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REVIEWS

Swimming performance of marine fish larvae: review of a universal trait under ecological and environmental pressure

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Abstract The larval phase of marine teleost fishes is characterized by important morphological and physiological modifications. Many of these modifications improve the larvae's ability to swim, which satisfies a suite of crucial biological and ecological functions. Indeed, larval fish swimming performance has been considered a good proxy for overall condition, a predictor for growth and survival, and particularly helpful in assessing effects of natural and anthropogenic stress. Several methodologies have been developed to test larval fish swimming performance; however, measured swimming capabilities can strongly depend on the methodology utilised and developmental stage investigated. The aims of this review were, therefore, to link the ontogenetic development of swimming performance in early life stages of marine fishes, particularly the anatomical and physiological processes around the fins, muscles, and gills, with both the experimental methodologies used and the environmental stressors tested. We conducted a literature search and found 156 research papers relevant to swimming performance of marine teleost fish larvae. We found swimming performance to be highly variable among species and driven by temperature. In a meta-analysis focusing on the impacts of environmental stress on larval swimming performance, we found that prey reduction had the greatest impact on swimming. Methods used to evaluate swimming should keep the ontogenetic stage a focus, as forced swimming experiments are unfit for larvae prior to flexion of the notochord. Overall, while the data are deficient in some areas, we are able to highlight where the field of larval fish swimming could be directed and provide insight into which methods are best used under certain ecological scenarios, environmental stressors, and developmental stages.

Keywords Early life history · Teleosts · Performance · Anthropogenic stress · Swimming methodology · Developmental biology

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Introduction

With an estimated 17,000 known species, marine fishes are the most speciose group of vertebrates on the planet, and their importance for ecosystem function

and global fisheries cannot be understated (Appeltans et al. 2012). Marine fishes act at all trophic levels (e.g., planktivores and herbivores, up to apex predators) and occur in a large range of ecosystems and latitudes (polar ice shelfs to tropical coral reefs). In order to maintain their populations, marine fishes rely on a continuous supply of larvae. At hatch, oviparous marine fishes are among the smallest free-living vertebrates (2–3 mm total length) and generally do not possess many of the physical characteristics of juvenile and adult conspecifics (e.g., fins; Osse and Van den Boogaart 1999). Consequently, larvae are highly vulnerable to changes in environmental conditions, starvation, and predation, resulting in high mortality rates ($\sim$ 99.9% during the entire larval phase; Fuiman and Cowan 2003; China and Holzman 2014). Indeed, the larval phase of marine fishes is a period of developmental change characterised by morphological and physiological modifications. These changes enhance performance traits that subsequently support rapid development, improve chances of survival, and enable potential recruitment to the adult population. Since the early 1900s, fisheries biologists have attributed changes in marine fish population dynamics to larval fish survival; however, there is still a need for assessing the development of performance to better predict larval survival, in particular under changing environmental conditions (Houde 2008). A highly relevant performance trait that encompasses important aspects of any marine fish's ontogeny, physiology, and ecology is swimming performance.

Swimming is a form of physical exercise powered by physiological and neuromuscular processes that enables fish to perform vital activities including foraging, avoiding predators, and undertaking daily and seasonal movements in their environment (Webb 1984; Domenici and Blake 1997; Hinch et al. 2005; Domenici and Kapoor 2010). The appropriate anatomical structures for swimming and the physiological processes mediating them primarily develop during the larval phase and can be assessed by a number of metrics and techniques that have been developed to study the swimming performance of fish (Batty 1984; Stobutzki and Bellwood 1994; Fuiman and Batty 1997). These methods have been used to investigate effects of different intrinsic and extrinsic factors on swimming performance, and to assess their implications for ecologically-relevant processes. For example, swimming is directly impacted by abiotic factors, such as temperature (Batty and Blaxter 1992; Wieser and Kaufmann 1998; Hunt von Herbing 2002; Green and Fisher 2004; Moyano et al. 2016) and carbon dioxide (CO_2) levels (Pimentel et al. 2014, 2016; Silva et al. 2016), and biotic factors such as prey availability (Illing et al. 2018). Knowledge as to how larvae respond to such changes is not only key for their individual survival, but also for predicting important events, such as dispersal or recruitment to adult stocks (Hufnagl and Peck 2011; Huebert and Peck 2014; Huebert et al. 2018).

Considering the increasing anthropogenic pressure on marine fishes, the use of larval fish swimming as a universal performance trait holds great potential for both a better mechanistic understanding of organismal performance and for assessing consequences on larger-scale levels, such as predicting dispersal and recruitment. However, there is a need to integrate the ontogenetic development of swimming performance, the metrics by which swimming is measured, and how changes in the environment will impact swimming at different stages of larval development. The aims of this review are, therefore, to (1) integrate morphological and physiological perspectives with the development of swimming performance, (2) evaluate the ecological relevance of commonly used methodologies to measure swimming, and (3) assess how (anthropogenic) environmental stressors affect swimming performance of marine fish larvae. Additionally, throughout the review, we attempt to disentangle the effects of latitudinal background, (i.e., the climatic region) and taxonomic origin on development and environmental impacts on swimming performance.

