagrass = 0.010. Estimated oxygen consumption (LM): Slope sand = 11.75; Slope seagrass = 7.70). For *E. aequareus*, both ventilation and estimated oxygen consumption were higher in the sand than in the seagrass habitat, but the rate of increase was the same (Ventilation rate: Intercept sand = 4.5203, Intercept seagrass = 4.2208. Estimated oxygen consumption: Intercept sand = 47.78, Intercept seagrass = 46.15). For *S. rostellatus*, although there were differences in the ventilation (Intercept sand = 4.6103, Intercept seagrass = 4.5253), we found no differences in oxygen metabolism between sand and seagrass substrates. Fish weight had not significant effect on ventilation frequency for any of the four species (*S. typhle* $z = -1.889$, $p = 0.0590$; *S. rostellatus* $z = -0.326$, $p = 0.7441$; *N. ophidion* $z = -1.487$, $p = 0.137101$; *E. aequareus* $z = 0.352$, $p = 0.725$).

The maximum flow velocity withstood by pipefish varied between the species but was generally lower when the seagrass substratum was removed. *S. typhle* and *E. aequareus* were the most resilient species in this regard, with some individuals coping with flow velocities of 18 cm/s in both substrata (Figure 4). None of the *S. rostellatus* were able to swim against the highest flow velocity (18 cm/s) in sand but 30% of them swam against it on seagrass. On

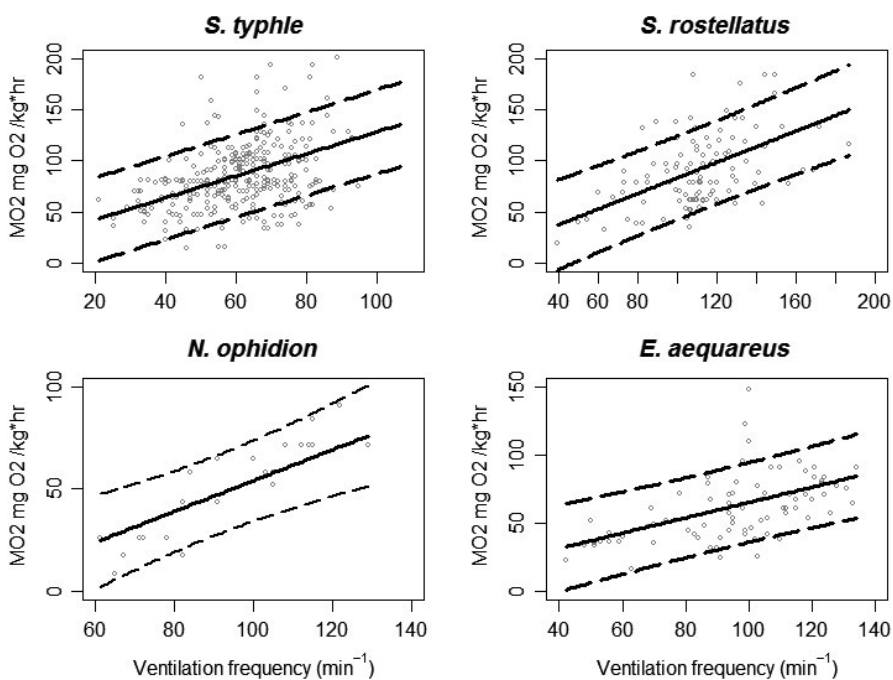


FIGURE 2 Generalized linear mixed effect models fitted to the relationship between metabolic rate (MO_2) and ventilation frequency mean of all individuals (solid black line), and confidence intervals of the mean (dashed black lines). Open circles show each ventilation frequency/metabolic rate determination. *Syngnathus typhle* $n = 34$; *Syngnathus rostellatus* $n = 11$; *Nerophis ophidion* $n = 2$; *Entelurus aequareus* $n = 7$

TABLE 1 Mean fitted slope estimate to the relationship between metabolic rate and Ventilation frequency for each pipefish species. 95% confidence intervals are shown in parentheses. Statistical significance is marked with asterisks

Species	Factor	Position			
		Estimate (conf. int)	SE	z-value	p
<i>Syngnathus typhle</i>	Ventilation	1.0712 (1.2557–0.8867)	0.0941	11.380	<0.0001***
<i>Syngnathus rostellatus</i>	Ventilation	0.7609 (0.9915–0.5303)	0.1177	6.467	<0.0001***
<i>Nerophis ophidion</i>	Ventilation	0.7530 (1.1571–0.3488)	0.2062	3.652	<0.0001***
<i>Entelurus aequareus</i>	Ventilation	0.5610 (0.3201–0.8019)	0.1229	4.564	<0.0001***

