Received: 5 November 2020 | Revised: 16 April 2021 | Accepted: 6 May 2021
DOI: 10.1111/faf.12580

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

The influence of habitat association on swimming performance in marine teleost fish larvae

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Abstract

Latitude and body size are generally considered key drivers of swimming performance for larval marine fishes, but evidence suggests that evolutionary relationships and habitat may also be important. We used a comparative phylogenetic framework, data synthesis and case study approach to investigate how swimming performance differs among larvae of fish species across latitude. First, we investigated how swimming performance changed with body length, and we found that temperate reef fishes have the greatest increases in swimming performance with length. Secondly, we compared differences in three swimming performance metrics (critical swimming speed, *in situ* swimming, and endurance) among post-flexion larvae, whilst considering phylogenetic relationships and morphology, and we found that reef fishes have higher swimming capacity than non-reef (pelagic and non-reef demersal) fishes, which is likely due to larger, more robust body sizes. Thirdly, we compared swimming performance of late-stage larvae of tropical fishes with oceanographic data to better understand the ecological relevance of their high-capacity swimming. We found that reef fishes have high swimming performance and grow larger than non-reef fish larvae, which we suggest is due to the pressures to find a specific, patchily distributed habitat upon which to settle. Given the current bias towards studies on percomorph fishes at low latitudes, we highlight that there is a need for more research on temperate reef fish larvae and other percomorph lineages from high latitudes. Overall, our findings provide valuable context to understand how swimming and morphological traits that are important for dispersal and recruitment processes are selected for among teleost fish larvae.

KEYWORDS
early life history, fish evolution, fish exercise physiology, ontogeny, phylogenetic comparative methods, recruitment strategies

1 | INTRODUCTION

A 2015 study suggested that Marine Protected Areas (MPAs) should encompass approximately 10% of the ocean's surface by the year 2020 (Andrello et al., 2015). Generally, MPAs attempt to preserve marine biodiversity, reduce exploitation of marine resources, and assist in the recovery of exploited or disturbed habitats. As such, MPAs represent a conservation and management policy with broad implications for protecting biodiversity, helping coastal human communities, and maintaining healthy stocks that supply young fish to overfished or damaged habitats (Andrello et al., 2015; Harrison et al., 2020). However, to be effective, MPAs must be self-sufficient (e.g. self-recruitment of early life stages) and linked with other marine habitats—protected or not—to promote recovery from disturbances (Planes et al., 2009). Thus, management of the marine environment relies on understanding the spatial scale of the movement of species and their habitat ranges through time (e.g. timing of migrations, movements to nurseries, influx of larvae, etc. Barbut et al., 2019; Lowerre-Barbieri et al., 2017).

Connectivity among geographically separated marine populations is critical, not only for MPA management, but for general ecosystem function, population structure, genetic diversity, and for improving ecosystem resilience to natural and anthropogenic disturbances (Barbut et al., 2019; Ramos et al., 2017). Dispersal is a key driver of connectivity and is also a measure of the adaptive capacity of a species to influence habitat range on temporal and spatial scales. For species with bipartite life histories, such as marine teleost fishes (i.e. especially those with site-attached juveniles and adults, such as demersal fishes), dispersal generally occurs during larval stages and is largely influenced by physical processes (e.g. hydrodynamics of the ocean) as well as by individual species traits (Lacroix et al., 2018). Due to the high mortality rates of fish larvae that lead to fluctuations in annual recruitment, dispersal is critical for maintaining population structure/dynamics and resilience to disturbances within fish populations (Lacroix et al., 2018). Several biotic and abiotic factors contribute to differences in dispersal potential among marine fishes, especially at different latitudes. Leis, Caselle, et al. (2013) and Leis, Hay, et al. (2013) describe how several of these factors, such as larval duration, community structure, spawning mode, hydrodynamic conditions, water temperature, and larval behaviour, contribute to latitudinal differences in dispersal potential among coastal fish larvae. The focus of the current study will expand upon how an influential and universal performance trait among larval fishes—swimming behaviour—differs in relation to the habitat used by the adults (e.g. reef, non-reef demersal, and pelagic) in high and low latitude groups of marine fishes.

For most marine teleost fishes, regardless of latitude, locomotor capabilities develop during larval stages (Downie et al., 2020). The focus of many early studies investigating swimming performance of marine teleost larvae was on commercially important pelagic and non-reef demersal species such as herrings (Order Clupeiformes), cods (Order Gadiformes), and flatfishes (Order Pleuronectiformes) that inhabit cold, temperate (i.e., high latitude) environments (Miller et al., 1988). These fishes are generally poor swimmers as larvae (<10 cm s^{-1}, throughout larval period), and the ability for influential horizontal swimming occurs during late larval or early juvenile life stages (Miller et al., 1988). Early generalizations suggested that marine fish larvae were planktonic organisms that passively drifted with ocean currents with no influence over where they ended up, regardless of latitude, and this had large implications for modelling connectivity and dispersal patterns of larval fishes (e.g. Roberts, 1997). This perspective changed with the discovery that, under laboratory conditions, late-stage tropical coral reef fishes were capable of swimming at high speeds (>40 cm s^{-1}; Stobutzki & Bellwood, 1994). This was further confirmed with *in situ* observations of actively swimming tropical reef fish larvae (Leis et al., 1996), as well as studies that underscored their high endurance capacity (Fisher & Bellwood, 2001; Stobutzki & Bellwood, 1997). These findings highlight the potential that tropical reef fishes have to influence their own dispersal. For example, several studies have shown that tropical reef fishes can return to natal reefs (e.g. anemonefishes, Pomacentridae, returning to within a few metres of natal anemones) or disperse using currents and swimming behaviour tens of kilometres to find a new reef home (Harrison et al., 2012; Jones et al., 1999, 2005). Swimming performance among fishes in warm tropical waters (i.e. low latitudes) has been considered to be higher compared to fish from cool latitudes because warmer temperatures increase the kinetic reactions within muscle tissues (Fisher et al., 2005; Leis, 2006, 2007). However, recent evidence suggests that larvae of temperate reef fishes are also capable of high swimming speeds (>40 cm s^{-1}; Faillettaz et al., 2018; Leis et al., 2012; Pattrick & Strydom, 2009), despite swimming in 10°C cooler water than larvae of tropical fishes, suggesting that other factors besides temperature may be influencing swimming performance.

Given that evolutionary success is a result of the integration of all life history components across the lifetime of the organism, it is likely that the habitat used by the adults may play a role in larval life history strategies. Both tropical and temperate demersal fishes live in close association with the benthos, but their eggs and larvae are carried by oceanic and reef currents, leaving larvae to develop in the open ocean (Leis, 2006). After a species-specific duration of time, the larvae return to a reef using a combination of current drift and active swimming with and against strong, directional reef currents (Leis, 2006). This contrasts with pelagic fishes that remain in open waters as juveniles and adults after their larval phase, suggesting the environmental pressures associated with swimming may be more consistent across life history stages. However, larvae of reef fishes have been shown to be better swimmers than larvae of non-reef demersal fishes (e.g. groups like cods, Order Gadiformes, and flatfishes, Order Pleuronectiformes, that do not settle onto reef habitat). The pressure to find a specific, yet suitable, patchily distributed coral or rocky reef habitat with distinct differences in hydrology (e.g. currents and tidal energy) on which to settle may influence swimming performance in particular groups of reef-associated fishes across latitudes.

Life history and morphology could play a critical role influencing swimming behaviours among different groups of fishes. For example, oxygen uptake rates among marine fishes scale differ with mass depending on lifestyle (e.g. benthic vs. pelagic; Killen et al., 2010). Since larvae of temperate reef fishes swim at impressive swimming speeds (>40 cm s^{-1}; e.g., Leis et al., 2012) when compared to those of pelagic temperate fishes (swimming speed ranged from 10–20 cm s^{-1}; e.g., Miller et al., 1988), interspecific differences in swimming ability may be related to more than previously established factors (e.g. latitude) alone. Body morphology could be one such factor, as body shape has been found to predict swimming performance among tropical reef fish larvae (Fisher & Hogan, 2007). Given the variety of body shapes among different fish groups at the taxonomic level (e.g. circular shapes of butterflyfishes, Order Chaetodontiformes and ribbon-like shapes of herrings, Order Clupeiformes) and how certain families and orders dominate fish communities at specific latitudes (e.g. percomorph fishes are the most abundant group in warm, coastal habitats, and non-percomorph fishes, such as fishes from Orders Gadiformes and Clupeiformes, are more dominant in cold, pelagic habitats), certain body shapes may be more specialized to high performance swimming. In short, more robust body forms may have greater muscle mass than more slender-shaped morphologies. In addition, confirming interspecific differences in performance using phylogenetic comparative methods would show how swimming performance varies among species while accounting for ancestral relationships and whether the magnitude of swimming ability is correlated with species relatedness. Moreover, such analyses may highlight gaps in knowledge and/or biases from certain taxonomic groups. To date, such information is missing from the fish ecology and physiology literature but would provide critical information for understanding larval dispersal potential and population connectivity of fishes associated with coastal and pelagic habitats.

Here, we used comparative phylogenetics, data synthesis, and a case study approach to understand several factors that influence swimming performance in marine teleost fish larvae. Our overarching hypothesis is that, regardless of latitude, larvae of reef-associated species are better swimmers than non-reef larval fishes (i.e. pelagic and non-reef demersal species), as the pressure to find a specific patchily distributed coastal reef habitat at the end of their larval duration requires higher swimming performance than simply remaining in the pelagic environment or finding a common benthic habitat. To investigate this hypothesis, we divided our study into three distinct aims where we compared swimming performance among larvae of species that inhabit different habitats (reef, non-reef demersal, and pelagic) across latitude (temperate and tropical).

For the first aim (Aim I), we investigated the relationship between swimming ability and growth (using changes in body length as a proxy for growth) across habitats throughout early ontogeny (pre-flexion to post-flexion), using *in situ* and laboratory estimates. We predicted that both tropical and temperate reef-associated fishes would have greater increases in swimming speed with growth when compared to temperate and tropical non-reef fishes in order to achieve faster swimming speeds into later, post-flexion stages. The post-flexion stage represents the point where larvae begin to resemble adult morphologies, and swimming ability has the greatest influence on dispersal (Fisher et al., 2000). Therefore, in our second aim (Aim II), we (I) incorporated phylogenetic comparative analyses to investigate differences in swimming performance among post-flexion larvae from different habitats using three measures of swimming performance (endurance, *in situ*, and critical swimming speed) and (II) determined the relationship between morphology (body size, body shape, muscle area, and caudal fin area) and swimming performance. We predicted that tropical reef fishes will have the strongest swimming capabilities across all three measures of swimming performance when compared to the other groups, likely due to larger body sizes. Consequently, we predicted that larvae that exhibit more robust body shapes would have higher swimming performance than more slender-shaped species. In general, tropical reef fishes have more robust shapes, and therefore, we predicted this would support their high swimming performance. Lastly, in our third aim (Aim III), we used a case study approach to investigate why tropical reef fishes swim to high capacities. We did this by comparing swimming data with oceanographic current data in a representative reef habitat (i.e. Lizard Island, Australia), to place performance within a relevant ecological context. We predicted that tropical reef fishes, which presumably exhibit larger body sizes and robust body shapes, may have high swimming performance in order to surpass fast currents around Lizard Island. Overall, swimming is a critical trait that enables larvae to grow, develop, find a suitable habitat, and ultimately contribute to the supply of new individuals required to support adult populations. Our perspective on the role habitat selection may play in influencing swimming performance among fish larvae across latitude may enhance our understanding of dispersal and recruitment strategies of fishes, and our findings will provide critical information for spatial management of fisheries and reserves.

2 | METHODS

2.1 | Data collection

2.1.1 | Literature search

To collect data on marine fish larvae swimming performance, a systematic literature search was performed (ISI Web of Knowledge, Clarivate Analytics, Core collection) using the following search terms: *(swim* OR sust* OR prolong* OR* U_{crit} *OR in situ) AND (early life stage* OR larv*) AND (marin* OR sea*) AND (fish* OR teleost*)*. Studies were manually checked for appropriateness for our analysis—mainly if the larvae were swum using endurance, *in situ*, or critical swimming speed tests and whether the body length each larva was provided (the exception being endurance swimming, as most studies did not provide body length). Generally, we extracted swimming data on an individual fish level either directly from the paper or from the supplementary materials, as most studies expressed swimming as scatter plots (swimming metric vs. size). Swimming data were extracted from the selected studies using WebPlotDigitizer (Version 4.2, Ankit Rohatgi). Other data extracted from the sources included fish length (standard length; mm) and experimental water temperature (°C). We used fish standard length as our proxy for size, as it was the most common metric across all selected studies.

2.1.2 | Swimming metrics investigated and general data organization

We focussed on studies that measured the following swimming metrics: critical swimming speeds (U_{crit}), *in situ* swimming speeds, and endurance capacity. This allowed us to investigate swimming performance of marine teleost larvae over a wide range (e.g. slow to fast performance) of metrics. Critical swimming speed tests are performed in a laboratory flume using a stepped velocity test, where fish swim against an incrementally faster flow over set time periods until fatigue, and this type of test is an estimate of fast, prolonged swimming speeds that fishes can maintain for short periods of time (Brett, 1964). Of the three investigated swimming metrics, U_{crit} represents the fastest swimming speeds larvae can maintain aerobically (i.e. fatigue endpoint is caused by mainly aerobic and partly anaerobic processes; Downie & Kieffer, 2017; Illing et al., 2021) and represents the upper limit of their swimming performance that may influence their dispersal capabilities (e.g. overcoming fast currents over a short period of time). *in situ* swimming speeds represent preferred swimming speeds of larvae under natural conditions and are measured by a scuba diving team observing the larvae in the ocean (Leis et al., 1996; and see Leis, 2006 for discussions on potential methodoloigcal biases). Lastly, endurance swimming represents the maximum distance that larvae can swim until fatigue. Generally, fish are forced to swim at a fixed velocity in a laboratory flume until fatigue (e.g. Majoris et al., 2019).