Methods

We conducted a systematic literature search to find all relevant studies (ISI Web of Knowledge, Clarivate Analytics, Core collection search on 19.02.2019 using the term: ((swim* OR sust* OR prolong* OR burst* OR cruis* OR routin* OR Ucrit OR endur*) AND (early life stage* OR larv*) AND (marin* OR sea* OR brack*) AND (fish* OR teleost*))). This search resulted in 1,938 papers that were then checked for suitability, subsequently providing 156 studies relevant to our aims (see S2 for details). We proceeded to extract data from the aforementioned 156 studies using WebPlotDigitizer (Version 4.2, Ankit Rohatgi). We grouped the retrieved data into climatic regions

and taxonomic orders based on information provided in Fishbase (Froese and Pauly 2017). Average daily growth and pelagic larval duration information incorporated into Fig. 3 was obtained from Fishbase (Froese and Pauly 2017). Furthermore, we compared the swimming performance (expressed as Reynold's Number; *Re*) of marine larvae across different ontogenetic stages and climatic regions. All statistical analyses were conducted in R (R Development Core Team 2013), e.g., model selection, diagnostics, and post-hoc tests ('lme', 'emmeans', and MuMin). Studies assessing the effects of environmental stress on swimming performance were grouped into categories of ocean acidification (OA), ocean warming (OW), ocean acidification and warming (OAW), prey reduction, and toxicants. We did not include studies that expressed swimming performance as percentage active vs. inactive, as we compared all studies using an absolute value for swimming performance (e.g., cm s^{-1}). We conducted a multivariate meta-analysis to determine the effect of the respective environmental stressors on swimming performance of marine fish larvae, using R and the package "metafor" (Viechtbauer 2010). For details on statistical analyses, please refer to Supplementary Materials.

Ontogenetic development and hydrodynamic limitations

The early life history of most marine fishes is characterised by a larval phase, which is spent in the open ocean and often referred to as the pelagic larval duration (PLD; Cowen and Sponaugle 2009). This period can be further divided into a pre-competent and a competent phase (Jackson and Strathmann 1981). These two phases are essentially separated by the ability of a fish larva to overcome hydrodynamic processes affecting its dispersal (e.g., ocean currents). This transition is influenced by extrinsic (i.e., effects from the abiotic and biotic environment) and intrinsic (i.e., development of key swimming structures and the physiological processes mediating them) factors.

At hatch, most marine teleost larvae are not fully developed and lack many important structures crucial for swimming: (1) the caudal fin, the most important structure for horizontal swimming, has not been formed yet, (2) gills are not present (cutaneous oxygen uptake is sufficient), and (3) muscles are undifferentiated (Fig. 1; Blaxter 1988; Müller and Videler 1996). This simple form, known as the pre-flexion stage, limits swimming capabilities regardless of climatic region or taxonomic group (Fig. 2b, c); however, it does allow larvae to change their horizontal displacement by swimming vertically in the water column (Fig. 1; Voesenek et al. 2018). Without a properly formed caudal fin, most larvae use high amplitude body undulations to swim (e.g., such as anguilliform swimming representative of many herring species), which can be energetically expensive (Fig. 1; Müller et al. 2008; Yavno and Holzman 2017). Indeed, at this developmental stage swimming can use up to 80% of a larval fish's energy budget (e.g., Atlantic cod; *Gadus morhua*; Ruzicka and Gallager 2006). A crucial developmental milestone is the flexion of the notochord, a rudimentary support structure for the vertebral column, which forms the caudal fin (Fig. 1). This stage, known as post-flexion, marks an increase in swimming competency for marine fish larvae and enables them to effectively overcome the limitations of their hydrodynamic environment. Notochord flexion generally occurs in conjunction with gill and muscle development to facilitate oxygen delivery to tissues and increase locomotor output, respectively. Cutaneous respiration becomes inefficient as larvae increase in size, which is based on species-specific growth rates and species-specific oxygen requirements per unit mass (QO_2; Blaxter 1988), and thus gills are crucial to provide sufficient oxygen to all aerobically driven tasks. Generally, upon gill formation, fish larvae possess high mass-specific oxygen uptake rates compared to adult conspecifics, which is associated with high metabolic rates to support rapid tissue development (Post and Lee 1996; Killen et al. 2007; Peck and Moyano 2016). However, the body of literature on oxygen consumption rates of marine teleost larvae is sparse, mainly due to the logistics of measuring oxygen consumption of small sizes of marine larvae (Peck and Moyano 2016). In fact, few studies have investigated the oxygen consumption rates of swimming larvae, and $> 95\%$ of the existing studies have tested only temperate fish larvae (Peck and Moyano 2016). Gill development also occurs in concert with muscle tissue differentiation (El-Fiky et al. 1987). As muscle tissue separates and forms red and white muscle types (i.e., differentiation) and muscle fiber abundance increases (i.e., hyperplasia), fish start