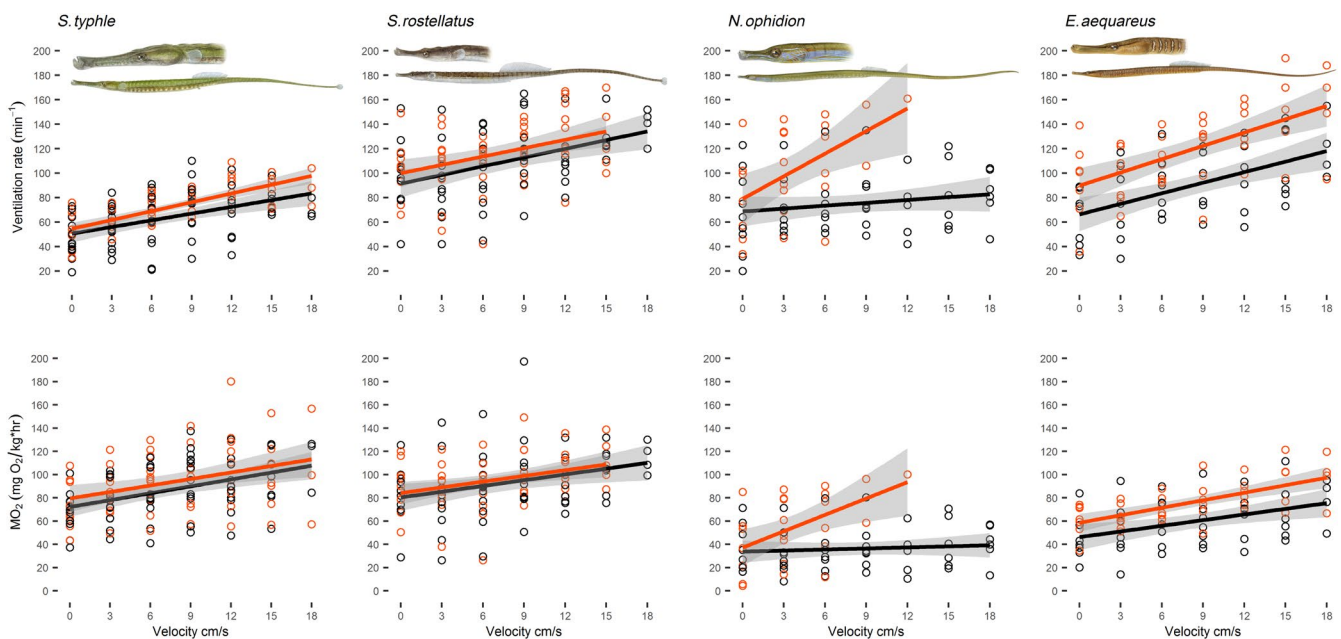


FIGURE 3 Response of pipefish ventilation frequency and estimated metabolic rate (MO_2) exposed to increasing flow velocities in a hydrodynamic flume. Fish response was tested on two substrata sand (orange) and seagrass (black). Four species were tested: for *Syngnathus typhle*, *Syngnathus rostellatus*, *Entelurus aequareus* and *Nerophis ophidion*. Open circles represent individuals, lines and shadow area represent the fitted model and confidence interval. (Illustrations: Karl Jilg/SLU Artdatabanken)

the sand substrate, most *N. ophidion* could only maintain positions in velocities ≤ 6 cm/s, and the maximum velocity they tolerated over sand was 12 cm/s. In contrast, in the seagrass substratum, 66% of the *N. ophidion* were able to maintain positions in the 18 cm/s current. Substratum and current velocity explained between 53% (*S. typhle*) and 33% (*S. rostellatus*) of the total variance of ventilation frequency. Fish identity explained a 53% and 24% of the ventilation frequency variance for *S. rostellatus* and *S. typhle* respectively (Table 3).

Regarding behaviour, the probability of finding *N. ophidion* holding seagrass leaves increased with rising current velocities (Figure 5; Table 4). On the contrary, *S. rostellatus* swam more frequently when current velocity increased (Figure 5; Table 4). The probability of

finding *S. typhle* and *E. aequareus* swimming or holding the leaves was not affected by current velocity (Figure 5; Table 4). Regarding position in the column water, all species were more likely to be near the bottom when seagrass was present independently of current speed. Over sand, *S. typhle* were more frequently found in the top half of the tank at low current speeds, but they tended to transition to the bottom as the speed increased. *S. rostellatus* and *N. ophidion* moved near to the bottom of the flume when velocity increases and this movement toward the bottom was more pronounced in the presence of seagrass. On sand, *E. aequareus* tended to move to the upper half of the tank the as the current velocity increased (Figure 6; Table 4). No significant changes in fish orientation to the current were found for any of the species. In total, 72.74% of the fish with

TABLE 2 Generalized linear mixed model of the effect of substratum and current velocity on fish ventilation rate and linear model of the effect of substratum and current velocity on fish metabolic rate. Statistical significance ($p < 0.05$) are marked with asterisks

Species	Factor	Ventilation frequency				Metabolic rate			
		Estim	SE	z-val	p	Estim	SE	t-val	p
<i>Syngnathus typhle</i> n = 14	Substratum	0.0712	0.0388	1.834	0.067	5.4873	5.6974	0.963	0.337
	Velocity	0.0318	0.0029	11.059	<0.0001***	2.4031	0.4389	5.475	<0.0001***
	Subst × Vel	0.0037	0.0040	0.919	0.3578	0.2386	0.6388	0.373	0.709
<i>Syngnathus rostellatus</i> n = 12	Substratum	0.1346	0.0312	4.320	<0.0001***	6.9497	7.8382	0.887	0.3770
	Velocity	0.0316	0.0023	13.845	<0.0001***	1.6089	0.5782	2.783	<0.01**
	Subst × Vel	-0.0062	0.0034	-1.814	0.0697	0.2688	0.9014	0.298	0.7660
<i>Nerophis ophidion</i> n = 9	Substratum	0.1544	0.0419	3.685	<0.0001***	6.3562	8.3424	0.762	0.4485
	Velocity	0.0138	0.0028	4.936	<0.0001***	0.6690	0.5144	1.301	0.1975
	Subst × Vel	0.0408	0.0064	6.375	<0.0001***	4.0347	1.4216	2.838	<0.01**
<i>Entelurus aequareus</i> n = 7	Substratum	0.2863	0.0396	7.231	<0.0001***	12.4612	6.2335	1.999	<0.05*
	Velocity	0.0279	0.0027	10.311	<0.0001***	1.5960	0.4325	3.690	<0.0001***
	Subst × Vel	-0.0008	0.0036	-0.229	0.819	0.5895	0.6234	0.946	0.347

seagrass shelter preferred to rest at the centre of the flume compared with 63.15% of the fish that preferred to be at the flume edge in sand assays.

4 | DISCUSSION

Here, we have experimentally demonstrated that structural complexity of the habitat (i.e. presence vs. absence of seagrass) reduces the energy expenditure for three out of four pipefish species when exposed to increasing current speeds. Ventilation frequency and estimated metabolic rate were consistently higher for all species when they experienced current on sand substratum than on vegetated substratum. Vegetation also increased the maximum flow velocities that fish could tolerate without losing position to the current. Despite some variability between species, we demonstrate the importance of plant canopy in providing hydrodynamic shelter for pipefishes, with potential implication for other cryptobenthic, substrate-associated fishes. The increase in energy expenditure is thus another threat for the persistence of substrate-associated fishes as seagrass habitats areal extent declines (Hughes et al., 2009; Waycott et al., 2009).