We then grouped each species from our selected studies by "Environmental Habitat," which represents a combination of latitude and habitat (temperate reef, temperate pelagic, temperate demersal, tropical reef, tropical pelagic, and tropical demersal), based on each species' description from their respective study. Experimental water temperature was generally confounded with "Environmental Habitat," with the exception of temperate demersal and temperate pelagic species, which were swum across a wide range of temperatures. Temperate demersal species (e.g. Atlantic cod, *Gadus morhua*, Gadidae; Guan et al., 2008; European plaice, *Pleuronectes platessa*, Pleuronectidae; Silva et al., 2015) from colder habitats were generally swum between 3 and 8.5°C. Some temperate demersal species were from warmer habitats, primarily the East coast of Australia (e.g. Australasian snapper *Pagrus auratus*, Sparidae; Japanese meagre *Argyrosomus japonicus*, Sciaenidae; yellowfin bream *Acanthopagrus australis*, Sparidae; Clark et al., 2005) and were swum between 20 and 23°C and the Gulf of Mexico (e.g. red drum *Sciaenops ocellatus*, Sciaenidae; Faria et al., 2009) and were swum at summertime temperatures of 26°C. Temperate pelagic species from colder habitats were swum at 7°C (e.g. Atlantic herring *Clupea harengus*, Clupeidae; Moyano et al. 2016) and 15°C (e.g. European pilchard *Sardina pilchurus*, Clupeidae; Silva et al., 2014); whereas, temperate pelagic species from warmer waters were swum at 17.5°C (e.g. sand smelt *Atherina presbyter*, Atherinidae; Faria et al., 2014) and 20°C (e.g. alewife *Alosa pseudoharengus*; Clupeidae; Klumb et al., 2003). Temperate reef fishes were swum within a narrow range of temperatures, spanning 18.5–20°C. Tropical fishes (pelagic, demersal, and reef) were swum between 26 and 30°C.

The criteria used to classify a species as "reef-associated" was whether they settled to adopt a close association with a benthic coral (tropical) or rocky coastal (temperate) habitat after a pelagic phase as a larva. Here, we define demersal fishes as fishes that settle in association with benthic habitats that are not reefs (e.g. gravel, muddy, or sandy bottoms) after a pelagic phase. Pelagic fishes remain in the water column across ontogenetic stages (i.e. larvae to adult). We classified each individual larva in the entire analysis based on ontogenetic stage, either pre-notochord flexion or post-notochord flexion (which also contained flexion-stage larvae). Pre-notochord flexion larvae generally have underdeveloped swimming fins and muscles and have limited ability to control horizontal movement (Downie et al., 2020). Over a narrow species-specific length range, the notochord flexes, and the caudal fin forms, marking an increase in horizontal swimming ability (post-notochord flexion; Downie et al., 2020). These classifications were based on when this transition between pre- and post-notochord flexion stages occurs, as per each species' body length, which was indicated by their respective studies.

2.2 | AIM I: Development of swimming performance over growth

2.2.1 | Data organization

Swimming speed across length (standard length; mm) was collected from marine teleost larvae, focussing on U_{crit} and *in situ* metrics, as not enough studies measured endurance swimming over development. We only included studies that measured swimming over the entire larval duration (pre- and post-flexion) of the study species, versus focussing on one stage (e.g. studies that exclusively swam post-flexion fish). All six "Environmental Habitats" were analysed for U_{crit}; however, "Temperate Reef" and "Temperate Pelagic" species were not present in the literature for *in situ* analyses.

2.2.2 | Statistical analyses

All statistical analyses for Aim I were performed using R (ver 3.6.1. http://www.R-project.org/). Prior to statistical analyses, data were checked for normality using visual diagnostic tests (Q-Q plots) and the Shapiro–Wilk test. The swimming data (U_{crit} and *in situ* swimming speeds) and body length were log-transformed prior to analyses for normality. Linear models, and "emtrends" function from the "emmeans" package (Lenth, 2016), were used to compare slopes between "Environmental Habitats" as swimming speed changed with body length. "Environmental Habitat" was considered a categorical variable in the model, swimming speed (U_{crit} or *in situ*) was a response variable, and body length was a continuous variable. The most appropriate model tested swimming speed (U_{crit} or *in situ*) as a function of the interaction of "Environmental Habitat" (categorical) and body length (continuous). This model was selected based on the lowest Akaike Information Criterion (AIC) using the "MuMIn" package (Barton, 2009). Upper and lower confidence intervals were determined using the "emmeans" package using the best fitting model. We set an $\alpha = 0.05$ to compare slopes between "Environmental Habitats."

2.3 | AIM II. Comparing swimming performance of post-flexion larvae

2.3.1 | Data organization

We used post-flexion-stage larvae from all six "Environmental Habitats" and three swimming metrics—U_{crit}, *in situ*, and endurance—for analyses. We expressed U_{crit} and *in situ* swimming in absolute (cm/s) terms. For endurance data, we only included studies that had swum fish at similar flow speeds (10–13 cm/s) and did not feed their larvae during the experiment so that the studies would be comparable.

At the post-flexion stage, fish larvae exhibit a wide range of body sizes, which is confounded with "Environmental Habitat," as tropical species are generally larger than temperate species. We investigated the influence of body length on swimming performance among "Environmental Habitats" in two different ways. The first model investigated differences in swimming performance over all sizes, with the exception being endurance swimming tests because body length data were not readily available. Generally, covariates should be within a similar range, and data outside that range should be omitted from the analysis (Quinn & Keough, 2002). Thus, we created a second model, where we sub-set the body length data to compare U_{crit} among our "Environmental Habitats" within a range of sizes common among all groups (16–22 mm SL) because there are large size differences between groups (e.g. tropical reef vs. temperate pelagic and temperate demersal groups). We could not perform similar analyses on *in situ* swimming, as there was not enough overlap in body sizes (Figure 7).

2.3.2 | Body shape analyses

To perform the analyses on body morphology and swimming performance, we extracted images from the literature (e.g. the studies that swum the fish), larval fish guides and online sources (see Supplementary Materials S3 for reference list). For any particular post-flexion-stage individual or representative of a species, we found images that were of similar size (<5 mm difference between the size of the image and size of the fishes swum in their respective study). We were able to find images for 80% of the species of post-flexion-stage larvae within an appropriate size range (see Supplementary Materials S3 for species list), and on average, the difference between the size of the individual swum and the images used for body shape analyses was 1.5 mm ± 1.5 mm (mean ± standard deviation). Following the procedures of Fisher and Hogan (2007), we measured total length, body depth, body area, propulsive area, muscle area, caudal fin height and caudal fin area in ImageJ (Figure 1). We were then able to calculate body shape as the ratio of body length to body depth, following Fisher and Hogan (2007). While we measured propulsive area and body area, these metrics did not add to the model and were omitted from the analyses, but we maintained the body shape data in the raw data data files.

2.3.3 | Statistical analyses

Model diagnostics were the same as in Aim I. We then created size distributions for each "Environmental Habitat" to highlight the differences in sizes (length, mm) at settlement between the groups. Bin size (4 mm) was uniform across "Environmental Habitats." First,

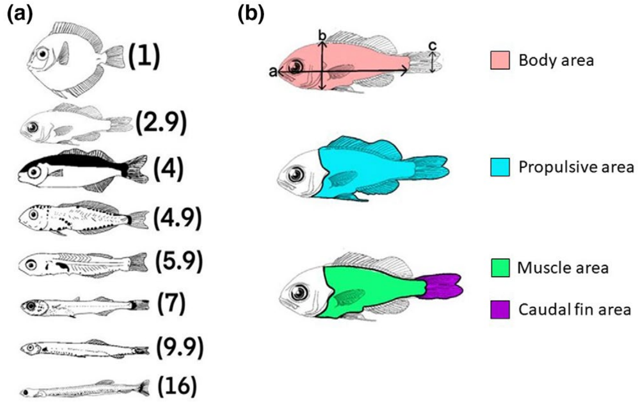

FIGURE 1 Images showing body shapes and measurements of morphology used to predict swimming capacity among fishes in our analyses. Body shape represents the ratio of body length to body depth and was calculated from reference photographs for each species within a narrow size range (see Methods 2.3.2 for details). (a) The representatives for different body shapes, spanning the most robust (body length:body depth = 1) to the most ribbon-like (body length:body depth = 16) body shapes. (b) The morphological features measured in each photograph: *a* standard length, *b* body depth and *c* caudal fin depth. From each photograph, we also measured body area, propulsive area, muscle area and caudal fin area (see Methods 2.3.2 for details)

linear models were used to compare swimming performance (U_{crit}, *in situ*, or endurance) between "Environmental Habitats" as a function of body length. "Environmental Habitats" were considered fixed, categorical factors in the model, and values for swimming performance (U_{crit}, *in situ*, and endurance) and body length were continuous variables. For U_{crit}, two models were tested: U_{crit} in response to the interaction of "Environmental Habitat" across the complete body length range of all species and U_{crit} in response to the interaction of "Environmental Habitat" and at a common body length range of 16–22 mm SL across all "Environmental Habitats." For *in situ* swimming speed, only one model could be tested: *in situ* swimming speed in response to the interaction of "Environmental Habitat" and body length (i.e. all body lengths). For endurance swimming, only one model could be tested: endurance distance in response to "Environmental Habitat," as body length data were not widely available. Second, a linear model was used to test U_{crit} in response to the interaction between "Environmental Habitat" and body shape. Third, linear models were used to test for differences in morphology (i.e. muscle area and caudal fin area) in response to "Environmental Habitat" as a function of body length. For both muscle area and caudal fin area, two models were tested: muscle or caudal fin area in response to "Environmental Habitat" (all body lengths) and muscle or caudal fin area in response to the interaction of "Environmental Habitat" and a common body length range from 16 to 22 mm SL. Morphology metrics (body shape, muscle area and caudal fin area) were all continuous variables. For body shape, swimming performance, morphology, and body length were log-transformed for statistical analyses (as data were not normally distributed) but then back-transformed to the response scale for plotting figures. The most appropriate model, including an interaction with body length, was selected based on the lowest Akaike Information Criterion (AIC) using the "MuMIn" package (Barton, 2009). For all swimming tests (U_{crit}, *in situ*, and endurance) and body shape analyses versus "Environmental Habitat" analyses, estimated marginal means were calculated using the "emmeans" package (Lenth, 2016) based on the best fit model and provided *p*-values from all our models. Significant differences were determined using a Tukey's post hoc test ($\alpha = 0.05$).

2.3.4 | Comparative phylogenetic analyses

Comparative phylogenetic methods were performed in R (R Development Core Team, 2013) using the "ape" (Paradis & Schliep, 2019) and "phytools" (Revell, 2012) packages. We used a pre-existing phylogenetic tree representing all extant fishes for our analyses accessed using the "fishtree" package (Chang et al., 2019; Rabosky et al., 2018). The scientific names of the species we selected were validated using the "rfishbase" package (Boettiger et al., 2012), and we pruned the entire tree based on these species. We pruned the phylogenetic tree down to tips that represented species sampled for each swimming metric (U_{crit}, *in situ*, or endurance swimming) using the function "drop.tip" from the "ape" package. We tested three models: swimming speed (U_{crit}, *in situ*) or swimming distance (endurance) were continuous response variables that were modelled in response to "Environmental Habitat" as a fixed factor and body length as a continuous factor (except for endurance swimming). The best model for phylogenetic analyses, including an interaction with body length, was selected based on the lowest AIC rankings using the "MuMIn" package. A Phylogenetic General Least Squares (PGLS; $\alpha = 0.05$) model ("nlme" package; Pinheiro et al., 2019) was used to investigate patterns of variation in swimming performance between species from different "Environmental Habitats" while accounting for phylogeny. Trees and their associated physiological traits (U_{crit}, *in situ*, and endurance swimming) were plotted using the "ggtree" package (Yu et al., 2017, 2018).

2.4 | AIM III: Case study: swimming performance over ontogeny versus Lizard Island current speeds

2.4.1 | Swimming performance over ontogeny versus Lizard Island current speeds

We used swimming data from Fisher et al. (2000) for this first objective. In their study, they measured U_{crit} daily over the entire larval duration, from hatch until the point of settlement, of three tropical reef fishes, including Ambon damselfish (*Pomacentrus amboinensis*, Pomacentridae), cinnamon anemonefish (*Amphiprion melanopus*, Pomacentridae), and pyjama cardinalfish (*Sphaeramia nematoptera*, Apogonidae). The two pomacentrid species (*P. amboinensis* and *A. melanopus*) have demersal eggs; whereas, the apogonid (*S. nematoptera*) has orally brooded eggs. For our analysis, we first calculated Reynold's Number (*Re*) for each U_{crit} measurement per species. The Reynold's number is a dimensionless metric that provides an estimate of the resistive forces of a fluid against an object in relation to the speed and length of the object moving through the fluid (Taylor, 1951). When *Re* is <300, this indicates that the viscosity of the fluid is too great for the object to move through it for prolonged periods, conditions that may be characteristic of fish larvae prior to notochord flexion. Swimming is inefficient and cannot be maintained for long periods; although, short movements for feeding and vertical migrations are possible. When *Re* is >1,000, this indicates that the object is capable of horizontal movements against the fluid. *Re* was calculated as:

$$\mathrm{Re} = U * L * V^{-1}$$

where U is U_{crit} (m s^{-1}), L is fish length (*m*), and V is the kinematic viscosity of seawater (m^2 s^{-1}) at the respective experimental temperature (Fuiman & Batty, 1997; Taylor, 1951). This allowed us to estimate when each species was capable of swimming under an inertial swimming regime ($Re > 1{,}000$) and therefore when swimming would be expected to have some capacity to influence dispersal potential. Johansen (2014) measured currents at three distinct reef habitats (i.e. exposed, oblique, and sheltered reefs at three replicate sites per habitat) around Lizard Island on the northern Great Barrier Reef, Australia, using a custom-built flow meter at depths of 3 and 9 m below the surface. The three reef habitats vary with respect to physical cover from the south-easterly trade winds, with "exposed reefs" having little cover, "oblique reefs" having some cover, and "sheltered reefs" having ample cover from the winds (see Johansen, (2014) for a schematic of the reefs). The depth range measured by Johansen (2014) represents a range of depths at which reef fishes swim when they approach the reef (see review by Leis, 2006). Current speeds were measured every 10 s, and on average, the current meter at each replicate site (3) per habitat per depth recorded 251 ± 47 hr (mean ± standard error; *s.e.*) of current data (Johansen, 2014). We used the averaged current speed for each habitat (averaged across the three replicate sites) for the depths of 3 and 9 m (i.e. as per Figure 4 in Johansen, 2014) for our case study. We superimposed the averaged annual current speed from each habitat and depth onto the swimming speed data in Figures 12 and 13. We could then compare the ages of larvae swimming under inertial regimes, factoring the average flow rates around the island at different depths, to infer whether remaining near the reef during the larval stage would be feasible.

2.4.2 | Swimming performance of settlement-stage coral reef fishes versus Lizard Island current speeds

Following a similar approach to Fisher, (2005), we used the same oceanographic data from 2.4.1. of the current study and superimposed it onto the speeds of different swimming metrics (i.e. estimated minimum swimming speed, average *in situ* speed, and average U_{crit}) of settlement-stage tropical coral reef fishes. Swimming data were adapted from (Leis & Fisher, 2006) in which U_{crit} and *in situ* speeds were measured in 30 species of settlement-stage reef fish larvae. To understand whether reef fishes swim at or beyond the minimum requirements of their habitats prior to settlement, we first had to define a "minimum" for each species. To do this, we calculated, for each species, the swimming speed at which *Re* would be 1,000 (i.e. the lowest *Re* at which an animal is predicted to overcome the viscosity of water). We then combined these data with average *in situ* speed (cm/s) and average U_{crit} (cm/s) for species within each family. Superimposing the swimming data on to the oceanographic data (Johansen, 2014) would then provide an estimate as to whether *in situ* or maximum swimming is sufficient to swim against reef currents at specific depths for each habitat and at which speeds, relative to minimum performance, fishes operate. We included swimming speeds for a tropical pelagic fish species and a tropical demersal fish species, where *in situ* and U_{crit} were available for the same species, to compare with the reef fishes.