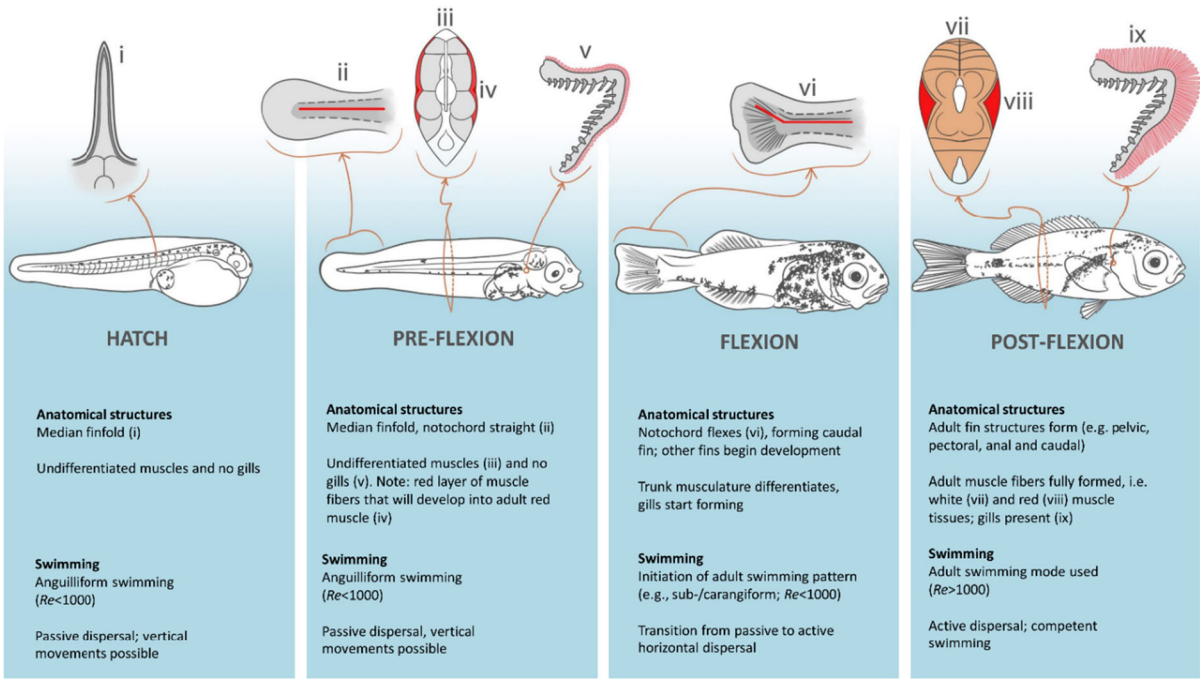

Fig. 1 Generalized overview of how swimming capabilities develop throughout early ontogeny in marine fishes. Each ontogenetic stage is described in terms of the anatomical structures that form (e.g., muscles, gills, and fins, highlighted by cross-sectional or top views), and how they influence swimming performance (e.g., Reynold's Number (*Re*), swimming mode, and vertical/horizontal swimming capabilities)

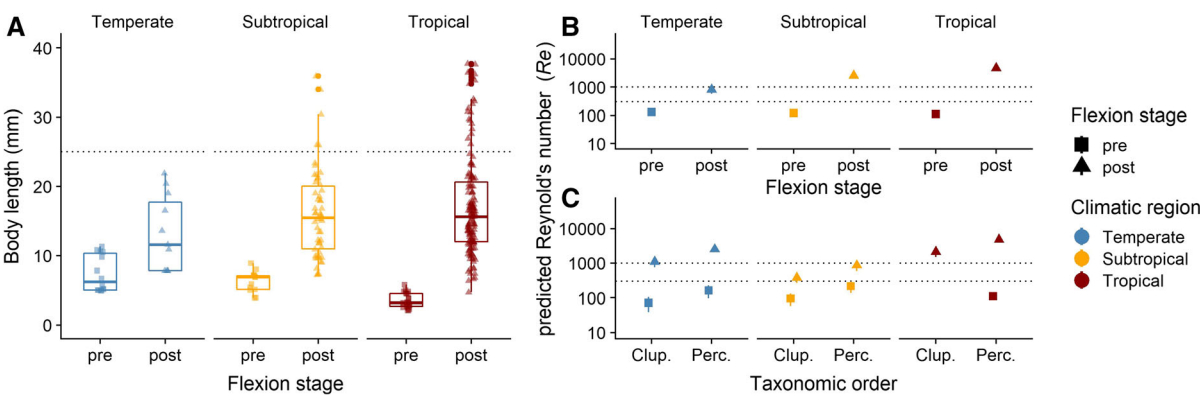

Fig. 2 **a** Body lengths of pre- and post-flexion stages of marine fish larvae from three climatic regions. Marine fish larvae develop faster in warmer climatic regions, and undergo the flexion of the notochord, a developmental milestone for improving swimming performance, at smaller body sizes. Original data were retrieved from a systematic literature search (see methods). We used body length, the inverse of the kinematic viscosity of seawater, and critical swimming performance (U_{crit}) data to calculate the Reynold's number (*Re*), a dimensionless unit describing the ratio of inertial to viscous forces. Limiting the body length data set to < 25 mm (dotted line) did not provide better model results. **b** Modelled means (± 95% CI) of the Reynold's number that marine fish larvae experience in waters of different climatic regions, separated by pre-and post-flexion stages (total body length range 2–38 mm). **c** Modelled means (± 95% CI) of the Reynold's number that pre- and post-flexion stages of marine Clupeiform (Clup.) and Perciform (Perc.) fish larvae experience across climatic regions. Dotted lines indicate the transition area from the viscous to the inertial zone, where competent swimming is achieved (*Re* = 300–1000; note logged y-axis scales in panels B + C). See supporting information S1 for further details on the linear regression models

utilizing a swimming mode analogous to the adult stage (e.g., sub-carangiform or carangiform, see references in Müller 2008; Fig. 1). The thin layer of muscle responsible for cutaneous respiration will develop into red muscle tissue characteristic of adult stages that powers sustained swimming behaviours (Fig. 1; Rombough 1988). Taken together, these anatomical and physiological modifications help fish larvae to become competent swimmers and escape their viscous environment.