The magnitude of such a threat for fishes in other biogenic habitats in decline, such as coral reefs, mangroves or kelp forests, should be carefully determined. Previous works evidence the importance of structural complexity in biogenic habitats to attenuate waves (Harris et al., 2018; Narayan et al., 2016) and flow velocity (Johansen et al., 2008), reduce sediment transport and resuspension (Pomeroy et al., 2017) with structural complexity creating fish refuges likely reducing turbidity and energy expenditure in resident fish in those systems (Johansen et al., 2008). The loss of habitat hydrodynamic shelter might thus be an under-appreciated consequence of global warming, particularly relevant for small fishes with limited dispersal capability (Brandl et al., 2018; Fagan et al., 2002; Kalinkat et al., 2017). Shelter availability negatively correlated with Atlantic salmon *Salmo salar* growth rate (Finstad et al., 2007) and the total absence of shelter led to an increase of juvenile *S. salar* metabolic cost by as much as 30% (Millidine et al., 2006). These results support that the hydrodynamic energy may have consequences on individual energy budgets as fish are forced to allocate more energy to swimming.

The structural complexity in biogenic habitats reduces wave energy and flow velocities (Harris et al., 2018; Luhar et al., 2013; Rosman et al., 2007). Higher current velocity caused an increase in ventilation frequency and estimated oxygen consumption for all the fish species regardless the substratum. The reductions in hydrodynamic shelter can drive large increases in metabolic rates of pipefishes when seagrass meadows disappear. Such increases in metabolic rates, and consequently energy expenditure, may, therefore, reduce the energy available for important processes such as growth and reproduction, potentially impairing population resilience (Adams, 1999). Most of the individuals (of all species) had problems to cope with the highest velocities tested (15–18 cm/s), particularly on sand substratum. However, increasing current velocities produced different responses in the different species. While *N. ophidion*

FIGURE 4 Number of individuals of each pipefish species that were not dragged before the end of the experimental period when flow velocity was increased in 3 cm/s intervals: sand (orange) and seagrass (black)

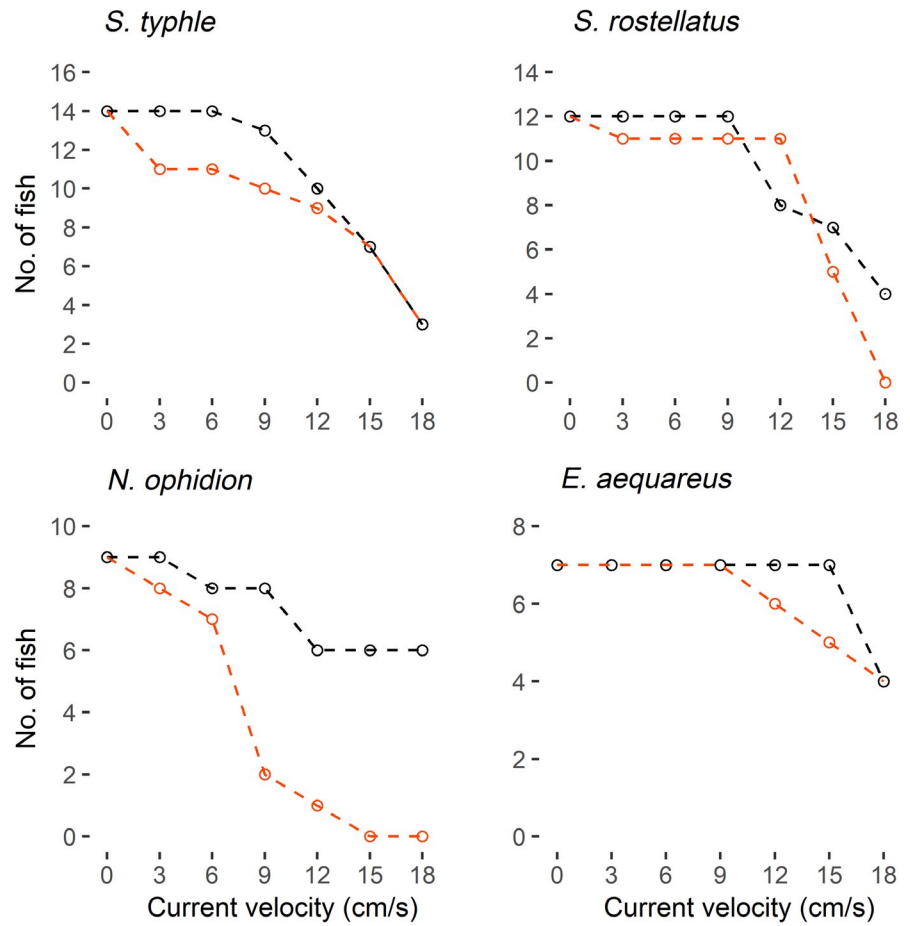


TABLE 3 Variance of ventilation frequency explained by the fixed (substratum and current velocity) and the random (fish individual) factors of the linear mixed effect model

Species	Fixed factors	Random factors
<i>Syngnathus typhle</i>	53.48	24.24
<i>Syngnathus rostellatus</i>	33.94	53.86
<i>Nerophis ophidion</i>	45.13	41.67
<i>Entelurus aequareus</i>	49.04	40.09

and *S. typhle* looked for shelter in the seagrass when flow velocities increased, *S. rostellatus* and *E. aequareus* tackled increasing flows by increasing their swimming effort.

Syngnathus rostellatus had a lesser an increase of oxygen consumption when exposed to hydrodynamic energy compared to the rest of the species. The influence of seagrass presence for this species was negligible in our results. Interestingly, it has also been found to be the local pipefish species affected the least by loss of seagrass meadows, with a decline in abundance of about 30% (Pihl et al., 2006). Previous published evidence shows that *S. rostellatus* can be found associated to sandy estuarine bottoms (Quigley, 2009) where they can migrate seasonally to facilitate reproduction (Power & Attrill, 2003). Hence, this species may have behaviour and physiology that is more adaptable to different habitats. On the contrary,

N. ophidion and *E. aequareus* which showed drastic reductions in abundance by the loss of Swedish meadows (Pihl et al., 2006), displayed noticeable increases in estimated metabolic rate in the absence of seagrass and were strongly influenced by current velocity. A particularly elongated shape, without (*N. ophidion*) or vestigial (*E. aequareus*) caudal fin could condition the high sensitivity of these species to hydrodynamic challenges. Particularly, *N. ophidion* showed the strongest dependence on seagrass shelter when current velocity increased, and responses (i.e. ventilation frequency, estimated oxygen consumption, position, behaviour and maximum tolerated current velocity) even more divergent to the other species when seagrass shelter was not available. This result is explained by the strategy of *N. ophidion* to resist hydrodynamics, which lacks caudal, anal and pectoral fins and instead relies on the use of a prehensile tail to hold the leaves (Neutens et al., 2017). On sand substrates, without the ability to hold on to vegetation, currents of above 12 cm/s will drag them and likely threaten their survival.