3 | RESULTS

3.1 | Search results

The literature search resulted in 37 relevant studies for our analyses. Our analyses, across all three aims, comprised 209 species (including 19 species only to genus level and 26 species only to Family level) from 44 families in 25 orders of teleost fishes. For a summary, see Table 1, and for a complete species list (scientific names, common names, and families), refer to Supplementary Materials S1 and the raw data files.

3.2 | AIM I

Correlation between body size and critical swimming speed was highest among temperate ($r^2 = 0.80$) and tropical ($r^2 = 0.64$) reef fishes. (Figure 2). In contrast, temperate pelagic fishes had the narrowest range in U_{crit} relative to length, and swimming speed was poorly correlated with body size ($r^2 = 0.0056$; Figure 2). Temperate reef fishes had the highest increase in U_{crit} with increasing body size ($\mathrm{Log}(U_{crit}) = 2.7\mathrm{Log}(\mathrm{Length}) - 4.25$; Figure 2), and temperate pelagic fishes were found to have the lowest increase in U_{crit} with increasing body size ($\mathrm{Log}(U_{crit}) = 0.29\mathrm{Log}(\mathrm{Length}) + 0.6$; Figure 2). The relationship between increasing body length and U_{crit} was generally different between all groups, except for temperate demersal and tropical demersal ($p = 0.99$), temperate demersal and tropical pelagic ($p = 0.78$), tropical demersal and tropical pelagic ($p = 0.73$), and tropical demersal and tropical reef ($p = 0.77$) (Figure 2; also, see Supplementary Materials S2.1.1 for details on statistical output). However, the way that *in situ* swimming changes with increasing size was similar between groups (i.e. tropical reef, tropical pelagic, tropical demersal, and temperate demersal), as slopes were not significantly different (Figure 3; $p > 0.3$ for all combinations of groups;

TABLE 1 Summary of taxonomic groups (Order and Family level) used for the analyses in this study (AIMS I, II, and III), organized into “Environmental Habitat” (Tropical Reef, Tropical Pelagic, Tropical Demersal, Temperate Reef, Temperate Pelagic, Temperate Demersal), swimming metrics (critical swimming speed U_{crit}, *in situ*, and endurance), and the number of species swum for each metric. Refer to Supplementary Materials for species list (scientific and common names).

Order	Family	Environmental habitat	U_{crit} (G)	*in situ* (G)	U_{crit} (PF)	*in situ* (PF)	End. (PF)
Acanthuriformes	Acanthuridae	Tropical Reef	0	0	5	0	0
Atheriniformes	Atherinidae	Temperate Pelagic	1	0	1	0	0
Blenniiformes	Blenniidae	Tropical Reef	0	0	4	0	0
	Grammatidae	Tropical Reef	1	0	1	0	0
	Pomacentridae	Tropical Reef	3	0	40	0	30
		Temperate Reef	1	0	1	0	0
Carangiformes	Carangidae	Tropical Reef	0	0	2	0	1
		Tropical Pelagic	2	1	2	1	1
	Rachycentridae	Tropical Reef	0	0	1	0	0
Centrarchiformes	Perichthyidae	Temperate Demersal	0	0	0	0	1
	Terapontidae	Tropical Reef	0	0	1	0	0
Chaetodontiformes	Chaetodontidae	Tropical Reef	0	0	8	0	10
	Leiognathidae	Tropical Demersal	1	1	1	1	1
Clupeiformes	Clupeidae	Temperate Pelagic	1	0	3	0	0
		Tropical Pelagic	0	0	2	0	0
Ephippiformes	Ephippidae	Tropical Reef	1	1	1	1	0
Gadiformes	Gadidae	Temperate Demersal	1	0	1	0	0
Gobiesociformes	Gobiesocidae	Temperate Reef	2	0	0	0	0
Gobiiformes	Gobiidae	Tropical Reef	2	0	2	0	0
Gonorynchiformes	Chanidae	Tropical Pelagic	1	0	1	0	0
Holocentriformes	Holocentridae	Tropical Reef	0	0	2	0	0
Istophoriformes	Polynemidae	Tropical Demersal	1	1	1	1	1
Kurtiformes	Apogonidae	Tropical Reef	1	0	22	0	1
Labriformes	Labridae	Tropical Reef	0	0	7	0	0
Lobotiformes	Moronidae	Temperate Reef	1	0	1	0	0
	Sciaenidae	Temperate Demersal	3	2	3	2	1
Lophiiformes	Ogcocephalidae	Tropical Reef	0	0	1	0	0
Lutjaniformes	Haemulidae	Tropical Reef	0	0	1	0	0
	Lutjanidae	Tropical Reef	1	1	10	1	0

(Continues)

TABLE 1 (Continued)

Order	Family	Environmental habitat	U_{crit} (G)	*in situ* (G)	U_{crit} (PF)	*in situ* (PF)	End. (PF)
Perciformes	Psychrolutidae	Temperate Demersal	1	0	1	0	0
	Sebastidae	Temperate Reef	5	0	0	0	0
	Serranidae	Tropical Reef	4	2	5	2	0
Pleuronectiformes	Pleuronectidae	Temperate Demersal	1	0	1	0	0
Scombriformes	Nomeidae	Tropical Pelagic	0	0	1	0	0
Spariformes	Lethrinidae	Tropical Reef	0	0	1	0	0
	Nemipteridae	Tropical Reef	0	0	2	0	0
	Pomacanthidae	Tropical Reef	0	0	2	0	0
	Siganidae	Tropical Reef	0	0	1	0	0
	Sparidae	Temperate Reef	5	0	10	0	1
		Temperate Demersal	2	1	2	1	2
		Tropical Reef	1	0	0	0	0
Syngnathiformes	Mullidae	Tropical Reef	0	0	1	0	1
	Sphyraenidae	Tropical Reef	0	0	1	0	0
	Syngnathidae	Tropical Reef	0	0	1	0	0
Tetraodontiformes	Balistidae	Tropical Reef	0	0	2	0	0
	Diodontidae	Tropical Reef	0	0	1	0	0
	Monacanthidae	Temperate Reef	0	0	0	0	1
		Tropical Reef	0	0	6	0	0
	Ostraciidae	Tropical Reef	0	0	2	0	0
	Tetraodontidae	Tropical Reef	0	0	3	0	0

Note: G, U_{crit} and, *in situ* over growth studies (AIM I); PF, Post-Flexion larvae used for U_{crit}, *in situ*, and endurance studies (AIM II and III).

refer to Supplementary Materials S2.1.2. for details on statistical output).

3.3 | AIM II

Upon completion of flexion, tropical reef fishes are generally larger than larvae from other "Environmental Habitats" (Figure 4). Among the tropical reef fishes, and from the available studies, we see the largest individuals and, overall, larger size classes with the highest frequency of individuals. Among the temperate reef fishes at or beyond flexion stages, there is a higher frequency of larger size classes than in temperate pelagic and demersal fishes (Figure 4).

When considering all sizes of post-flexion larvae, tropical reef fishes have the highest critical swimming speed (U_{crit}; Figure 5a). Temperate pelagic fishes had the lowest U_{crit} values of all "Environmental Habitats" (Figure 5a). Temperate reef fishes swim faster than tropical pelagic fishes ($p = 0.036$) but not significantly different than tropical demersal fishes ($p = 0.79$; refer to Supplementary Materials S2.2.1 for details statistical output; Figure 5a). Comparing U_{crit} within a similar size range (16–22 mm SL) revealed that tropical reef, tropical demersal, and temperate reef fishes swim at similar speeds ($p > 0.1$ for all combinations; refer to Supplementary Materials S2.2.2 Figure 5b).

Upon accounting for phylogenetic relationships among species (PGLS), we found significant differences in U_{crit} between settlement-stage larvae with respect to environmental habitat and body length ($p < 0.0001$ and $p < 0.0001$, respectively; refer to Supplementary Materials S2.2.10 for details on statistical output; Figure 6). The majority of reef-associated fishes for which data exist on swimming larvae, especially in the tropical latitudes, are from Percomorpha; whereas, larvae from temperate regions include species from the non-percomorph orders (e.g. Orders Clupeiformes and Gadiformes; Figure 6).

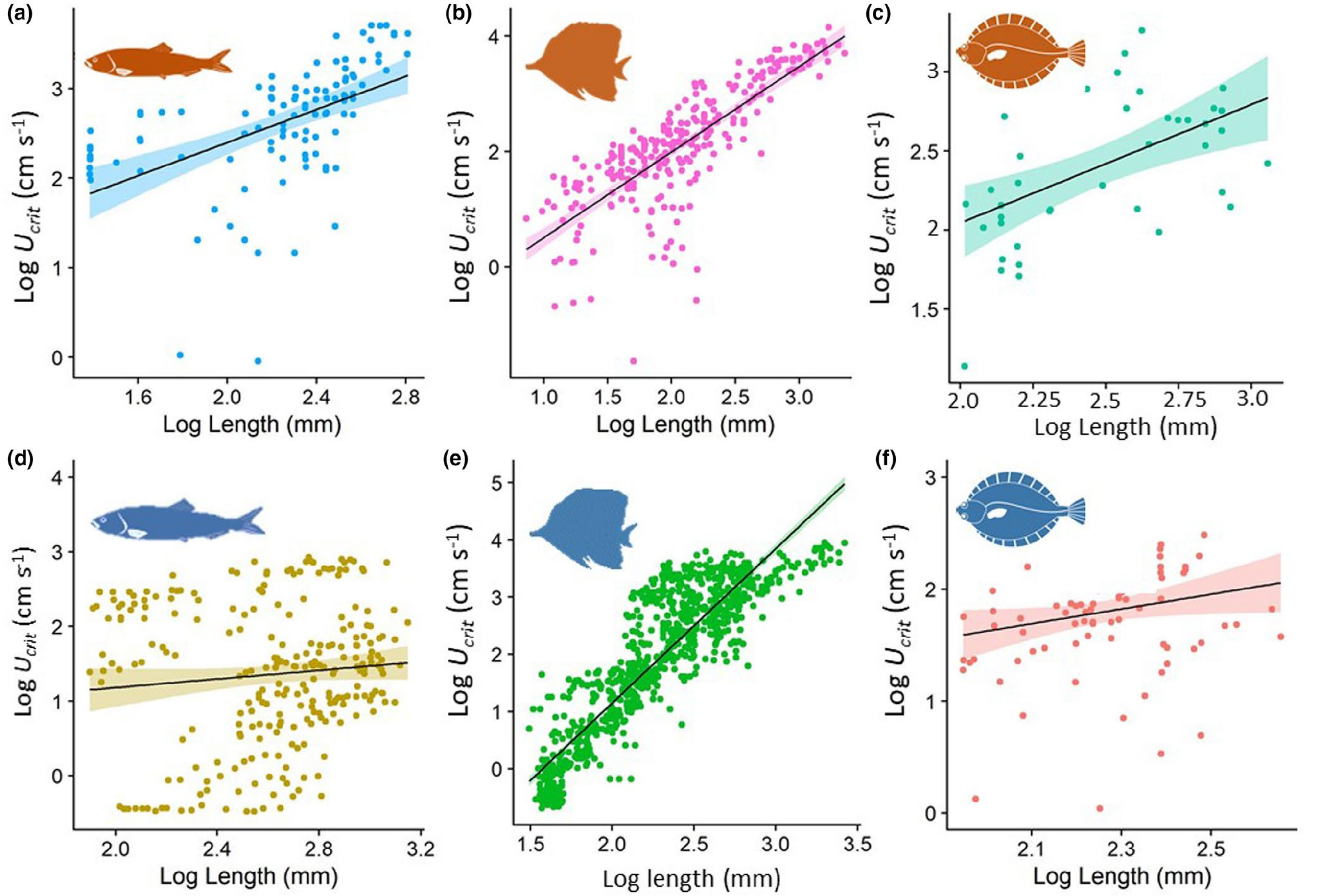

FIGURE 2 The relationship of critical swimming speed (U_{crit}; cm/s) with length (standard length; mm) for marine teleost fishes from six "Environmental Habitats": (a) tropical pelagic, (b) tropical reef, (c) tropical demersal, (d) temperate pelagic, (e) temperate reef, (f) temperate demersal. A herring symbol represents pelagic fish species, a butterflyfish symbol represents reef fish species, and a flatfish symbol represents demersal fish species. Blue-coloured symbols represent temperate species, and orange-coloured symbols represent tropical species. Raw data are included onto each panel respective to "Environmental Habitat" and represent an individual larva. Linear models are presented with 95% confidence intervals. The regression equations for each "Environmental Habitat" are based on the best fitting linear model (refer to supplementary materials), and the equations are as follows: tropical pelagic: $\text{Log}(U_{crit}) = 0.93\text{Log}(\text{Length}) - 0.97$ $r^2 = 0.26$; tropical reef: $\text{Log}(U_{crit}) = 1.48\text{Log}(\text{Length}) - 0.97$ $r^2 = 0.64$; tropical demersal: $\text{Log}(U_{crit}) = 1.25\text{Log}(\text{Length}) - 0.38$ $r^2 = 0.51$; temperate pelagic: $\text{Log}(U_{crit}) = 0.29\text{Log}(\text{Length}) + 0.6$ $r^2 = 0.0056$; temperate reef: $\text{Log}(U_{crit}) = 2.7\text{Log}(\text{Length}) - 4.25$ $r^2 = 0.8$; temperate demersal: $\text{Log}(U_{crit}) = 1.16\text{Log}(\text{Length}) - .6$ $r^2 = 0.35$

Similar to larvae used in U_{crit} experiments, larvae swum for *in situ* experiments from tropical reef habitats were larger at post-flexion stages, and a higher frequency of larger size classes was represented when compared to larvae from temperate non-reef and tropical non-reef habitats (Figure 7). Temperate larvae were generally smaller and showed a higher frequency of smaller size classes than tropical fishes (Figure 7). Among post-flexion larvae swimming *in situ*, we found that tropical reef fish larvae were swimming significantly faster than the other groups of fishes ($p < 0.03$ for all combinations; for details on statistical output refer to Supplementary Materials S2.2.3; Figure 8). We did not find a significant effect of length ($p = 0.92$) or "Environmental Habitat" ($p = 0.51$) on *in situ* swimming performance when accounting for phylogeny (refer to Supplementary Materials S2.2.11 for details on statistical output). Across all three "Environmental Habitats" from this sub-set of analyses, the fishes were exclusively percomorphs.