The viscosity of water has a proportionally stronger effect on smaller organisms compared to larger organisms and therefore hinders effective swimming of many marine fish larvae. A dimensionless metric, called the Reynold's number (*Re*), describes the ratio of the viscous forces of water against an animal and the inertial forces of an animal moving through water (Taylor 1951; Fuiman and Batty 1997). A low *Re* (< 300) indicates that the animal's swimming capabilities are not strong enough to overcome the viscosity of the water (viscous zone; pre-competent phase); whereas, high *Re* (> 1000) is attributed to inertial forces of the swimming animal being greater than the resistive forces of the water (inertial zone; competent phase; Fig. 1; Ngo and McHenry 2014; Moyano et al. 2016). Several factors impact the *Re*, including size, swimming speed, and water viscosity, all of which are highly temperature-dependent (Figs. 2, 3; Hunt von Herbing 2002). Thus, for example, the higher *Re* of fish larvae inhabiting tropical latitudes

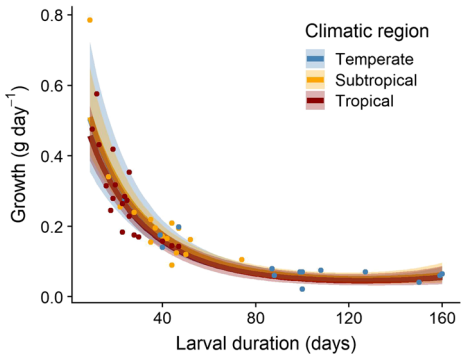

Fig. 3 Average growth (g body mass day^{-1}) of marine fish larvae from different climatic regions and their larval duration (days before metamorphosis). Data were extracted from Fish Base, and each data point represents an individual species. An exponential curve was fit through the data (log (growth) $\sim$ larval duration + climatic region + I(larval duration^2); $df = 44$, $p < 0.001$, $R^2 = 0.85$). Bands represent 95% CI

compared to fishes of temperate environments is partially attributed to warmer water temperatures (Fig. 2b). Regardless of climatic region, investing energy into anatomical structures designed for swimming mitigates the challenges of such a viscous environment, which can mean "the difference between acquiring energy and being acquired energy" (Goolish 1991).

To date, much of what we know about the development of marine fishes relates to those that inhabit temperate environments. Marine fishes inhabiting tropical and polar (stenothermal) habitats may have some differences in their developmental patterns when compared to their temperate water counterparts. However, in contrast, most available data on swimming performance is from tropical perciform fishes, likely due to the large number of species occurring in the tropics, and the high number of species encompassed by Perciformes (Leis 2007; Leis et al. 2013). Regardless, at any given size, tropical marine fish larvae, particularly those that hatch from demersal eggs (e.g., anemonefishes), are better developed (e.g., in terms of fin and sensory systems), and have higher growth rates than their temperate counterparts, such as herrings or cods (Leis and McCormick 2002; Leis 2007; Leis et al. 2013). Flexion of the notochord appears to occur at a smaller body size for tropical compared to temperate larvae (Fig. 2a). After extracting data from the original literature, we first predicted *Re* with an overall linear model ($\log(Re) \sim$ Region $\times$ Stage; $df = 250$, $p < 0.001$, $R^2 = 0.67$) in which we accounted for an interaction between developmental stage and climatic region, across all taxonomic groups. Using Tukey's post-hoc tests, no differences in *Re* were observed in pre-flexion life stages across climatic regions ($p > 0.05$), whereas all post-flexion life stages differed significantly from another ($p < 0.01$). Many factors, such as life history traits (e.g., developmental rates), morphology, and evolutionary history are hypothesized to contribute to this difference in marine fish ontogeny and swimming performance; however, temperature is widely regarded as a leading factor (Leis et al. 2013).

To investigate whether taxonomy or latitude has the greater impact on swimming performance (represented by *Re*), we compared two taxonomic groups of fishes, Order Perciformes and Order Clupeiformes. These are the only two orders with sufficient swimming data available across a wide latitudinal range

(temperate, subtropical and tropical climate regions) and for most developmental stages (Fig. 2c). Perciformes are more speciose in the tropics, and are considered better swimmers than Clupeiformes, which are more abundant in temperate regions. We analyzed a subset of the data (only Clupeiform and Perciform fishes) and added taxonomic order as a fixed factor to the model ($\log(Re) \sim$ Order + Stage × Region; $df = 221$, $p < 0.001$, $R^2 = 0.68$). We used Tukey post-hoc tests for pairwise comparisons between the groups, and found no significant differences in *Re* between taxa when compared within the respective developmental stage (pre- and post-flexion; $p > 0.05$; Fig. 2c; see S1 for further details on the statistical analysis). While this is based on comparing two groups with limited data, it may suggest that temperature is a greater driver of performance than taxonomic group alone, as larvae of marine fish species living in warmer climatic regions posses a higher capacity for swimming, regardless of taxonomic order.

Methodologies and ecological relevance

The most widely utilised methodology to measure larval fish swimming performance is routine swimming, which is evaluated by measuring the swimming speed of undisturbed larvae or quantifying behaviour as 'percent active versus inactive' (e.g., Fisher and Bellwood 2003). Routine swimming tests provide valuable information as to how larvae naturally interact with their environment under both natural (e.g., swimming speed as larvae develop; Ryland 1963; Fuiman et al. 1999; Fisher and Bellwood 2003; Arndt et al. 2016; Garrido et al. 2016; Højgaard et al. 2018) and modified environmental conditions in laboratory settings including stressors, such as prey reduction (Chick and Van den Avyle 2000), ocean warming (Moyano et al. 2016) and ocean acidification (Rossi et al. 2015), or exposure to toxins (Benítez-Santana et al. 2012, 2014). Some studies, mainly on coral reefs, have quantified routine swimming performance of larval fishes in the field, whereby divers released captured tropical coral reef fish larvae back onto the reef and followed them in situ to quantify their swimming speed, depth, orientation, and interactions with other fishes (Leis et al. 1996; Leis and Carson-Ewart 1997, 1998, 1999, 2000, 2002). Measuring routine swimming in the field provides (1) valuable information regarding natural swimming speeds of larvae as they swim toward the reef to settle (Leis and Carson-Ewart 1997, 1998, 1999, 2000, 2002) and (2) allows for comparisons to be made between in situ swimming speeds and other laboratory measures (Fisher et al. 2005; Fisher and Leis 2010). Unfortunately, the effect that the diver has on swimming performance of the observed larvae is not known (Leis 2006). Yet, routine swimming, especially in situ swimming speeds, would provide highly valuable information for dispersal models, as these are minimum speeds larvae swim at under natural conditions.