The drivers of unexplained variance of ventilation frequency are elusive. It could be explained by variation in individual behaviour (beyond the measured behaviours), daily patterns or the exact fish position in the flume: Fish closer to the side and the bottom or deeper in the vegetation may experience lower local velocities and therefore show lower ventilation than expected for each velocity.

Our results supports the predictive mechanism of Crain and Bertness (2006) that postulates that under harsh environmental

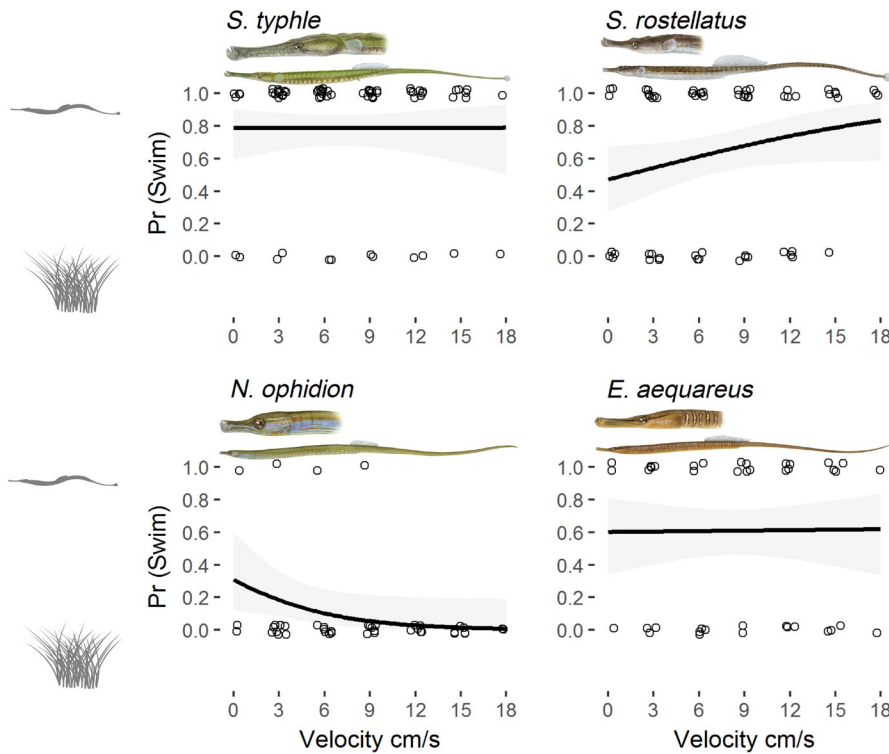


FIGURE 5 Behaviour response of four species of pipefish exposed to increasing flow velocities in a hydrodynamic flume. Probability of *Syngnathus typhle*, *Syngnathus rostellatus*, *Entelurus aequareus* and *Nerophis ophidion* to be found swimming with increasing current velocity on seagrass (black line). Fish behaviour was categorized in swimming and holding/clinging to substratum so this figure also shows the probability of found pipefish holding. Zero indicates low probability and one high probability of being found swimming (and the opposite for holding). Only the results on seagrass substratum are shown because fish on sand cannot cling the substratum and exposed to flow they were always categorized as swimming (or dragged at the end of the experiment)

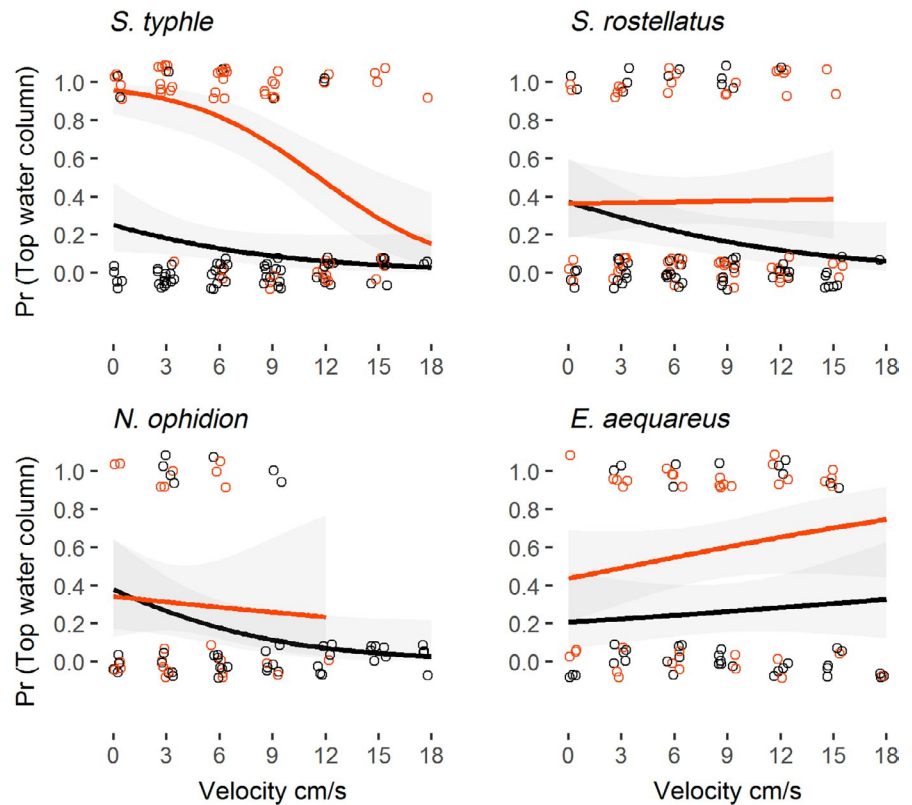
TABLE 4 Logistic regression of the effect of substratum and current velocity on fish position (i.e. probability of being in the upper half of the column water) and behaviour (i.e. probability of being swimming). Statistical significance ($p < 0.05$) are marked with asterisks