While temperate reef fish larvae at flexion stages were, on average, capable of swimming for longer distances (average = 30.8 ± 11.9 km) at constant speeds (10–13 cm/s) than fish from other groups, there were no statistical differences in endurance swimming between temperate reef fishes, tropical reef fishes (24.98 ± 3.1 km), tropical demersal fishes (14.32 ± 2.4 km) and tropical pelagic fishes (16.13 ± 4.3 km) ($p > 0.05$; Figure 9; also, for details on statistical output, refer to Supplementary Materials S2.2.4). Temperate demersal fishes had less endurance capacity than fishes from all of the other "Environmental Habitats" ($p < 0.0001$; Figure 9). Similar to our findings with *in situ* swimming performance, we found no significant effect of "Environmental Habitat" ($p = 0.47$) when we accounted for phylogenetic relatedness (for details on statistical output, refer to Supplementary Materials S2.2.12).

Fishes with more robust body morphologies typically had higher swimming performance than thinner, more ribbon-like species

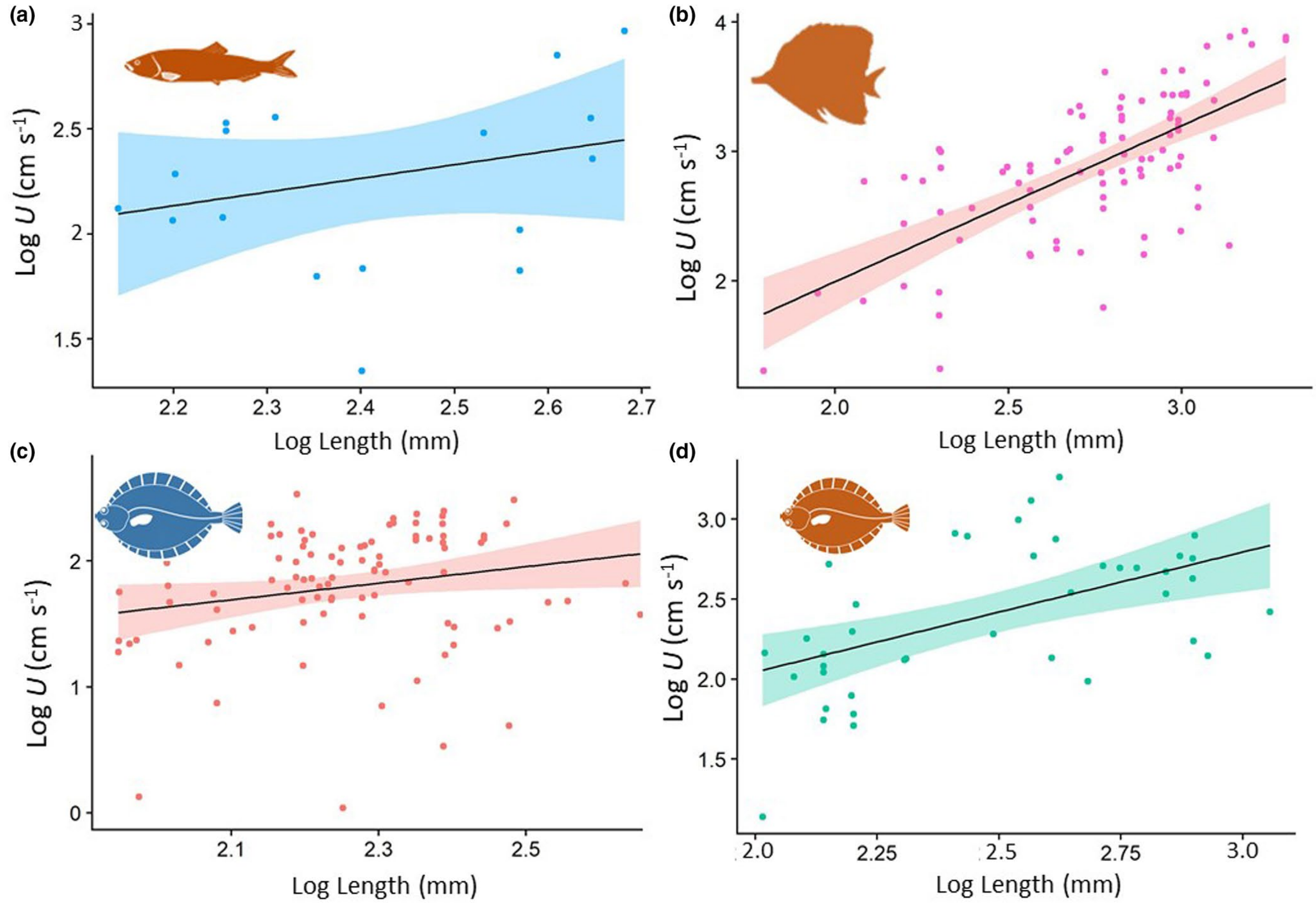

FIGURE 3 The relationship between *in situ* swimming (U; cm/s) and length (standard length; mm) for marine teleost fishes from four “Environmental Habitats”: (a) tropical pelagic, (b) tropical reef, (c) temperate demersal, (d) tropical demersal. A herring symbol represents pelagic fish species, a butterflyfish symbol represents reef fish species, and a flatfish symbol represents demersal fish species. A blue-coloured symbol represents temperate species, and an orange-coloured symbol represents tropical species. Raw data are included onto each panel respective to “Environmental Habitat” and represent an individual larva. The regression equations for each “Environmental Habitat” are based on the best fitting model (refer to supplementary materials), and the equations are as follows: tropical pelagic: $\mathrm{Log}(U) = 0.65\mathrm{Log}(\mathrm{Length}) + 0.7$ $r^2 = 0.02$; tropical reef: $\mathrm{Log}(U) = 1.2\mathrm{Log}(\mathrm{Length}) - 0.42$ $r^2 = 0.44$; temperate demersal: $\mathrm{Log}(U) = 0.66\mathrm{Log}(\mathrm{Length}) + 0.31$ $r^2 = 0.034$; tropical demersal: $\mathrm{Log}(U) = 0.75\mathrm{Log}(\mathrm{Length}) + 0.55$ $r^2 = 0.25$

(Figure 10). Tropical reef fishes largely exhibited more robust body shapes than other groups, and as a consequence, had higher swimming performance than the species from the other habitats (Figure 10). Temperate demersal fishes and tropical pelagic species ($p = 0.13$) as well as temperate reef fishes and tropical demersal fishes ($p = 0.42$) had similar swimming capabilities and similar body shapes (Figure 10), which were less robust than tropical reef species (for details on statistical output, refer to Supplementary Materials S2.2.5; Figure 10). Temperate pelagic species had the most elongated body shapes, and as a consequence, had the poorest swimming capabilities (Figure 10). Post-flexion larvae of tropical reef fishes have high muscle and caudal fin area across all body sizes when compared to fishes from the other “Environmental Habitats” ($p < 0.0001$ for all combinations; refer to Supplementary Materials S2.2.6 and S2.2.8 for details on statistical output; Figure 11). However, when comparing at a common body size (16–22 mm SL), there was no difference in these metrics between tropical reef and tropical pelagic fishes (refer to Supplementary Materials S2.2.7 and S2.2.9 for details on statistical analyses; Figure 11).

3.4 | AIM III

3.4.1 | Swimming performance over ontogeny versus Lizard Island current speeds

The three reef fish species (i.e. *Pomacentrus amboinensis*, *Amphiprion melanopus*, and *Sphaeramia nematoptera*) where U_{crit} was measured in laboratory-reared larvae across days post-hatch (dph) from hatch until settlement, attained influential swimming abilities ($Re > 1{,}000$) at very different ages. *P. amboinensis* became capable of influential swimming at 12 dph (~11 cm/s; ~7.5 mm TL; settlement at 20 dph; Figure 12). *A. melanopus* became capable of influential swimming at 6 dph (~12 cm/s; 8.05 mm TL; settlement at 9 dph; Figure 9). *S. nematoptera* became capable of influential swimming at 18 dph (~9.9 cm/s; 9.9 mm TL; settlement at 23 dph; Figure 12). On exposed reefs, none of these species at either the age when swimming becomes influential ($Re > 1{,}000$) or the age at settlement (last day of PLD) exhibited U_{crit} values that were faster than currents at 3 m

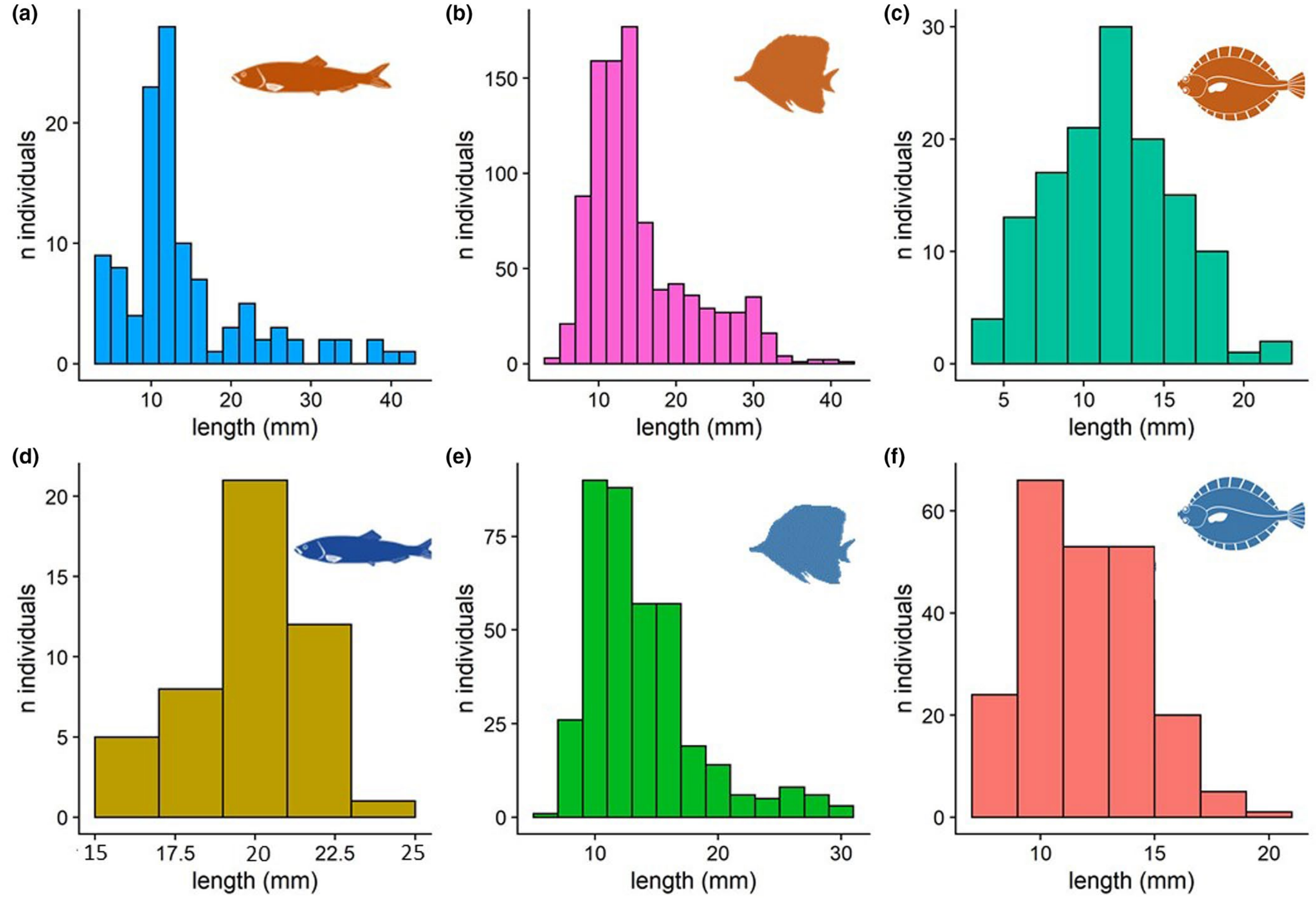

FIGURE 4 Size distributions (*n* individuals) for post-flexion stage larvae used in U_{crit} experiments from (a) tropical pelagic, (b) tropical reef, (c) tropical demersal, (d) temperate pelagic, (e) temperate reef, and (f) temperate demersal "Environmental Habitats." A herring symbol represents pelagic fish species, a butterflyfish symbol represents reef fish species, and a flatfish symbol represents demersal fish species. A blue-coloured symbol represents temperate species, and an orange-coloured symbol represents tropical species

depth (Figure 12). In contrast, on sheltered reefs, all three species possessed U_{crit} values that were sufficient for them to swim against shallow and deep currents at the settlement stage (Figure 12). Settlement-stage larvae from all three species would be capable of swimming against deep currents on exposed, oblique and sheltered reefs (Figure 12). In contrast, *A. melanopus* and *P. amboinensis* would be capable of swimming against shallow currents on oblique reefs upon settlement; whereas, *S. nematoptera* would not (Figure 12).

3.4.2 | Swimming performance of settlement-stage coral reef fishes versus Lizard Island current speeds

On average, across 10 families (30 species), settlement-stage tropical coral reef fishes swim (i.e. U_{crit}), on average, 420 ± 54% above the minimum speed required to overcome the viscosity of seawater. This range of overcompensation spanned from 124% (yellow-striped cardinalfish *Apogon cyanosoma*; Apogonidae) to 1,400% (gulf damselfish *Pristotis obtusirostris*; Pomacentridae). Upon excluding species from Families Apogonidae and Pomacanthidae, the average U_{crit} for all other species of fish examined would have been sufficient for the remaining fish species to swim against the fastest currents, which were the shallow currents on exposed reefs (Figure 13). *in situ* swimming speeds were sufficient for settlement-stage larvae of all coral reef species to surpass the deepest currents for exposed, oblique, and sheltered reefs and the shallowest currents on sheltered reefs, except in species from Family Apogonidae (Figure 13). In contrast, U_{crit} swimming speeds of pelagic and demersal fishes would only suffice on sheltered reefs at the shallowest depths (Figure 13). Additionally, for demersal and pelagic fishes, *in situ* speeds would only suffice at deeper depths in any of the reef habitats and only at shallow depths on sheltered reefs (Figure 13).