An endurance swimming test involves swimming a fish at a fixed water velocity until the fish fatigues, and is generally repeated using different flow intensities [e.g., high-water flow, such as U_{crit}, see below, down to routine swimming speeds of 1 body length (BL s^{-1})]. This helps create a fatigue curve to determine (1) how long fish can swim at various ecologically-relevant speeds (e.g., different oceanic currents or tides; see Peake et al. 1997) and (2) when fish transition between different modes of swimming (e.g., sustained, prolonged, and burst; see Beamish 1978). For many temperate fish larvae, competent swimming is not possible until much later in ontogeny, generally when fish approach the juvenile phase. However, it may be an important metric for tropical fish larvae, due to their remarkable swimming capabilities early in their development (for examples of swimming speeds and notes on ecological relevance, see Stobutzki and Bellwood 1994; Leis et al. 1996; Jones et al. 1999; Fisher et al. 2005; Fisher and Leis 2010). For example, when provided a routine feeding regime, cinnamon anemonefish (*Amphiprion melanopus*) larvae [5.5–7.6 mm total length (TL)] are capable of swimming at 7 cm s^{-1} for 50 h (maximum of 120 h) and covering 12 km (maximum of 30 km; Fisher and Bellwood 2001). While it has not been evaluated to date, information on energy requirements for sustained swimming performance at ecologically-relevant flow velocities would be valuable in determining cost of transport (COT; amount of energy required to move a unit distance) during dispersal, settlement, and recruitment processes. Integrating oxygen uptake, a proxy for energetic costs, into physiologically-coupled biophysical models will help improve predictive power and help assess potentially increased costs under changing environmental conditions.

The most widely used metric to measure swimming performance of adult fishes, and also common among larval fishes, is the critical swimming test (U_{crit}; Brett 1964). The U_{crit} test (Brett 1964) is a stepped-velocity test, whereby water velocity increases by reliable increments (generally 1 BL s^{-1}) after a fixed time interval until the fish fatigues. The U_{crit} test has been used to evaluate how swimming performance develops throughout the larval phase of many marine fishes (Leis et al. 2006, 2012; Faria et al. 2009; Faria and Gonçalves 2010), compare swimming competencies of different species/families (e.g., Fisher et al. 2005), and evaluate how environmental changes impact swimming performance (Green and Fisher 2004; Guan et al. 2008; Koumoundouros et al. 2009; Munday et al. 2009; Moyano et al. 2016). However, the test has been criticized for a few reasons: (1) altering the time and speed intervals may drastically change U_{crit} (Farlinger and Beamish 1978; Downie and Kieffer 2017, but see Hogan and Mora 2005), (2) swimming the fish until fatigue involves anaerobic metabolism (i.e., the U_{crit} test is not an obligatory aerobic measure per se), and (3) fish do not generally swim at U_{crit} for time periods relevant to daily/seasonal movements. As such, U_{crit} should be used with caution when modelling dispersal, and thus, endurance swimming and routine swimming should be considered as more accurate metrics (see reviews by Plaut 2001; Fisher and Leis 2010; Majoris et al. 2019). We recommend the use of U_{crit} when comparing the magnitude by which an environmental stressor impacts swimming performance. A valuable application for U_{crit} would be to measure oxygen uptake at each swimming speed so that a COT/fatigue graph over a wide range of water flow velocities could be created to determine swimming efficiency. Also, aerobic scope (an animal's energy budget) can be calculated from swimming fish, which may be a more accurate method than static respirometry (Rummer et al. 2016). While this would increase the experimental time (i.e., 10–20 min per step interval, versus the generally used 2–5 min per interval), the data would be invaluable in determining, for example, the costs for swimming at different speeds, whether the oxygen budget changes over ontogeny, and the impact of environmental stress.

Burst swimming is associated with larvae capturing prey and avoiding predators (e.g., Batty et al. 1993) and produces the fastest swimming speeds. Burst swimming is generally captured using a high-speed camera and software to quantify these fast movements (see review by Domenici and Blake 1997). Burst swimming has been used to understand effects of varying prey densities (Faria et al. 2010, 2011) or chemicals (e.g., Alvarez et al. 2006; Johansen et al. 2017). Several studies have also investigated how burst swimming develops throughout the larval phase and across taxa (notable examples include Masuda et al. 2002; Masuda 2006; Benítez-Santana et al. 2007; Chesney 2008; Olivier et al. 2013). The implications for burst performance have been incorporated into individual-based models (IBMs) associated with growth and survival, across many developmental stages (Peck and Hufnagl 2012), and the methods are of particular interest in determining how fish larvae may be impacted by environmental stress (e.g., Allan et al. 2015).