Species	Factor	Probability of being in the top (upper-half)				Probability of swimming			
		Estim	SE	z-val	p	Estim	SE	z-val	p
<i>Syngnathus typhle</i>	Intercept	-1.0930	0.5001	-2.185	<0.05*	1.2976	0.4697	2.763	<0.01**
	Substratum	4.2207	0.9216	4.580	<0.0001***				
	Velocity	-0.1369	0.0790	-1.733	0.0831	0.0010	0.0541	0.019	0.9845
	Subst x Vel	-0.1323	0.1081	-1.224	0.2210				
<i>Syngnathus rostellatus</i>	Intercept	-0.5246	0.4747	-1.105	0.2691	-0.1131	0.4318	-0.262	0.7934
	Substratum	-0.0396	0.6728	-0.059	0.9530				
	Velocity	-0.1226	0.0652	-1.880	0.060	0.096	0.0518	1.853	0.0639
	Subst x Vel	0.1291	0.0866	1.490	0.1363				
<i>Nerophis ophidion</i>	Intercept	-0.4962	0.5474	-0.907	0.3647	-0.8054	0.6110	-1.318	0.1874
	Substratum	-0.1557	0.8370	-0.186	0.8525				
	Velocity	-0.1721	0.0832	-2.069	0.0385*	-0.2272	0.1165	-1.950	0.0512
	Subst x Vel	0.1279	0.1574	0.813	0.4162				
<i>Entelurus aequareus</i>	Intercept	-1.3431	0.6274	-2.141	0.0323*	0.4082	0.5362	0.761	0.446
	Substratum	1.0917	0.8246	1.324	0.1855				
	Velocity	0.0347	0.0591	0.588	0.5568	0.0040	0.0528	0.076	0.940
	Subst x Vel	0.0395	0.0820	0.481	0.6304				

conditions, ecosystem engineers (e.g. seagrass) will modify the constraining variables in the system (e.g. hydrodynamics), alleviate physical conditions and consequently allow the expansion of distributional limits for diverse species. It is possible this mechanism by seagrass allows pipefish, and, in particular, of *N. ophidion*, to inhabit areas that would otherwise be uninhabitable. This contrasting

response among pipefish species appear similar to the facultative and obligate species of fish that live in live coral and their respective differential vulnerability to coral structure loss (Pratchett et al., 2006; Wismer et al., 2019). It also suggests the importance of protection of seagrass and vegetated bottoms to conserve pipefish populations.

FIGURE 6 Vertical position of four species of pipefish exposed to increasing flow velocities in a hydrodynamic flume. Fish position with increasing flow velocity was tested on two substrata sand (orange) and seagrass (black). The figure shows the probability of finding *Syngnathus typhle*, *Syngnathus rostellatus*, *Entelurus aequareus* and *Nerophis ophidion* in the upper half of the flume column water. Zero indicates low probability while one indicates high probability of finding fish in the upper middle of the water column (and the opposite for the lower middle)



In addition to hydrodynamic shelter, vegetated canopy allows pipefish crypsis and protects them from predators such as Atlantic cod *Gadus morhua* (Hindell et al., 2000; Kleiber et al., 2011). Shelter absence seems to trigger fish shelter search reflex, even in experimental conditions without predators. In our study, when seagrass was absent, pipefish appeared to search for protection along the flume walls, similar to observations reported for salmonid juveniles (Millidine et al., 2006). *E. aequareus* and *S. rostellatus* had lower ventilation frequency and estimated oxygen consumption when seagrass shelter was available regardless of current velocity, suggestive of reduced stress when shelter was available. The access to shelter structure, rather than the use of it, reduced metabolic rate in our study and in Millidine et al. (2006). However, *S. typhle* did not clearly react to seagrass shelter availability at 0 cm/s velocity and showed the narrowest range of ventilation response with increasing current velocity. This may suggest that *S. typhle* is more flexible in its habitat requirements and perhaps more resilient to hydrodynamical changes.

Ventilation frequency was used as a proxy for metabolic rate, representing a non-invasive indicator of activity and energy expenditure. Ventilation frequency can be determined visually, however, it only allows quantification of frequency and not of the volume of the ventilation, both of which can affect oxygen uptake (Rooij & Videler, 1996). Moreover, the percentage of oxygen that is extracted from the ventilatory current may vary as well (Rooij & Videler, 1996). Ventilation frequency may thus not fully reflect the intensity of stressors, which is another reason for caution when using it as indicator of stress (Barreto & Volpato, 2004). Therefore, the correlation between ventilation frequency and oxygen uptake has to

be investigated case by case, and data interpretation needs to be cautious. However, the literature contains several examples in which the correlation between ventilation rate and oxygen consumption is reliable; this is the case for adults and juveniles of the coral reef fish *Sparisoma viride* at naturally varying temperatures (Rooij & Videler, 1996) as well as for *Sander lucioperca* tested at temperatures between 13 and 28°C (Frisk et al., 2012). Ventilation and metabolic rates were also well correlated in *Salmo salar* at five levels of activity: initial settling, resting immobile, feeding-digestion, responding to disturbance (Millidine et al., 2008). Our results strengthen the utility of using ventilation frequency (when statistically robust correlations are found) for fish metabolic rate assessment in natural environments. This method could be used to estimate field metabolic rates, as was successfully done for Atlantic salmon using a semi-natural stream (Reid, Armstrong, & Metcalfe, 2011, 2012).

Predicting the effects of global change on species diversity, abundance, distribution or body condition requires integrating effects and responses at several organization levels (from physiological to populations and ecosystems). Information about variability of environmental conditions at relevant scales is essential for this challenge (Buckley et al., 2018; Helmuth et al., 2005). Our results link large spatial scale processes, such as habitat structure degradation, with individual physiological response (i.e. metabolic rate increase) and suggest a mechanism that might partially explain the observed decline of species diversity and decline of individual body condition in fishes in degraded habitats.

In conclusion, our results demonstrate the dependence of pipefishes on seagrass structural complexity for shelter against

hydrodynamic stress, and that degradation of such habitats can dramatically increase energy expenditure in pipefishes. Similarities in morphology, dispersal capability, size and lifestyles could mean that our results may also be generalizable not only for other pipefish species but also for other fishes in various habitats. The general decline, fragmentation and loss of structural complexity in biogenic habitats worldwide (Pandolfi et al., 2003; Waycott et al., 2009) is likely driving a significant reduction in hydrodynamically sheltered habitats, and triggering an increase in energy expenditure of associated fauna that could contribute to population declines. Future management actions designed to conserve and restore coastal habitats would therefore aid in protecting weak swimmers such as pipefishes.

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COMPETING INTERESTS

The authors declare no competing financial or non-financial interests.