4 | DISCUSSION

Our study supports several decades of research showing that the larvae of reef-associated teleost fish species are impressive swimmers. While tropical reef species have received much of the research attention, we show that temperate reef fish larvae are swimming to similar capacities as tropical pelagic and demersal species, despite the 10°C difference in water temperature. The interactions

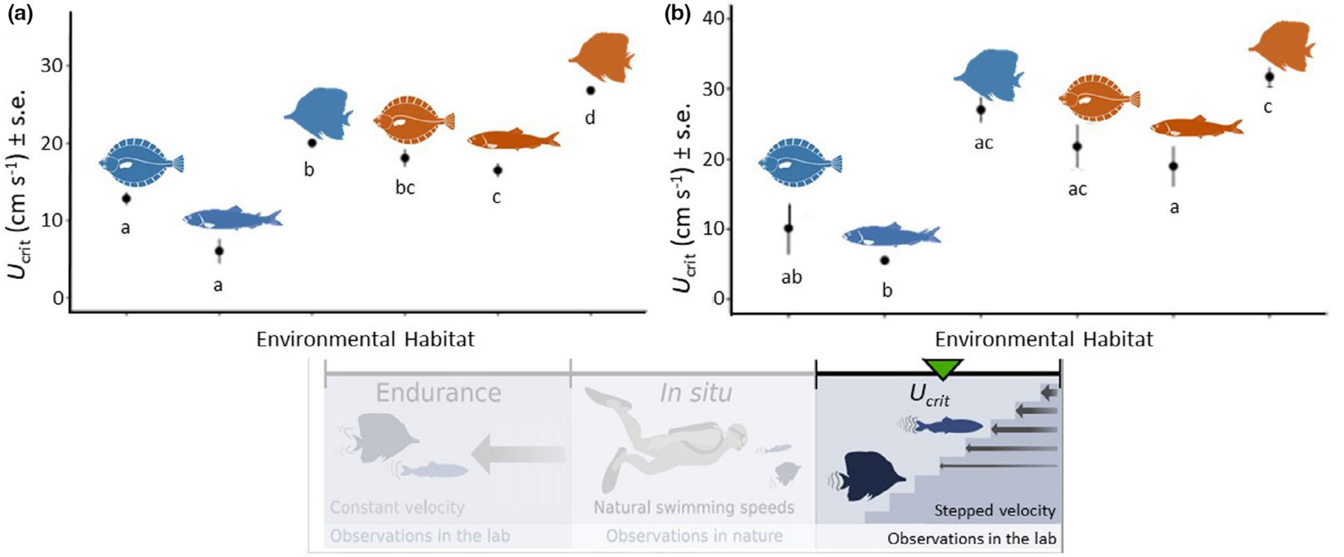

FIGURE 5 Average critical swimming speed (mean U_{crit}; cm/s; ± standard error, *s.e.*) of post-flexion-stage marine teleost larvae from six "Environmental Habitats," based on latitude (orange = tropical, blue = temperate) and habitat (herring symbol = pelagic, butterflyfish symbol = reef, flatfish symbol = demersal) (a) comparing swimming speeds of post-flexion larvae across all sizes and (b) comparing swimming speeds at a common size range (16–22 mm SL). Linear models included body length (standard length; mm) as a covariate, and different lower-case letters represent statistical differences between groups (α = 0.05)

among biotic and abiotic factors that contribute to annual fluctuations in larval fish recruitment and dispersal are complex. One of these factors is the spatial scale in which fish larvae move, which suggests that swimming can play an important role in fish dispersal. Indeed, swimming performance is a critical trait that is universal among marine fishes, contributes to dispersal and recruitment processes, and is impacted by many biotic and abiotic factors (Downie et al., 2020). Although it had been well established that latitude and body size influence larval fish species' swimming speed (e.g. Hunt von Herbing, 2002), our analyses of the present larval fish swimming literature also suggest that the habitat with which adults associate (i.e. reef, demersal, or pelagic) may have an important role in selecting for swimming traits of larvae over evolutionary history. Post-flexion-stage larvae of tropical and temperate reef fishes swim to a much higher capacity than non-reef counterparts, likely attributable to larger body sizes achieved by these groups at a similar stage of development and more robust body morphologies (particularly tropical reef species) that may accommodate higher muscle mass. This may suggest that the physiological and morphological requirements of finding and selecting a patchy habitat (e.g. coral or rocky reefs) with different hydrodynamic conditions (e.g. strong nearshore currents, especially near the surface) on which to settle and transition to older life history stages—as opposed to living strictly in the pelagic realm or selecting other benthic habitats—may have underpinned selection for larger body sizes/robust body morphologies to produce higher performance among larval reef fishes. However, it is important to note that latitude is conflated with phylogeny, as percomorph species dominate warmer waters, and species of other non-percomorpha orders (e.g. Clupeiformes, and Gadiformes) dominate cooler waters (Leis, Caselle, et al., 2013;). Therefore, it would be of interest to investigate more species from orders or families with wide latitudinal ranges. However, despite the obvious differences in temperatures between latitudes, it is important to note that our analyses found that: (a) at the same latitude (e.g. experiments were conducted at 26–30°C) tropical reef fish larvae swim to a higher capacity than tropical pelagic and demersal fish larvae, and (b) temperate reef fish larvae were able to swim to similar speeds as tropical demersal and tropical pelagic species, despite the 10°C difference in experimental water temperatures.

4.1 | AIM I

Absolute swimming speed (cm/s) generally increases with body length (relative swimming speed, body lengths/s, levels off with increasing size in adults; Kolok, 1999) and is correlated with temperature (Moyano et al., 2016), growth rate (Billerbeck et al., 2001), and diet composition/ration size (Arnott et al., 2006). We found similar trends when comparing swimming speed (U_{crit} and *in situ*) with body length across "Environmental Habitats." Larvae of tropical species generally had greater increases in U_{crit} with increasing body length than temperate pelagic and temperate demersal species. Interestingly, we found that temperate reef fish larvae had the fastest increase in U_{crit} with increasing size, thus highlighting the complexities of modelling swimming performance in relation to ontogeny across latitude for marine teleost larvae, as many biotic and abiotic factors contribute and occasionally affect each other (Leis, Caselle, et al., 2013;). Several studies focussing on fishes (e.g. Atlantic cod Sylvestre et al. 2007; Atlantic silverside *Menidia menidia*, Atherinopsidae

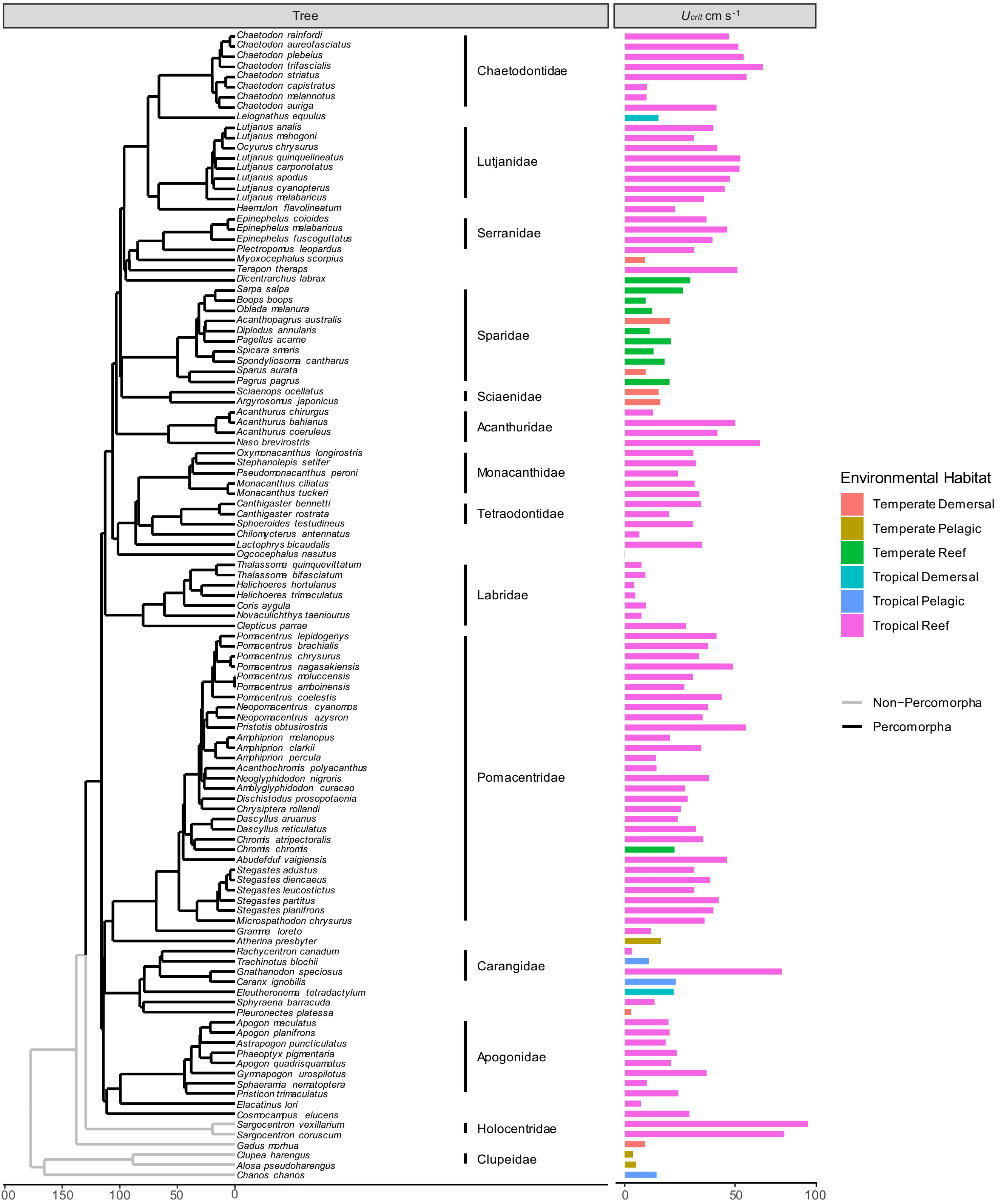

FIGURE 6 Time calibrated phylogeny of fishes (modified from Rabosky et al. 2018) and the distribution of average critical swimming speed (U_{crit}) of post-flexion-stage teleost larvae from six "Environmental Habitats" (tropical reef, tropical demersal, tropical pelagic, temperate reef, temperate demersal, and temperate pelagic). Percomorph lineages are indicated by black coloured branches, and non-percomorph lineages are indicated by grey-coloured branches. For species list (scientific names, common names and families), refer to Supplementary Materials S1

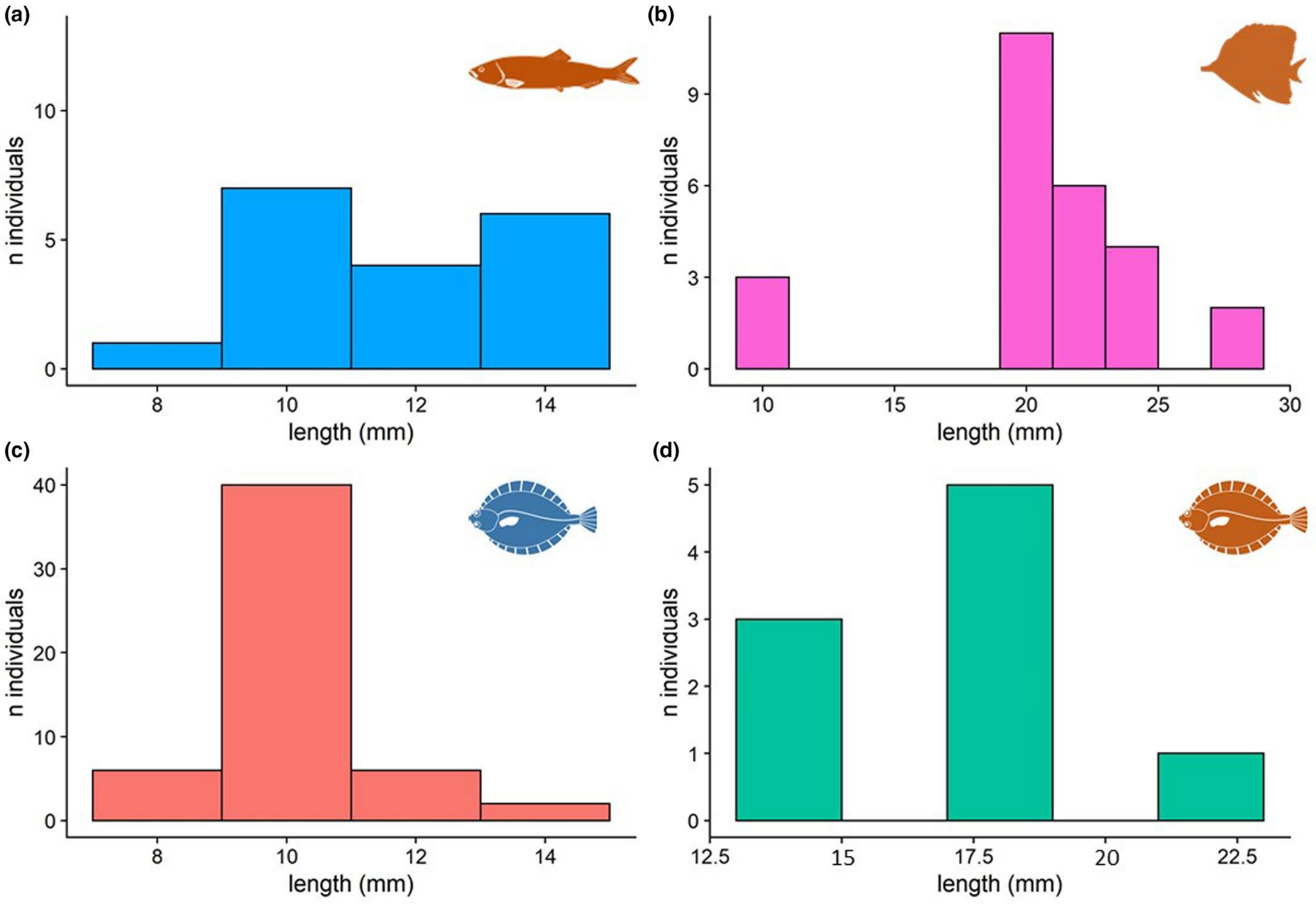

FIGURE 7 Size distributions for post-flexion-stage larvae used in *in situ* swimming observations from (a) tropical pelagic, (b) tropical reef, (c) temperate demersal, and (d) tropical demersal "Environmental Habitats." A butterflyfish symbol represents reef fish species, the herring symbol represents pelagic fish species, and a flatfish symbol represents demersal fish species. A blue-coloured symbol represents temperate species, and an orange-coloured symbol represents tropical species

Billerbeck et al., 2000; Billerbeck et al., 2001) support countergradient variation, whereby some species inhabiting colder habitats have faster growth rates than species inhabiting warmer habitats (reviewed by Kingsolver & Huey, 2008). These studies found that the caveat to faster growth in high latitude species included significant changes in other physiological properties, notably decreased swimming performance and increased standard metabolic rate and specific dynamic action (Billerbeck et al., 2000, 2001; Gregory & Wood, 1998; Kolok & Oris, 1995). This caveat may not hold true for temperate reef fish larvae during early larval stages in terms of swimming performance (see AIM II), but trade-offs with other physiological traits may exist.