Environmental impacts

Ocean acidification (OA)

Ocean acidification (OA) is defined as the decline in ocean water pH due to the absorption of atmospheric CO_2 (Lopes et al. 2016). Adult and juvenile teleosts may be more resistant to OA, as they are quite capable of efficient acid–base regulation (Munday et al. 2009; Bignami et al. 2014; Rummer and Munday 2017); however, such regulation is energetically expensive and may have ripple effects on other physiological processes and overall performance and behaviour (Munday et al. 2009; Leis 2018). Teleost larvae are believed to lack many physiological mechanisms that allow more developed life-stages to tolerate environmental conditions, including OA, and consequently, it is hypothesized that early life stages of marine fishes are highly susceptible to the effects of acidification. (Bignami et al. 2013; Leis 2018). While several studies have shown negative, sub-lethal, impacts on larval fish predator avoidance (Dixson et al. 2010), vision (Chung et al. 2014), lateralization (Domenici et al. 2011), hearing (Simpson et al. 2011), learning (Ferrari et al. 2012), and activity rates (Munday et al. 2010), OA does not seem to impact swimming performance, regardless of climatic region or swimming methodology (Fig. 4). Tropical fishes, such as the common dolphinfish (*Mahi mahi),* possess high

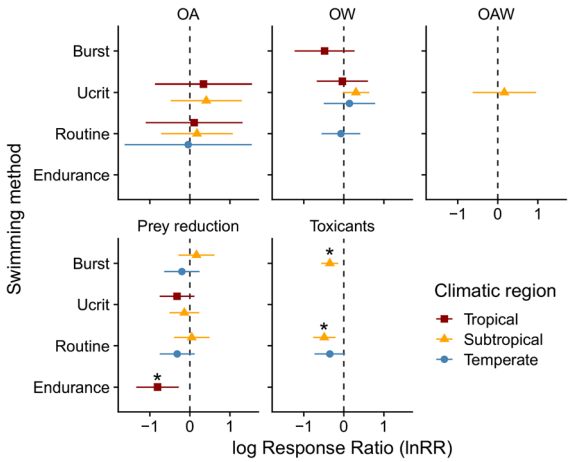

Fig. 4 Mean effect sizes (lnRR) of environmental factors on swimming performance measures of marine fish larvae. Studies investigating the effects of ocean acidification (OA), ocean warming (OW), the combination of ocean acidification and warming (OAW), prey reduction, and toxicants were retrieved by a systematic literature search in the Web of Science (n = 27). The original data were extracted, converted to swimming speeds in cm s^{-1}, and compared using multivariate meta-analyses (see methods for further details). Symbols indicate predicted mean effect sizes (± 95% CI), and are shape-and color-coded by climatic regions. Significant effects ($p < 0.05$) were observed where the confidence bands did not span zero (marked with asterisks)

metabolic rates, which may allow for increased ability to regulate pH (Bignami et al. 2013, 2014), and there is evidence that young *Mahi mahi* supress metabolic rates under OA conditions, creating a trade-off with a decreased growth rate (Pimentel et al. 2014). The larvae of barramundi (*Lates calcarifer*), a tropical, euryhaline fish, slightly decrease routine swimming activity in response to exposure to OA, which may have impacts on timing of recruitment and growth rates (Fig. 4; Rossi et al. 2015). Similarly, larvae of temperate fish, like herring, do not show a change in routine swimming capabilities (Fig. 4; Maneja et al. 2015).

Based on the limited data, it is possible that teleosts are capable of acid–base regulation to some capacity early in development (Lopes et al. 2016). The reallocation of resources and energy to acid–base regulation could explain the lack of significant change in swimming performance during exposure to OA conditions, and the negative impacts OA has on larval growth and development (Silva et al. 2016). Species inhabiting habitats with high natural fluctuation in pH, such as those on coral reefs, may be more resilient and able to keep acid–base balance under hypercapnic conditions (Michaelidis et al. 2007; Munday et al. 2009). While speculative, the exact mechanism underpinning the lack of impact OA has on swimming at such an early ontogenetic stage is unknown, and it cannot be understated that there is generally a lack of available studies on the subject.

Ocean warming (OW)

Temperature governs all biochemical processes and basic physiological functions. Thus, ectotherms, such as fishes, strongly depend on temperature, as it controls metabolism and regulates factors relevant for fast growth and developing structures required for swimming (Rummer and Munday 2017). However, these processes occur within an optimal temperature window, and any direction, warmer or colder, outside this window causes performance to deteriorate (Rombough 1997). Ocean warming (OW) is becoming an ever-present threat to our ecosystems, and ectotherms operating outside of their optimal thermal windows may face the risk of being unable to sustain their metabolic rates (Moyano et al. 2016). Teleost larvae are especially at risk, as they are believed to be incapable of physiologically multi-tasking between high growth rates, swimming, basic maintenance costs, and responding to stress (Killen et al. 2007). As a result, understanding how OW will impact swimming performance is crucial.

Generally, swimming speed increases with temperature due to a reduced viscosity of the water and an increase in the activity of swimming muscles (Batty et al. 1991, 1993). In concert with this, herring (*Clupea harengus*) larvae reared at warmer temperatures grew faster, achieved developmental milestones sooner, and performed better than conspecifics reared at lower temperatures (Moyano et al. 2016). Atlantic cod (*Gadus morhua*, 5 dph; 5 mm TL) swim circa 70% faster at 10 °C than at 0 °C (Hunt von Herbing and Keating 2003). Cinnamon anemonefish (*Amphiprion melanopus*) reared at 25 °C swam to a lesser capacity than those reared and swum at 28 °C (U_{crit} protocol; Green and Fisher 2004). However, Koumoundouros et al. (2009) found that the optimum swimming temperature for gilthead seabream (*Sparus aurata*) was 25 °C, as they found a decrease in U_{crit} at 28 °C. Additionally, the escape response of Ward's damselfish (*Pomacentrus wardi*) was reduced at elevated

temperatures due to a decrease in muscle power at high temperatures (Allan et al. 2015). These two studies show how operating outside of a fish's optimal thermal window many hinder performance and subsequently survival.