AUTHORS' CONTRIBUTIONS

I.C.-S., J.T., E.I. and F.J. conceived the study and designed methodology; I.C.-S. and T.N. collected the data; I.C.-S. and F.J. analysed the data; I.C.-S., J.T., E.I. and F.J. wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Digital CSIC Repository <https://doi.org/10.20350/digitalCSIC/12511> (Castejón-Silvo et al., 2020).

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REFERENCES

- Adams, S. M. (1999). Ecological role of lipids in the health and success of fish populations. In W. B. C. Arts M.T. (Ed.), *Lipids in freshwater ecosystems* (pp. 132–160). Springer. https://doi.org/10.1007/978-1-4612-0547-0_8
- Ahnesjö, I., & Craig, J. F. (2011). The biology of Syngnathidae: Pipefishes, seadragons and seahorses. *Journal of Fish Biology*, 78(6), 1597–1602. <https://doi.org/10.1111/j.1095-8649.2011.03008.x>
- Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J., Clark, J. A., & Ireland, P. L. (2003). Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biological Conservation*, 114(1), 127–141. [https://doi.org/10.1016/S0006-3207\(03\)00017-X](https://doi.org/10.1016/S0006-3207(03)00017-X)
- Barreto, R. E., & Volpato, G. L. (2004). Caution for using ventilatory frequency as an indicator of stress in fish. *Behavioural Processes*, 66(1), 43–51. <https://doi.org/10.1016/j.beproc.2004.01.001>
- Bejarano, S., Jouffray, J.-B., Chollett, I., Allen, R., Roff, G., Marshall, A., Steneck, R., Ferse, S. C. A., & Mumby, P. J. (2017). The shape of success in a turbulent world: Wave exposure filtering of coral reef herbivory. *Functional Ecology*, 31(6), 1312–1324. <https://doi.org/10.1111/1365-2435.12828>
- Bracciali, C., Guzzo, G., Giacoma, C., Dean, J. M., & Sarà, G. (2016). Fish functional traits are affected by hydrodynamics at small spatial scale. *Marine Environmental Research*, 113, 116–123. <https://doi.org/10.1016/j.marenvres.2015.12.002>
- Brandl, S. J., Goatley, C. H. R., Bellwood, D. R., & Tornabene, L. (2018). The hidden half: Ecology and evolution of cryptobenthic fishes on coral reefs. *Biological Reviews*, 93(4), 1846–1873. <https://doi.org/10.1111/brv.12423>
- Brandl, S. J., Johansen, J. L., Casey, J. M., Tornabene, L., Morais, R. A., & Burt, J. A. (2020). Extreme environmental conditions reduce coral reef fish biodiversity and productivity. *Nature Communications*, 11(1), 1–14. <https://doi.org/10.1038/s41467-020-17731-2>
- Brooks, M. E., Kristensen, K., & Van Benthem, K. J. (2017). *Modeling zero-inflated count data with glmmTMB*. <https://doi.org/10.1101/132753>
- Buckley, L. B., Cannistra, A. F., & John, A. (2018). Leveraging organismal biology to forecast the effects of climate change. *Integrative and Comparative Biology*, 58(1), 38–51. <https://doi.org/10.1093/icb/icy018>
- Burton, N. H. K., Rehfish, M. M., Clark, N. A., & Dodd, S. G. (2006). Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *Journal of Applied Ecology*, 43(3), 464–473. <https://doi.org/10.1111/j.1365-2664.2006.01156.x>
- Cakić, P., Lenhardt, M., Mičković, D., Sekulić, N., & Budakov, L. J. (2002). Biometric analysis of *Syngnathus abaster* populations. *Journal of Fish Biology*, 60(6), 1562–1569. <https://doi.org/10.1006/jfbi.2002.2011>
- Camphuysen, K., Ens, B. J., Heg, D., Hulscher, J. B., Van Der Meer, J., & Smit, C. J. (1996). Oystercatcher *Haematopus ostralegus* winter mortality in the Netherlands: The effect of severe weather and food supply. *Ardea*, 84, 469–492.
- Castejón-Silvo, I., Terrados, J., Nguyen, T., Jutfelt, F., & Infantes, E. (2020). Data from: Pipefishes use seagrass as hydrodynamic shelter for reducing energy expenditure [Dataset]. *DIGITAL.CSIC*, <https://doi.org/10.20350/digitalCSIC/12511>
- Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *Journal of Fish Biology*, 88(1), 81–121. <https://doi.org/10.1111/jfb.12845>
- Clark, T. D., Sandblom, E., & Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. *Journal of Experimental Biology*, 216(15), 2771–2782. <https://doi.org/10.1242/jeb.084251>
- Crain, C. M., & Bertness, M. D. (2006). Ecosystem engineering across environmental gradients: Implications for conservation and management. *Biosciences*, 56(3), 211–218. [https://doi.org/10.1641/0006-3568\(2006\)056\[0211:EEAEGI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)056[0211:EEAEGI]2.0.CO;2)
- Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloepfel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., Von Holle, B., & Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3, 479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Fagan, W. F., Unmack, P. J., Burgess, C., & Minckley, W. L. (2002). Rarity, fragmentation, and extinction risk in desert fishes. *Reports Ecology*, 83(12), 3250–3256. [https://doi.org/10.1890/0012-9658\(2002\)083\[3250:RFAERI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3250:RFAERI]2.0.CO;2)
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>