During the larval phase for marine fishes, swimming capabilities generally increase with length and girth (i.e. muscle mass) such that a specific level of performance can be accomplished to improve the chances of encountering prey items and achieve ontogenetic milestones that contribute to overall survival in their respective habitats. Additionally, the ability to swim faster and for longer periods may have a ripple effect on their dispersal potential, which is influenced further by environmental temperatures, resource abundance (Llopiz, 2013) and interspecific differences in muscle composition (e.g. proportion of red muscle and muscle mitochondria volume density; Johnston et al., 1998), active and standard metabolic rates (Peck & Moyano, 2016), food consumption rates, and morphology (e.g. body depth, fineness ratio and fin aspect ratio; Fisher & Hogan, 2007). How larval fishes metabolize energy over development and the extent to which energy is diverted to growth (i.e. organogenesis and hyperplasia and hypertrophy of muscle fibres), maintenance, and swimming performance at key developmental milestones (e.g. notochord flexion) are generally unknown across a wide range of species, but would be highly species-specific and likely driven by several biotic and abiotic factors (Wieser, 1995; Wieser & Kaufmann, 1998). However, even *in situ*, larvae of tropical reef fishes exhibit faster swimming speeds as they get larger when compared to tropical pelagic and temperate fishes. The exact physiological mechanisms and environmental pressures underpinning developmental rates and dispersal potential among temperate reef fishes are also generally unknown but clearly warrant further investigation to better understand how higher latitude species increase swimming performance with growth faster than lower latitude species.

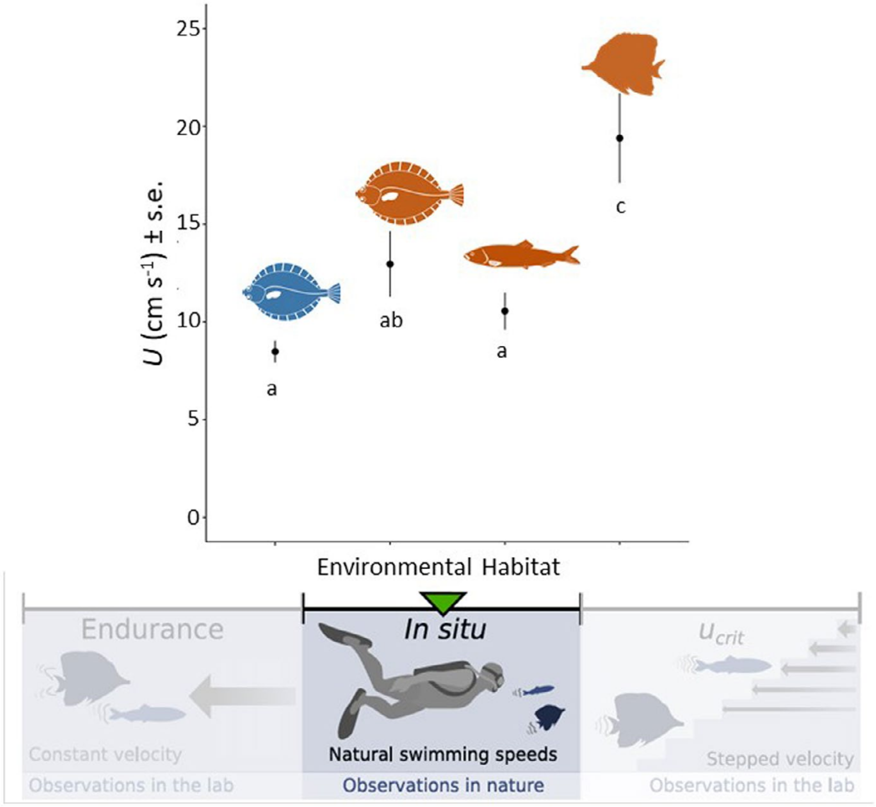

FIGURE 8 Average *in situ* swimming speed (mean U; cm/s ± standard error, s.e.) of post-flexion-stage marine teleost larvae from four "Environmental Habitats," based on latitude (orange = tropical, blue = temperate) and habitat (herring symbol = pelagic, butterflyfish symbol = reef, flatfish symbol = demersal). Linear models included body length (standard length; mm) as a covariate, and different lower-case letters represent statistical differences between groups ($\alpha = 0.05$)

4.2 | AIM II

Nearly all teleost fishes are ectotherms, and therefore, metabolic rate increases with increasing water temperature, which has strong, positive correlations with increased muscle function and swimming speed (Hunt von Herbing, 2002). Therefore, it is important to mention early in the discussion of our results that water temperature is generally confounded with "Environmental Habitat," which is an important factor to consider when comparing traits amongst these habitats. Temperate species were generally swum at temperatures below 15°C, and tropical species were swum between 26 and 30°C. Moreover, the differences between these groups with respect to swimming performance are apparent (e.g. Orders Gadiformes, Clupeiformes, and Pleuronectiformes from cold waters compared to tropical species). Comparing among tropical species clearly shows that reef fishes swim to a higher capacity than pelagic and demersal species, despite the common temperature. Interestingly, some of the temperate species (i.e. temperate reef fishes) swum between 15 and 20°C exhibited swimming performance that was comparable to tropical species, despite the 10°C difference in water temperature. These species were from warm-temperate regions, such as the Mediterranean Sea (e.g. Faillettaz et al., 2018) and south eastern coast of Australia (e.g. Clark et al., 2005), regions that naturally experience wide fluctuations in annual temperatures. For example, surface temperatures in the Mediterranean Sea have high seasonal fluctuations (9.0–17.7°C in winter and 20.8–28.3°C in summer; Shaltout & Omstedt, 2014). In contrast, tropical and cold temperate regions do not experience such dramatic shifts in annual sea surface temperatures (see references discussed in Methods section in Illing et al., 2020). Additionally, Downie et al. (2020) found no overall change in swimming performance in response to thermal stress of species from warm–temperate regions. Tolerance to a wide thermal regime may attribute to the high swimming capacity of the larvae of temperate reef fishes, especially if the upper thermal limits of their habitat are similar to temperatures experienced by tropical species. It may be of interest to swim temperate fishes that naturally experience wide seasonal variations in temperature across this thermal range. Regardless, across several metrics of performance, reef-associated species generally exhibit a stronger swimming performance than fishes from other groups.

In absolute terms (e.g. U_{crit} in cm/s), tropical reef fishes are capable of attaining higher U_{crit} and *in situ* speeds than temperate and tropical non-reef fishes (Clark et al., 2005; Fisher et al., 2005; Leis, 2010; Leis et al., 2006). While casually referred to as "athletes," this high-calibre performance in tropical reef fishes was widely considered to be driven by latitude (Downie et al., 2020; Leis, 2007; Leis & McCormick, 2002). These results are complimented by the fast speeds that settlement-stage tropical reef fishes exhibit *in situ*, especially when compared to temperate and tropical pelagic larvae, along with a suite of complex behaviours and sensory abilities exhibited by tropical reef fish larvae (e.g. swimming depth and orientation) that are associated with their ability to find and settle onto a reef habitat (Leis & Carson-Ewart, 1999; Leis et al., 1996; Leis, Hay, et al., 2009; Leis, Piola, et al., 2009). Several studies have found

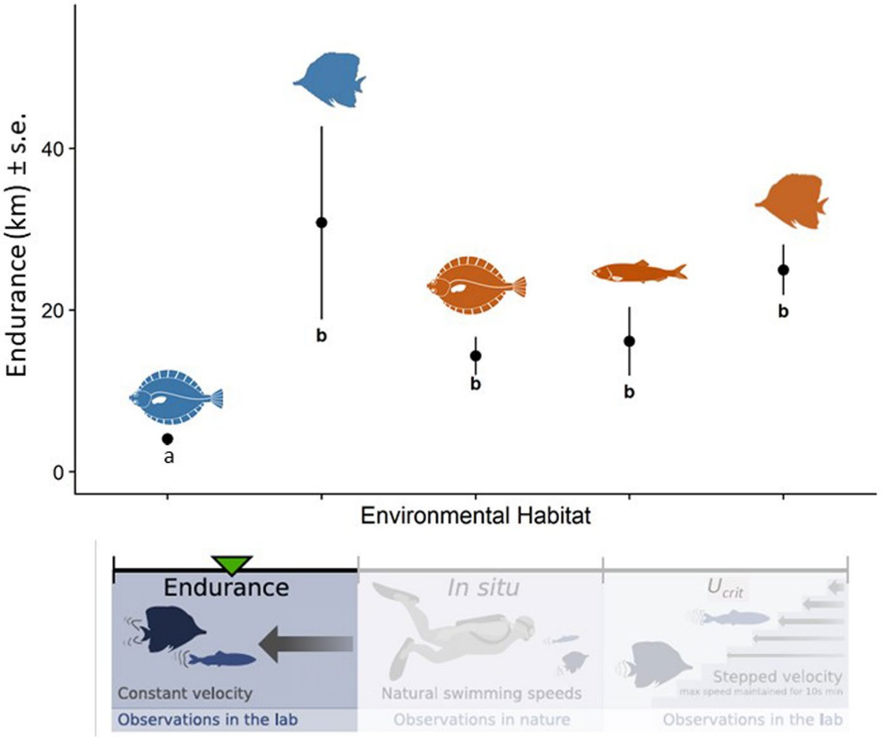

FIGURE 9 Average endurance distance (mean km ± standard error, s.e.) of post-flexion-stage marine teleost larvae from six "Environmental Habitats," based on latitude (orange = tropical, blue = temperate) and habitat (herring symbol = pelagic, butterflyfish symbol = reef, flatfish symbol = demersal). All larvae were swum at fixed speeds of 10–13 cm/s. Data were analysed using linear models, and different lower-case letters represent statistical differences between groups (α = 0.05)

interspecific differences in red muscle composition, oxygen uptake rates, and muscle mitochondria volume density between fishes at different latitudes and lifestyles, with fishes from low latitudes having higher respiration rates and aerobic properties in their muscle tissues than fishes living in colder habitats (Johnston et al., 1998; Killen et al., 2010). This may be further complimented by body size, in which propulsive area of swimming muscles and muscle mass increases with size (Fisher & Hogan, 2007). However, it is interesting that post-flexion temperate reef fishes are capable of swimming to a similar capacity as tropical pelagic and demersal species (Faillettaz et al., 2018; Leis et al., 2012), possibly attributed to the high growth rates during early larval ontogeny (see Aim I), as well as their wide thermal tolerance ranges. This is accentuated when body size is taken into account, and this relationship holds true in the endurance swimming data as well.

Larvae of tropical reef fishes were previously noted for having high dispersal potential based on long distances (>100 km) swum during endurance experiments (Fisher & Bellwood, 2001; Stobutzki & Bellwood, 1997). However, fishes from the Fisher and Bellwood, (2001) study were fed throughout endurance tests; whereas, food is generally withheld for at least 24 hr prior to most endurance tests (Downie et al., 2020). Our analyses excluded fishes that were fed during endurance tests, and as such, we found that temperate reef fishes were capable of similar endurance swimming distances as tropical fishes (e.g. Baptista et al., 2019; Clark et al., 2005; Dudley et al., 2000). Post-flexion-stage fishes, regardless of latitude, likely need strong endurance capacity to find patchily distributed resources in the open ocean, especially at low latitudes where these resources are more limited (Llopiz, 2013). Comparing energy reserves and metabolic rates between tropical and temperate groups within the context of endurance swimming may reveal more about this interesting contrast between endurance capacity. This endurance capacity is especially important when combined with findings from Nilsson et al., (2007); they found that tropical reef fish larvae have the highest oxygen uptake rates of any other teleost fish species during activity, suggesting that reef fish larvae are energy-efficient swimmers. Indeed, while reef fishes are among the fastest swimmers and capable of long-distance swimming, it is important to note the influence that body size has on such performance metrics.

There has been a focus on the relationship between body size and swimming performance when making interspecific and intraspecific comparisons among fishes across ontogeny (Kolok, 1999; Fisher et al., 2005; Fisher & Hogan, 2007; Fisher & Leis, 2010). Among settlement-stage larvae of 100 coral reef species from Australia and the Caribbean, ~70% of the variation in swimming speed (U_{crit}) was accounted for by body length and other morphological metrics, such as caudal peduncle depth and fin aspect ratio (Fisher & Hogan, 2007). Similarly, our models suggest that body length has a large influence on swimming performance, as temperate reef fishes and tropical pelagic, reef and demersal fishes of the same size range (16–22 mm SL) do not differ significantly in swimming performance, and the larger sizes of larval reef fishes in general—both temperate and tropical—may be driving this performance metric, particularly among tropical species (see Figures 1 and 2 in Leis, 2010). Given the phylogenetic overlap, in the form of a large bias towards percomorph species between tropical and temperate reef fish larvae, it is possible that these groups of fishes have inherited similar properties in their muscle tissue and

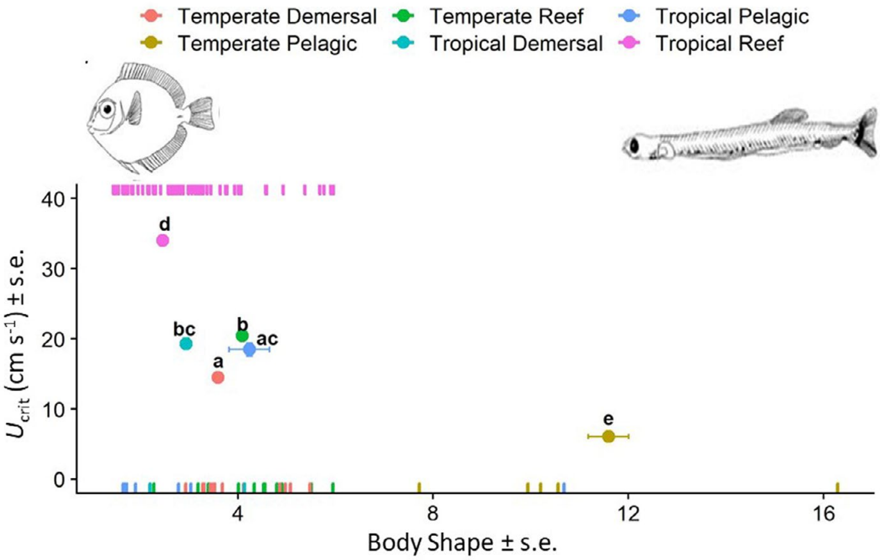

FIGURE 10 Average critical swimming speed (mean U_{crit}; cm/s ± standard error; *s.e.*) of post-flexion-stage marine teleost fishes from six "Environmental Habitats" (temperate demersal, temperate reef, temperate pelagic, tropical demersal, tropical reef, and tropical pelagic) versus body shape (ratio of body length to body width). Raw data (*x*-axis for tropical pelagic, tropical demersal, temperate reef, temperate demersal, and temperate pelagic habitats; tropical reef data placed above figure to mitigate cluttering of data points) show the spread of the body shapes per "Environmental Habitat." A representative example of the most robust body shape (surgeonfish Acanthuridae, left side of figure; body shape ratio [body length:body depth] = 1) and the most streamlined body shape (herring Clupeidae, right side of figure; body shape ratio [body length:body depth] = 16) are present on the figure to help visualize the shapes (refer to Figure 1 for full range of body shapes). Linear models were used to analyse data, and different lower-case letters represent statistical differences between groups ($\alpha = 0.05$)

metabolic rates at a similar size. However, we know very little about properties of muscles (e.g. mitochondrial volume densities) from tropical reef fishes, and we suggest that this is an area of particular interest for future studies. Furthermore, as evidenced by our analyses on changes in swimming speed with body length, interspecific growth rates may also contribute to the expression of swimming genotypes among groups of fishes (Billerbeck et al., 2000, 2001; Kolok & Oris, 1995). However, we found *in situ* swimming speed was still highest among larval tropical reef fishes, when compared to larvae of tropical pelagic, and demersal fishes, even when accounting for body size. While few studies have investigated the relationship between *in situ* swimming and laboratory estimates (e.g. U_{crit}), there appears to be no fixed relationship, and the relationship appears highly variable among species (Leis, 2020). Taken together, larvae of reef fishes from both high (i.e. temperate) and low (i.e. tropical) latitudes are capable of fast swimming speeds at settlement when compared to their non-reef counterparts. This may be attributed to the robust body morphologies found in the majority of reef fishes and the increased muscle mass exhibited by such morphologies—at least in the species studied thus far—that may be specialized for swimming.