Across all climatic regions and methods, we found no overall significant change in swimming performance for marine teleost larvae in response to OW (Fig. 4). This may be attributed to several factors, such as (1) high levels of individual variation (Moyano et al. 2016; Hunt von Herbing and Keating 2003), (2) narrow temperature ranges tested (Klumb et al. 2003), (3) pooling together pre- and post-flexion larvae for analyses (Hunt von Herbing and Keating 2003; Moyano et al. 2016), and (4) testing species with wide thermal windows (e.g., subtropical species) that are often not impacted by large increases in temperature (Koumoundouros et al. 2009). At the smallest sizes (i.e., generally pre-flexion), larvae are not fully developed (i.e., lacking proper muscles and fin structures; Fig. 1), and thus swim poorly, regardless of experimental temperature (Hunt von Herbing and Keating 2003; Moyano et al. 2016; see Fig. 2b, c). As larvae increase in size and develop further, temperature impacts swimming more, than the viscosity of the water (Hunt Von Herbing and Keating 2003). Temperate and subtropical larvae with wider thermal windows tend to increase their critical swimming performance, likely benefiting from faster growth and development at elevated temperatures (Fig. 4).

Ocean acidification and ocean warming (OAW)

Generally, most laboratory experiments test swimming performance of larvae against OA and OW scenarios separately. However, these processes are co-occurring, with the nature of the stressor interactions still being unclear (Laubenstein et al. 2018, 2019; Baumann 2019). Ocean acidification effects are often hypothesized to amplify OW effects, either additively or synergistically (Watson et al. 2018; Cominassi et al. 2019). Co-occurring warming and acidification effects potentially increase metabolic demands and may divert additional energy from growth to acid–base regulation (Bignami et al. 2016). However, evidence suggests that, in trials with concerted warming and elevated CO_2, elevated temperature has the greater impact on swimming performance (Fig. 4; Bignami et al. 2016; Watson et al. 2018; Cominassi et al. 2019). We are only aware, to date, of three studies combining OA and OW to investigate the effects on swimming performance (Bignami et al. 2017, Watson et al. 2018, Cominassi et al. 2019). Thus, it is difficult to draw final conclusions using such few studies, geographic regions represented, and methodologies used (Fig. 4). In the three present studies on subtropical fish larvae, OAW did not affect critical swimming performance (Fig. 4). However, multi-stressor experiments are the most promising approach to disentangle effects of co-occurring and interacting climate change factors. Future studies, with a focus on a wider taxonomic range, methods, developmental stages, and geographic regions will provide stronger evidence for how these combined stressors may impact swimming performance.

Prey reduction

The two main drivers of larval fish mortality are starvation and predation, and since the early 1900s, many experimental and field studies have shown slow-growing and low-performing fish to be more vulnerable to predation (e.g., Hjort 1914; Takasuka et al. 2004). Therefore, fast growing fish larvae that manage to optimize their feeding behaviour are positively selected for, rendering a flexible search behaviour as a key trait for survival in prey scarce environments. When prey is not limiting, larvae decrease swimming speed to save energy, and consequently decrease their encounter rate with predators (Chick and Van Den Avyle 2000; Mahjoub et al. 2011). When prey becomes limiting, however, some fishes increase their search behaviour until they reach a "point of no return" (Hempel and Blaxter 1963). Results from our meta-analysis on the effects of prey reduction on swimming performance indicate that most marine fish larvae show an overall trend toward a decrease in performance after periods of food shortage. Still, only endurance swimming was significantly negatively affected (Fig. 4). Several factors contribute to the variability in the findings. First, some studies investigated pre-flexion larvae that had not fully developed their swimming capacity (Faria et al. 2011). Second, the period that larvae fasted or were starved differed between studies (Skajaa and Browman 2007; Faria et al 2010, 2011; Mahjoub et al. 2011). Third, specifically for burst swimming, muscle glycogen stores may be maintained during periods of starvation

(Floyd and Anderson 2010). The maintenance of short-term swimming performance in prey-reduced environments may be a strategy to conserve energy and prioritize behaviours that help capture food when it becomes available again, and escape predators (Skajaa and Browman 2007; Faria et al. 2011).

Prey availability studies are the only larval fish swimming studies to use endurance tests as a metric for measuring swimming performance (Fisher and Bellwood 2001; Leis and Clark 2004; Faria et al. 2011). Feeding the larvae during endurance swimming experiments provides a more accurate measure as to how far a fish can travel, as they 'feed on the run', before switching to the juvenile and adult life styles and habitats (Leis and Clark 2004). Across all studies, larval fish, where food was withheld, swam shorter distances than larvae that were fed (Fig. 4; Fisher and Bellwood 2001; Leis and Clark 2004; Faria et al. 2011), and it has been suggested that endurance swimming is limited by energy reserves availability (Faria et al. 2011). Therefore, unfed larvae undergoing endurance experiments are an indicator of how far energy stores can take larvae (Stobutzki 1997). Regardless of climatic region, endurance swimming experiments, where fish are fed and their oxygen uptake quantified, will be an invaluable metric to evaluate travel distances of larvae and related costs.