- Finstad, A. G., Einum, S., Forseth, T., & Ugedal, O. (2007). Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology*, 52(9), 1710–1718. <https://doi.org/10.1111/j.1365-2427.2007.01799.x>
- Foster, S. J., & Vincent, A. C. J. J. (2004). Life history and ecology of seahorses: Implications for conservation and management. *Journal of Fish Biology*, 65(1), 1–61. <https://doi.org/10.1111/j.1095-8649.2004.00429.x>
- Freitas, V., Cardoso, J. F. M. F., Lika, K., Peck, M. A., Campos, J., Kooijman, S. A. L. M., & van der Veer, H. W. (2010). Temperature tolerance and energetics: A dynamic energy budget-based comparison of North Atlantic marine species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1557), 3553–3565. <https://doi.org/10.1098/rstb.2010.0049>
- Frisk, M., Vilhelm, P., & Fleng, J. (2012). Thermal optimum for pikeperch (*Sander lucioperca*) and the use of ventilation frequency as a predictor of metabolic rate. *Aquaculture*, 324–325, 151–157. <https://doi.org/10.1016/j.aquaculture.2011.10.024>
- Ghisalberti, M. (2009). Obstructed shear flows: Similarities across systems and scales. *Journal of Fluid Mechanics*, 641, 51–61. <https://doi.org/10.1017/S0022112009992175>
- Harris, D. L., Rovere, A., Casella, E., Power, H., Canavesio, R., Collin, A., Pomeroy, A., Webster, J. M., & Parravicini, V. (2018). Coral reef structural complexity provides important coastal protection from waves under rising sea levels. *Science Advances*, 4(2), eaao4350. <https://doi.org/10.1126/sciadv.aao4350>
- Helmuth, B., Kingsolver, J. G., & Carrington, E. (2005). Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annual Review of Physiology*, 67, 177–201. <https://doi.org/10.1146/annurev.physiol.67.040403.105027>
- Hindell, J. S., Jenkins, G. P., & Keough, M. J. (2000). Evaluating the impact of predation by fish on the assemblage structure of fishes associated with seagrass (*Heterozostera tasmanica*) (martens ex ascherson) den hartog, and unvegetated sand habitats. *Journal of Experimental Marine Biology and Ecology*, 255(2), 153–174. [https://doi.org/10.1016/S0022-0981\(00\)00289-6](https://doi.org/10.1016/S0022-0981(00)00289-6)
- Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, 8(1), 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- Hughes, A. R., Williams, S. L., Duarte, C. M., Heck, K. L., & Waycott, M. (2009). Associations of concern: Declining seagrasses and threatened dependent species. *Frontiers in Ecology and the Environment*, 7, 242–246. <https://doi.org/10.1890/080041>
- IUCN (2020). *IUCN Red List web site*. Retrieved from <https://www.iucnredlist.org/search?query=pipefish&searchType=species>
- Hylander, K., & Ehrlén, J. (2013). The mechanisms causing extinction debts. *Trends in Ecology & Evolution*, 28(6), 341–346. <https://doi.org/10.1016/j.tree.2013.01.010>
- Infantes, E., Orfila, A., Simarro, G., Terrados, J., Luhar, M., & Nepf, H. (2012). Effect of a seagrass (*Posidonia oceanica*) meadow on wave propagation. *Marine Ecology Progress Series*, 456, 63–72. <https://doi.org/10.3354/meps09754>
- Johansen, J. L., Bellwood, D. R., & Fulton, C. J. (2008). Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology Progress Series*, 360(May), 219–226. <https://doi.org/10.3354/meps07482>
- Kalinkat, G., Jähmig, S. C., & Jeschke, J. M. (2017). Exceptional body size-extinction risk relations shed new light on the freshwater biodiversity crisis. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E10263–E10264. <https://doi.org/10.1073/pnas.1717087114>
- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioural thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106(10), 3835–3840. <https://doi.org/10.1073/pnas.0808913106>
- Kleiber, D., Blight, L. K., Caldwell, I. R., & Vincent, A. C. J. J. (2011). The importance of seahorses and pipefishes in the diet of marine animals. *Reviews in Fish Biology and Fisheries*, 21(2), 205–223. <https://doi.org/10.1007/s11160-010-9167-5>
- Koch, E. W., Ackerman, J. D., Verduin, J., & Van Keulen, M. (2006). Fluid dynamics in seagrass ecology-from molecules to ecosystems. In A. W. D. Larkum, R. J. Orth, & C. M. Duarte (Eds.), *Seagrasses: Biology, ecology and conservation* (pp. 193–225). Springer Netherlands. https://doi.org/10.1007/978-1-4020-2983-7_8
- Koch, E. W., & Gust, G. (1999). Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*, 184, 63–72. <https://doi.org/10.3354/meps184063>
- Kooijman, S. A. L. M. (2010). Dynamic Energy Budget theory for metabolic organisation: Summary of concepts of the third edition. *Water*, 365, 68.
- Lambeck, R. H. D. (1990). Changes in abundance, distribution and mortality of winter oystercatchers after habitat loss in the delta area, SW Netherlands. *Acta XX Congressus Internationalis Ornithologici Christchurch, New Zealand 2–9 December 1990*, 2208–2218. New Zealand Ornithological Congress Trust Board.
- Lauder, G. V., & Drucker, E. G. (2004). Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE Journal of Oceanic Engineering*, 29(3), 556–571. <https://doi.org/10.1109/JOE.2004.833219>
- Lourie, S. A., Green, D. M., & Vincent, A. C. J. (2005). Dispersal, habitat differences, and comparative phylogeography of Southeast Asian seahorses (Syngnathidae: Hippocampus). *Molecular Ecology*, 14(4), 1073–1094. <https://doi.org/10.1111/j.1365-294X.2005.02464.x>
- Luhar, M., Infantes, E., Orfila, A., Terrados, J., & Nepf, H. M. (2013). Field observations of wave-induced streaming through a submerged seagrass (*Posidonia oceanica*) meadow. *Journal of Geophysical Research: Oceans*, 118(4), 1955–1968. <https://doi.org/10.1002/jgrc.20162>
- Magnusson, A., & Hilborn, R. (2003). Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific Coast. *Estuaries*, 26(4), 1094–1103. <https://doi.org/10.1007/BF02803366>
- Mantyka-Pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, 18(4), 1239–1252. <https://doi.org/10.1111/j.1365-2486.2011.02593.x>
- Marcoux, T. M., & Korsmeyer, K. E. (2019). Energetics and behavior of coral reef fishes during oscillatory swimming in a simulated wave surge. *Journal of Experimental Biology*, 222(4), jeb191791. <https://doi.org/10.1242/jeb.191791>
- Meysick, L., Infantes, E., & Boström, C. (2019). The influence of hydrodynamics and ecosystem engineers on eelgrass seed trapping. *PLoS ONE*, 14(9), 1–17. <https://doi.org/10.1371/journal.pone.0222020>
- Millidine, K. J., Armstrong, J. D., & Metcalfe, N. B. (2006). Presence of shelter reduces maintenance metabolism of juvenile salmon. *Functional Ecology*, 20(5), 839–845. <https://doi.org/10.1111/j.1365-2435.2006.01166.x>
- Millidine, K. J., Metcalfe, N. B., & Armstrong, J. D. (2008). The use of ventilation frequency as an accurate indicator of metabolic rate in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2081–2087. <https://doi.org/10.1139/F08-118>
- Mobley, K. B., Small, C. M., & Jones, A. G. (2011). June). The genetics and genomics of Syngnathidae: Pipefishes, seahorses and seadragons. *Journal of Fish Biology*, 78, 1624–1646. <https://doi.org/10.1111/j.1095-8649.2011.02967.x>
- Narayan, S., Beck, M. W., Reguero, B. G., Losada, I. J., van Wesenbeeck, B., Pontee, N., Sanchirico, J. N., Ingram, J. C., Lange, G.-M., & Burks-Copes, K. A. (2016). The effectiveness, costs and coastal protection benefits of natural and nature-based defences. *PLoS ONE*, 11(5), 154735. <https://doi.org/10.1371/journal.pone.0154735>