Fishes exhibit a wide diversity of body shapes, from dorsoventrally flattened (e.g. Order Pleuronectiformes) to streamlined (e.g. Order Scombriformes) (Walker et al., 2013). Body morphology and swimming performance are positively correlated, as more streamlined body morphologies reduce drag and enhance swimming performance (Fisher & Hogan, 2007). Additionally, the morphology of the caudal fin (e.g. depth and area) provides thrust for forward momentum (Webb, 1984), and unusually designed pectoral fins (e.g. members of the Family Labridae) enable adult tropical reef fishes to swim against strong reef currents (Fulton & Bellwood, 2004; Fulton et al., 2013). Near the end of their larval phase, the larvae of many fishes have already attained their adult morphologies in shape, despite their small sizes, and are generally swimming in inertial hydrodynamic regimes (e.g. $Re > 1{,}000$), making it therefore reasonable to use body shape as an important factor influencing swimming during early life stages (e.g. Fisher & Hogan, 2007). We found that body shape has an important influence on swimming performance among larval fishes across "Environmental Habitats." The best performers were generally round or streamlined in shape (body length:body depth ratio ranging 1 to 3), which were the morphologies most frequently exhibited by reef fishes. In contrast, temperate pelagic fishes were generally more "ribbon shaped" or slender in shape (e.g. Order Clupeiformes) and had weaker swimming performance. It is interesting that the rounded shaped/robust fishes had high swimming performance, as such body shapes would expect to create more drag. Swimming performance was found to be greatest among adult tropical reef fishes with high (e.g. more streamlined) finess ratios (relationship between body depth, length, and width) versus low finess ratios (circular shaped) (Walker et al., 2013). This suggests that the physiological requirements to swim towards a

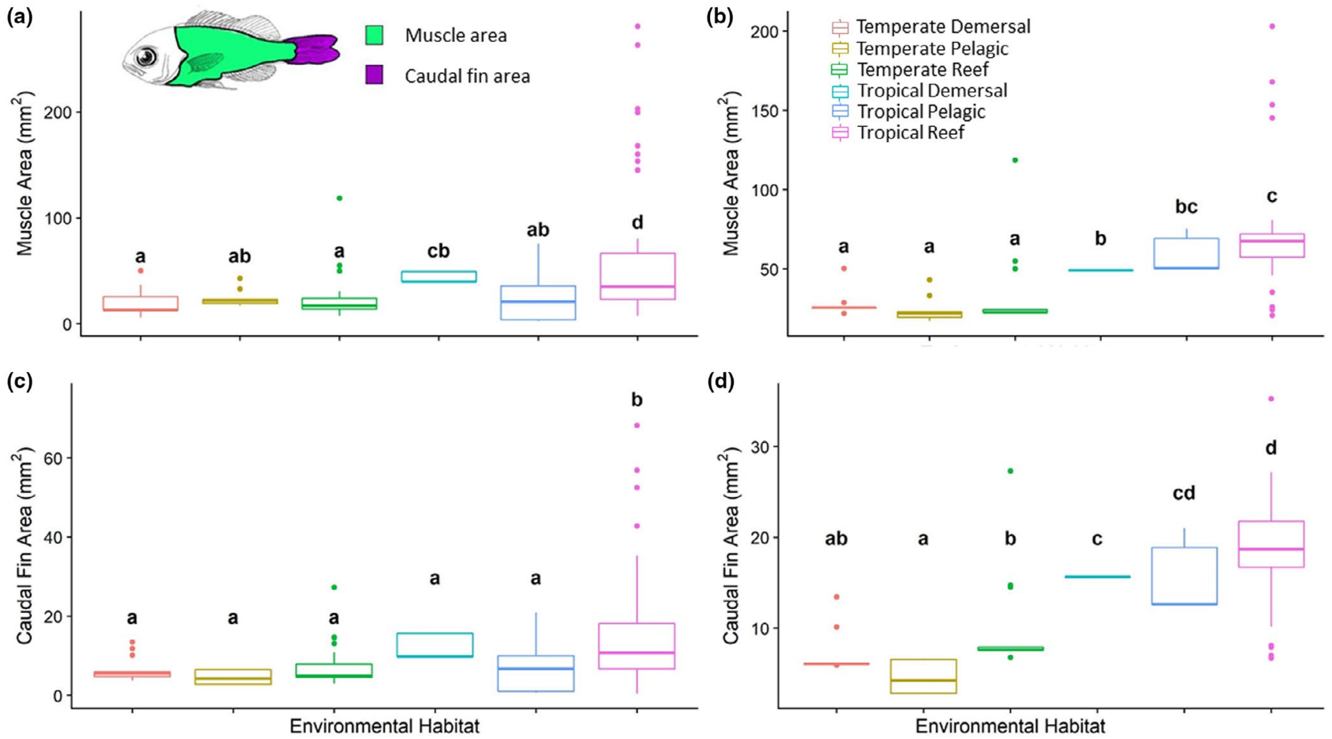

FIGURE 11 Comparison of morphological predictors of swimming performance among six "Environmental Habitats" (tropical reef, tropical pelagic, tropical demersal, temperate reef fish, temperate pelagic, temperate demersal). Muscle area (mm^2) and caudal fin area (mm^2) for each group across all size ranges (a) muscle area and (c) for caudal fin area and among a common size range (16–22 mm) for (b) muscle area and (d) caudal fin area. Linear models were used to analyse data (common body size as a covariate where appropriate), and different lower-case letters represent statistical differences between groups ($\alpha = 0.05$)

reef during early life may be different than the requirements and demands to stay on a reef as an adult (Fulton & Bellwood, 2004; Fulton et al., 2005; Walker et al., 2013). However, we found that the higher swimming performance of fishes with more robust body shapes may be because these morphologies had greater muscle areas than the thinner body morphologies. Therefore, growing larger to increase muscle mass may be a strategy for body morphologies that are more-susceptible to drag to swim faster against ocean currents. This also implies that physiological metrics that are involved in muscle function during exercise, such as oxygen uptake rates, mitochondria volume densities of red muscle and enzyme activities that are involved in cellular respiration, may be important predictors of swimming performance among settlement-stage larvae. Unfortunately, these metrics and the muscle development of reef fishes are unknown, and there is a general lack of knowledge with respect to aerobic properties of swimming muscles from tropical species, when compared to temperate, commercially important species (e.g. Orders Clupeiformes, Gadiformes, Pleuronectiformes, etc.), and this would be an area of particular interest for future studies. Growing larger to accommodate larger blocks of muscle, especially for robust species vulnerable to drag, allows larvae to swim faster, which may be valuable and selected for to enhance recruitment for reef fishes and subsequent performance during post-settlement processes.

4.3 | AIM III

In the field of exercise physiology, the aim is to better understand how and why animals move to the extents that they do (Bennett, 1991; Irschick, 2002; Irschick & Higham, 2016). Putting performance into an environmental context requires both natural and laboratory measures of a trait (Irschick, 2003). Fortunately, for tropical fishes, laboratory estimates of maximum, prolonged swimming speeds (U_{crit}) and *in situ* observations are available, and our case study approach incorporates both estimates. The large sizes of some (i.e. the species in our analyses) tropical coral reef fishes before they leave the pelagic environment likely contribute to the high U_{crit} and *in situ* speeds. However, upon hatching, larval marine fishes are tiny, and their swimming speeds are not sufficient for them to remain on reefs (Leis, 2006; Leis & McCormick, 2002). The few species in which a pelagic stage is lacking are mouth brooders (e.g. Apogonidae) or provide parental care, with parents keeping well-developed hatchlings sheltered in enclaves, caves, and among coral (e.g. spiny chromis; *Acanthochromis polyacanthus*, Pomacentridae). While some studies have attempted to explain/quantify the persistence of a pelagic larval duration among reef fishes (e.g. competition with adults for resources, predators, etc.; Bonhomme & Planes, 2000), the inability to remain on reefs due to underdeveloped swimming performance structures (e.g. fins and muscles) may provide a more straightforward answer. Most reef fishes have pelagic larval durations that span

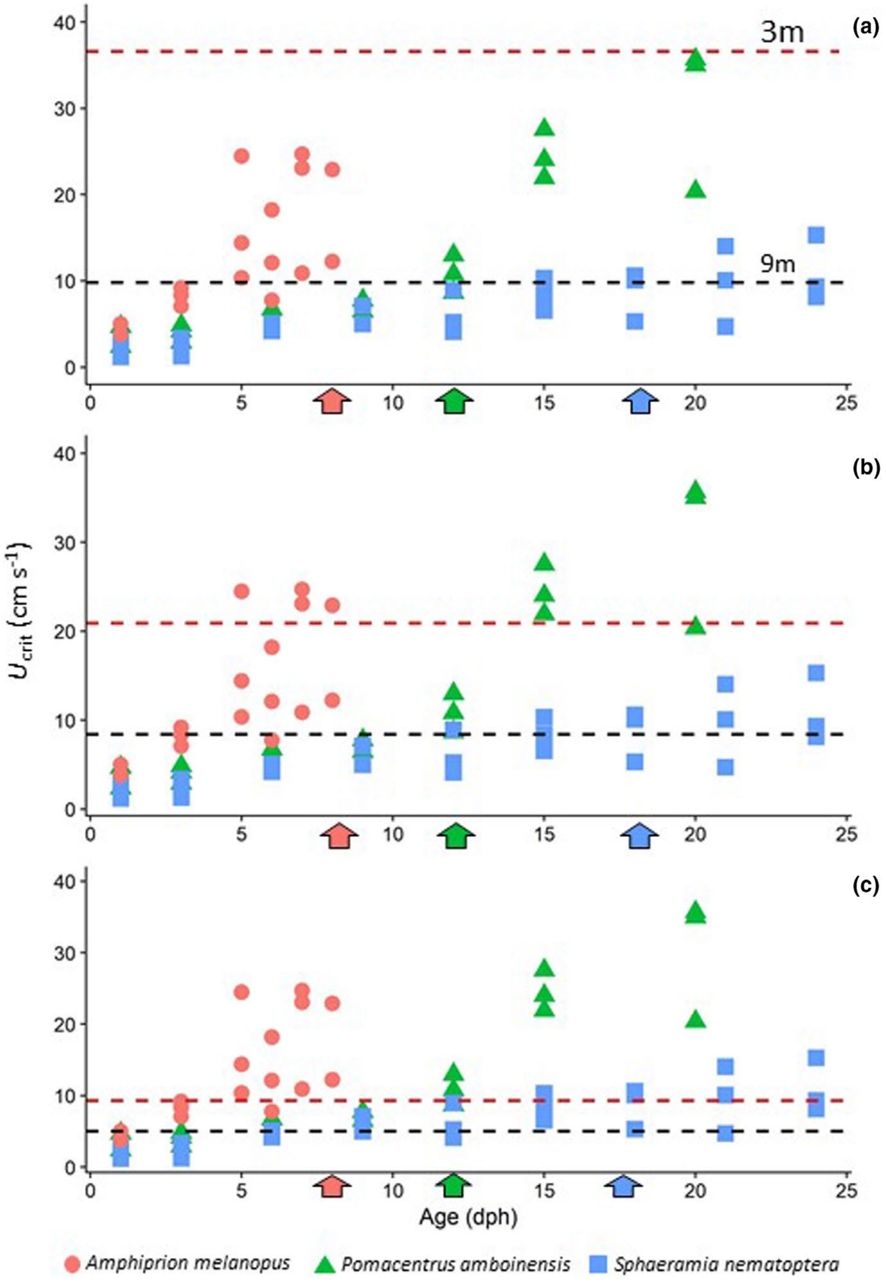

FIGURE 12 Critical swimming speed (U_{crit}; cm/s) over larval ontogeny (age; days post-hatch; dph) of laboratory-reared larvae of three coral reef fish species that hatch from demersal or brooded eggs (cinnamon anemonefish, *Amphiprion melanopus*, Pomacentridae ●, Ambon damselfish, *Pomacentrus amboinensis*, Pomacentridae ▲, and pyjama cardinalfish, *Sphaeramia nematoptera*, Apogonidae ■) (data adapted from Fisher et al., 2000) at different coral reef habitats on Lizard Island, Australia. (a) Exposed reef, (b) oblique reef, and (c) sheltered reef (adapted from Johansen, 2014). Habitats are based on their level of exposure to south-easterly trade winds. Current data were measured using a custom-built flow meter, which was positioned at three replicate sites per reef habitat at depths of 3 m (horizontal red dotted line indicates average speed at depth) and 9 m (horizontal black dotted line indicates average speed at depth) (Johansen, 2014). Upward arrows on the *x*-axis match colours of their respective species and represents the age when larvae are capable of swimming in an inertial hydrodynamic regime (Re > 1,000). The last data point from each species represents the age at settlement

several weeks to months (Leis, 2006). Once these larvae are capable of swimming (i.e. inertial *Re*), they have possibly been moving away from the reef for several days/weeks (Leis, 2006). Indeed, the need to influence control of their movement in the pelagic environment may allow them to seek out a specific habitat—either natal (e.g. Jones et al., 1999, 2005) or new (e.g. Harrison et al., 2012)—which may be an important driver influencing the fast swimming performance among reef-associated species.