Toxicants

The two main toxicants that have been used to evaluate the effects of chemicals on swimming performance were methylmercury and heavy oil. Methylmercury (MeHg) is a natural form of mercury produced by burning fossil fuels and coal that bio-accumulates in food webs and is an endocrine disrupting chemical and neurotoxicant (Alvarez et al. 2006). Routine and burst swimming of pre-flexion croaker (*Micropogonias undulatus*) were significantly reduced upon exposure, and model simulations predicted most exposed larvae would not survive a predator attack (Fig. 4; Alvarez et al. 2006). Heavy oil causes nervous system damage to early life stages of teleosts, results in chronic behavioural abnormalities, and impacts swimming performance (Kawaguchi et al. 2011; Irie et al. 2011; Johansen et al. 2017). Pufferfish (*Takifugu rubripes*) larvae displayed abnormal swimming patterns associated with central nervous system defects (Fig. 4; Kawaguchi et al. 2012). Both of these studies tested pre-flexion stages, which would be most sensitive to these chemicals. Knowledge on how marine fish larvae are affected by toxicants, such as heavy oil, continues to be highly relevant with ongoing use of off-shore oil platforms and underwater drilling activities that have potential spill hazards (e.g., Deepwater Horizon; Johansen and Esbaugh 2017). Taken together, swimming performance may be a useful metric for ecotoxicological assessment, to measure the direct impact that toxicants have on survivorship of marine fish larvae, regardless of ontogenetic stage.

Conclusion and future work

This review provides a comprehensive overview on the biology, physiology, and methodologies characterising swimming performance of marine fish larvae and is framed into an ecological context by assessing the effects of key environmental stressors on larval fish swimming. In summary, we found the following:

(1) The larval phase of marine fishes is highly dynamic and influenced by many intrinsic and extrinsic factors that control growth and development. Specific developmental milestones (e.g., notochord flexion) determine when a larva reaches the ability to effectively influence its own dispersal, and we found this competency to be rather temperature- than taxon-dependent. Regardless of taxonomic order, tropical and subtropical fish larvae develop faster and have higher capacity for swimming when compared to temperate fish larvae. Determining the timing of this competency is crucial for improving biophysical dispersal models and assessing connectivity and recruitment scenarios.

(2) Several methodologies exist to test the swimming performance of marine fish larvae. They are helpful for investigating different modes of swimming, but their relevance depends on the tested life stage and ecological question. For example, pre-flexion larvae are not competent swimmers, regardless of taxonomy and climatic region, and are best swum using routine swimming methods. Post-flexion larvae, however, can be tested against continuously increased velocities. For ecological questions related to

dispersal distance and connectivity, endurance swimming tests may be the most useful method. Burst swimming tests are valuable for evaluating when and how larvae try to escape predators.

(3) We analyzed the effects of key environmental stressors and found that, irrespective of the methodology and climatic region, ocean acidification, ocean warming, and the combination of both have no significant effects on the swimming performance of marine fish larvae. We discuss the potential reasons for the observed trends (e.g., high inter-individual variability, combining data of pre-and post-flexion stages) and provide suggestions for future research. Other stressors, such as reduced prey density or exposure to toxicants, had stronger effects on swimming performance, but depended on the experimental settings (e.g., the duration of prey absence). For example, prey reduction seems to affect prolonged swimming performance more than short-term/acute swimming performance (e.g., critical swimming or burst speeds). In general, we observed a lack of data across all stressors, with respect to developmental stages, methods, climatic regions, and taxonomic groups tested, which hampers better-informed conclusions on the effects of environmental stress on larval fish swimming performance.

Based on our findings, we recommend future studies to address and consider the following points. First, swimming performance should be tested across multiple developmental stages (e.g., both pre-and post-flexion). Currently, swimming performance is often assessed at a single point in time and extrapolated, thus ignoring the rapid changes in performance throughout ontogeny. For example, all recent studies on OA, most OW studies, and OAW have focused on post-flexion larvae. The impacts of these stressors, while not apparent on older larvae, may be more severe earlier in development (e.g., pre-flexion stages). Second, standard protocols for juvenile and adult fishes exist for quantifying the energetic costs of swimming, (e.g., through measurements of oxygen uptake), however, are rare in larval fishes. Future work should aim to add more physiological metrics, which will be invaluable for assessing whether sustaining a certain swimming performance comes with the trade-off of increased energetic costs. While difficult to construct, swim tunnels can be miniaturized enough to assess to the swimming performance of larvae, and fiber optic oxygen probes are available and can detect small changes in water oxygen levels. In more detail, this knowledge could help assess what developmental stages or taxa are most vulnerable to environmental stress, even if no significant differences in swimming performance are observed at first glance. Third, we stress that choosing the right swimming methodology is important: (1) the burst swimming method is ideal for evaluating predator escape performance in post-flexion larvae, (2) the routine swimming is a generalist method, and useful for assessing undisturbed swimming in both pre- and post-flexion stages, (3) the U_{crit} method should be used to evaluate short-term, high capacity swimming in post-flexion fish larvae, and (4) the endurance swimming method is most relevant for providing data that can be used for modelling dispersal and connectivity. All methods are obviously prone to result in different estimates, based on chosen speed increments and time intervals, and we suggest testing these effects to ease comparative approaches. On this note, we caution the use of U_{crit} to model dispersal distances, as larvae likely do not swim at those speeds for a long time; endurance swimming tests are more suited for modelling the dispersal of marine fish larvae in biophysical models. Lastly, we emphasize that testing swimming performance of early life stages of fishes under co-occurring environmental stressors will improve our understanding of how (anthropogenic) environmental stress affects individual fishes and therefore populations. We recommend testing environmental stress on pre-flexion larvae using unforced, routine swimming protocols, as U_{crit} and burst performance methods are more ecologically and physiologically relevant once larvae have further developed. Thus, comparing the swimming performance of larval fishes on an individual level, across developmental stages, taxonomic groups, and climatic regions, provides valuable information as to how population-level dynamics, such as recruitment and connectivity, may be affected by environmental stressors.

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