- Neutens, C., de Dobbelaer, B., Claes, P., & Adriaens, D. (2017). Prehensile and non-prehensile tails among syngnathid fishes: What's the difference? *Zoology*, 120, 62–72. <https://doi.org/10.1016/j.zool.2016.11.002>
- Pakkasmaa, S., & Piironen, J. (2000). Water velocity shapes juvenile salmonids. *Evolutionary Ecology*, 14(8), 721–730. <https://doi.org/10.1023/A:1011691810801>
- Pandolfi, J. M., Bradbury, R. H., Sala, E., Hughes, T. P., Bjorndal, K. A., Cooke, R. G., McArdle, D., McClenachan, L., Newman, M. J. H., Paredes, G., Warner, R. R., & Jackson, J. B. C. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301(5635), 955–958. <https://doi.org/10.1126/science.1085706>
- Peters, R. (1983). *The ecological implications of body size (Cambridge Studies in Ecology)*. Cambridge University Press. <https://doi.org/10.1017/cbo9780511608551>
- Pihl, L., Baden, S., Kautsky, N., Rönnbäck, P., Söderqvist, T., Max.Troell, & Wennhage, H. (2006). Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. *Estuarine, Coastal and Shelf Science*, 67(1–2), 123–132. <https://doi.org/10.1016/j.ecss.2005.10.016>
- Pomeroy, A. W. M., Lowe, R. J., Ghisalberti, M., Storlazzi, C., Symonds, G., & Roelvink, D. (2017). Sediment transport in the presence of large reef bottom roughness. *Journal of Geophysical Research: Oceans*, 122(2), 1347–1368. <https://doi.org/10.1002/2016JC011755>
- Power, M., & Attrill, M. J. (2003). Long-term trends in the estuarine abundance of Nilsson's pipefish (*Syngnathus rostellatus* Nilsson). *Estuarine, Coastal and Shelf Science*, 57(1–2), 325–333. [https://doi.org/10.1016/S0272-7714\(02\)00358-X](https://doi.org/10.1016/S0272-7714(02)00358-X)
- Pratchett, M. S., Wilson, S. K., & Baird, A. H. (2006). Declines in the abundance of *Chaetodon butterflyfishes* following extensive coral depletion. *Journal of Fish Biology*, 69(5), 1269–1280. <https://doi.org/10.1111/j.1095-8649.2006.01161.x>
- Purvis, A., Gittleman, J. L., Cowlshaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, 267(1456), 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>
- Quigley, D. T. (2009). Pipefishes and seahorses (Syngnathidae) in Irish and European waters. *Sherkin Comment*, 48, 6.
- R Core Team (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2011). Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. *Functional Ecology*, 25(6), 1360–1367. <https://doi.org/10.1111/j.1365-2435.2011.01894.x>
- Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2012). The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. *Journal of Animal Ecology*, 81(4), 868–875. <https://doi.org/10.1111/j.1365-2656.2012.01969.x>
- Rosman, J. H., Koseff, J. R., Monismith, S. G., & Grover, J. (2007). A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *Journal of Geophysical Research*, 112, 2016. <https://doi.org/10.1029/2005JC003430>
- Scapin, L., Cavararo, F., Malavasi, S., Riccato, F., Zucchetta, M., & Franzoi, P. (2018). Linking pipefishes and seahorses to seagrass meadows in the Venice lagoon: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(2), 282–295. <https://doi.org/10.1002/aqc.2860>
- Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuisen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 9(4), 306–312. <https://doi.org/10.1038/s41558-019-0412-1>
- Svendsen, M. B. S., Bushnell, P. G., & Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system for aquatic organisms. *Journal of Fish Biology*, 88(1), 26–50. <https://doi.org/10.1111/jfb.12797>
- Teske, P. R., Hamilton, H., Palsbøll, P. J., Choo, C. K., Gabr, H., Lourie, S. A., Santos, M., Sreepada, A., Cherry, M. I., & Matthee, C. A. (2005). Molecular evidence for long-distance colonization in an Indo-Pacific seahorse lineage. *Marine Ecology Progress Series*, 286(February), 249–260. <https://doi.org/10.3354/meps286249>
- Van Rooij, J. M., & Videler, J. J. (1996). Estimating oxygen uptake rate from ventilation frequency in the reef fish *Sparisoma viride*. *Marine Ecology Progress Series*, 132, 31–41. <https://doi.org/10.3354/meps132031>
- van Rooijen, A., Lowe, R., Ghisalberti, M., Conde-Frias, M., & Tan, L. (2018). Predicting current-induced drag in emergent and submerged aquatic vegetation canopies. *Frontiers in Marine Science*, 5, 449. <https://doi.org/10.3389/fmars.2018.00449>
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(19), 12377–12381. <https://doi.org/10.1073/pnas.0905620106>
- Widdows, J., Pope, N. D., Brinsley, M. D., Asmus, H., & Asmus, R. M. (2008). Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. *Marine Ecology Progress Series*, 358, 125–136. <https://doi.org/10.3354/meps07338>
- Wilson, N. G., Stiller, J., & Rouse, G. W. (2017). Barriers to gene flow in common seadragons (Syngnathidae: *Phyllopteryx taeniolatus*). *Conservation Genetics*, 18(1), 53–66. <https://doi.org/10.1007/s1059-2-016-0881-y>
- Wismer, S., Tebbett, S. B., Streit, R. P., & Bellwood, D. R. (2019). Young fishes persist despite coral loss on the Great Barrier Reef. *Communications Biology*, 2(1), 1–7. <https://doi.org/10.1038/s42003-019-0703-0>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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