High swimming performance among reef fish larvae may provide a good example of how an animal is truly a product of its environment. Several studies have shown intraspecific differences in swimming performance between isolated populations of fishes exposed to different riverine or oceanic flows, with individuals from higher flow habitats exhibiting better swimming performance (Nelson et al., 2003; Taylor & Foote, 1991; Taylor & McPhail, 1986). Therefore, over evolutionary history, the pressure to find a specific, patchily distributed reef habitat and surpass distinct oceanic and reef currents may have selected for the high performance of larval reef fishes, regardless of latitude. This may be why tropical and temperate larval reef fishes grow to larger sizes than larvae of pelagic and demersal fishes at similar latitudes. The U_{crit} and *in situ* swimming speeds of most tropical larval reef fishes are faster than the high reef currents at different depths and locations on Lizard Island in the northern Great Barrier Reef, which indicates, therefore, performing at a bare minimum (e.g. *Re* = 1,000) would not suffice against these currents. Across 57 species of tropical fish larvae surveyed via plankton tows at different locations around Lizard Island, 50% of post-notochord flexion larvae were found at depths of 6 m during the day, and 40% were found near the surface (<6 m) at night (Leis, 1986). Surface

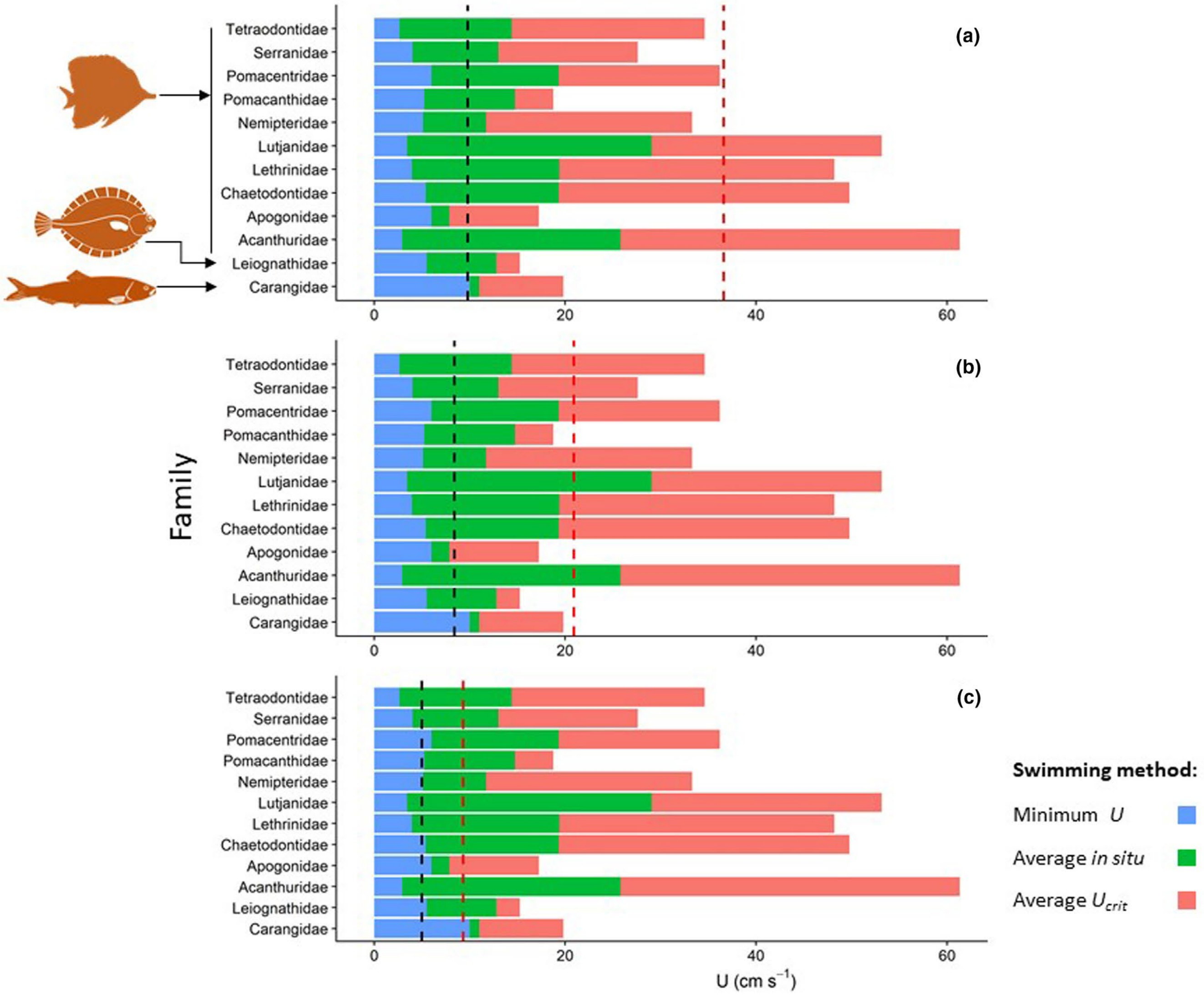

FIGURE 13 Comparison of different swimming performance (U; cm/s) metrics of settlement-stage larvae across 12 different families of tropical, reef and non-reef-associated fishes. Average oceanic current velocity (cm/s) data from three different coral reef habitats: (a) exposed, (b) oblique and (c) sheltered reefs on Lizard Island (Australia). Habitats are based on their level of exposure to south-easterly trade winds. Current data were measured by a custom-built flow meter, which was positioned at three replicate sites per reef habitat at depths of 3 m (vertical red line indicates average speed at depth) and 9 m (vertical black line indicates average speed at depth) (Johansen, 2014). "Minimum U" (🟦) represents the predicted minimum swimming speed required to overcome the viscosity of water (U, where $Re = 1{,}000$), "average *in situ*" represents the average swimming speed under natural conditions (🟩), and "average U_{crit}" is the mean swimming speed for larvae swimming at prolonged speeds (🟥). Reef fish families are indexed by a butterflyfish image. The pelagic fish family is indexed by a herring symbol. The demersal fish family is indexed by a flatfish symbol. Symbols are indexed on "Exposed" reef panels but are consistent with "Oblique" and "Sheltered" reefs. Swimming data were adapted from Leis & Fisher, (2006)

currents in these areas ranged from 3.5 to 37.5 cm/s, and currents at the deeper depths (7.5 m) ranged from 0.9–25.5 cm/s, depending on location (Leis, 1986). Some of these current speeds would not be surpassed by *in situ* swimming alone, but U_{crit} speeds would be greater than the current speeds. These currents are relatively high, and reef fish larvae captured by Leis (1986) and during other studies (e.g. Leis & Goldman, 1984, 1987) typically occur within the depths indicated by our case study. These reef currents, particularly on the exposed reefs, are too strong for non-reef tropical larvae. While simplistic in nature, comparing natural and laboratory measurements of swimming speeds with oceanographic data may further our understanding as to the degree by which ambient currents have influenced swimming performance in reef fishes (see Fisher, 2005 as an example).

Given the simplistic approach to this case study, however, we need to be cautious in our interpretation. Understanding the temporal (e.g. diurnal and seasonal patterns) variations in vertical distribution patterns of ichthyoplankton is complex and has been an area of particular interest since the 1980s for tropical species (possibly even longer in temperate waters), with the general consensus suggesting that distributions vary considerably with season, time of day, geographic location, taxa, thermocline, hydrology, and prey distribution patterns (Höffle et al., 2013; Leis, 1991; Olivar & Sabatés, 1997; Rodríguez et al., 2006). For example, in the North Sea, vertical distributions of larvae are taxon-specific, with members of Order Gadiformes selecting depths below 40 m during the day and members of Order Pleuronectiformes selecting depths ranging 20–90 m regardless of time of day (Höffle et al., 2013). In contrast, in the Mediterranean, some species were found consistently near the surface (e.g. bogue *Boops boops*, Sparidae; and white seabream *Diplodus sargus*, Sparidae), despite seasonal changes in hydrology (Olivar & Sabatés, 1997), and species found off the coast of Africa were consistently found at intermediate depths (Rodríguez et al., 2006). The vertical distributions of tropical reef fishes are variable, both temporally and spatially; yet, many species are consistently found near the surface at night (e.g. Leis, 1986) and some during the day (Leis, 1991). The role of the case study was to provide some environmental context as to why tropical reef fishes swim to such a high capacity. Ongoing research is examining the role of fish behaviour in relation to the hydrodynamic environment that tropical reef fishes experience as they approach a reef and how it contributes to dispersal, but evidence suggesting that tropical reef fishes display a high level of self-recruitment implies that swimming against currents likely plays a critical role (Christie et al., 2010; Jones et al., 1999; Saenz-Agudelo et al., 2011). The level of self-recruitment is generally unknown for temperate reef fishes, but is an area of particular interest for future studies. In contrast, temperate pelagic and demersal fishes like members from Orders Clupeiformes, Gadiformes and Pleuronectiformes rely more heavily on hydrodynamic processes (e.g. current stratification, wind) to bring larvae to nursery grounds, which may be some distance from spawning grounds and do not actively move horizontally against currents (i.e. they act more like plankton, making vertical movements) until much later in their development (Dickey-Collas et al., 2009; Lacroix et al., 2018; van der Molen et al., 2007; Tanner et al., 2017). While we only used one location on the Great Barrier Reef for our case study, the hydrodynamic and biological processes that occur on Lizard Island are representative of recruitment conditions encountered by settling reef fishes regardless of location. However, the spatial scale over which dispersal, recruitment and connectivity act is a critically important factor. Many studies investigating the self-recruitment and dispersal of tropical reef fish subpopulations occur among island reefs (e.g. Keppel Islands, Harrison et al., 2012; Lizard Island, Jones et al., 1999; Kimbe Island, Almany et al., 2007); however, some studies use larger spatial scales for better management practices for MPAs. For example, across a 10 000 km^2 sampling range, clownfish (orange clownfish *Amphiprion percula*, Pomacentridae) larvae consistently dispersed 10–15 km among local reserves over a two-year period (20% self-recruitment rate), and butterflyfish (vagabond butterflyfish *Chaetodon vagabundus*, Chaetodontidae) dispersed up to 64 km to local reserves (Almany et al., 2017). This shows that tropical reef fishes are targeting specific habitats within a specific spatial scale, and this may be consistent, temporally. The integration of species-specific larval behaviour into hydrodynamic models over appropriate spatial scales (e.g. within the maximum dispersal distances of larvae) will benefit the design of MPAs, and this is an area of ongoing investigation for both tropical and temperate regions. Future work on energetics, including oxygen uptake rates and muscle tissue development, that support swimming behaviour will assist in better understanding how active behaviours contribute to the dispersal processes of marine fishes.

4.4 | Conclusions

Swimming performance in marine teleost fish larvae is impacted by numerous biotic and abiotic factors, including latitude, habitat association, morphology, and body size, to name a few. The interactions among these factors are complex, and more information regarding species-specific metabolic rates, composition of swimming muscles, feeding rates, and energy utilization is needed in order to further differentiate swimming abilities. However, based on the available data, reef-associated percomorph fishes from high and low latitudes show impressive swimming capabilities when compared to pelagic and demersal counterparts, and we hypothesize this is due to the need to grow larger to swim against oceanic and reef currents in order to select for new or natal reef habitats on which to settle (e.g. Jones et al., 1999, 2005). The high performance of temperate reef fishes when compared to high and low latitude non-reef fishes warrants further investigation into the anatomical and physiological mechanisms underpinning such performance. Although it is surprising that temperate reef fishes have the greatest increase in U_{crit} with body length, this highlights that i) the way in which performance scales with ontogeny varies across taxa and latitude, and ii) the way in which fishes metabolize and utilize energy may be different among taxonomic and ecological groups. It is important to note, however, that there is a profound sampling bias in the larval fish swimming literature towards percomorph fishes (Leis, Caselle, et al., 2013; Leis, Hay, et al., 2013). While percomorph fishes represent the higher performing taxa, particularly on tropical reef habitats, this finding may be confounded by the bias that percomorph fishes constitute a greater proportion of low latitude coastal fish communities than high latitude communities. In other words, apparent influences of latitude are likely due to the species involved. Therefore, it would be invaluable for future research to investigate swimming performance of tropical species from taxonomic groups primarily found in high latitude areas (e.g. tropical members from Orders Pleuronectiformes and Clupeiformes) and vice versa. More information on the swimming performance of late-stage larvae from high latitudes would help minimize this bias in the data. Additionally, tropical and temperate reefs are heavily populated by cryptobenthic species (e.g. members from the Families Gobiidae and Blenniidae; Majoris et al. 2019) whose larvae are not well represented in the larval fish swimming literature, and such larvae may not readily swim in flume chambers. The absence of data on the swimming performance of these fishes during their pelagic stages may have influenced our findings, and therefore, it is important to emphasize that our findings are based on the available larval fish swimming literature. The species for which data on larval swimming are available are neither a representative nor a random sample of the fish communities from various latitudes or habitats. Therefore, we do note that caution should be taken when making gross generalizations from our results. Regardless, as more information becomes available on a wider range of species, our hypothesis that reef association influences swimming performance among fish larvae should still be considered. Ultimately, by placing swimming performance of marine teleost fish larvae within a phylogenetic framework and accounting for key biological factors impacting performance, we can further our understanding of swimming capacity in different groups of fishes. This, in turn, may provide a broader understanding of the ecological and biological drivers of fish life history, including connectivity, mortality, feeding, dispersal, and recruitment.

ACKNOWLEDGEMENTS

We thank R. Fisher, with much gratitude, for providing us with her raw data from some of her previous work. We thank B. Illing and I. Bouyoucos for advice on statistical analyses and for helpful feedback on the manuscript. Figure illustrations were designed by E. Walsh. We also thank the two anonymous reviewers for useful comments on the manuscript.

CONFLICTS OF INTEREST

The authors deem no conflicts of interest in this work.

AUTHOR CONTRIBUTIONS

A.T.D, P.F.C, J.M.L., M.I.M, and J.L.R. conceived the study. A.T.D. collected the data and performed analyses, with help from P.F.C. for the comparative phylogenetic analyses. A.T.D. wrote the first draft of the manuscript with substantial contributions on subsequent drafts from P.F.C., J.M.L, M.I.M. and, J.L.R.

DATA AVAILABILITY STATEMENT

The following study largely used data extracted from the published literature. We generated new data from our body shape analyses. All data used for analyses, species/reference list and statistical outputs for all analyses are available (DOI: https://doi.org/10.1111/faf.12580).

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SUPPORTING INFORMATION

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

How to cite this article: Downie AT, Leis JM, Cowman PF, McCormick MI, Rummer JL. The influence of habitat association on swimming performance in marine teleost fish larvae. *Fish Fish*. 2021;22:1187–1212. https://doi.org/10.1111/faf.12580