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Measurement of swimming ability in larval marine fishes: comparison of critical speed with *in situ* speed

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ABSTRACT: For much of their pelagic larval dispersal (PLD) stage, larval perciform fishes are able to directly influence their dispersal by horizontal swimming, but it is unclear which means of measuring swimming ability is most appropriate for modelling dispersal and studying demographic and genetic connectivity. Most studies use critical speed (Ucrit), a laboratory flume measure derived by increasing flow until larvae can no longer maintain their position. Most swimming ability data on fish larvae are Ucrit, usually for larvae nearing the end of PLD. Recognizing that a forced laboratory measure is inappropriate for dispersal, researchers have used decreased Ucrit values, usually by 50%, and have argued that Ucrit is strongly correlated with more relevant swimming measures. Here I examined the suitability of Ucrit versus *in situ* speed (ISS), wherein speed of larvae is measured by divers following them in the ocean with a flow meter. Considerations of dispersal require inclusion of swimming ontogeny. Swimming speed regressions of speed on size of 10 species in 8 families showed that Ucrit and ISS are not well correlated. The Ucrit:standard length (SL) slope was greater than the ISS:SL slope in 6 species, and did not differ in the other 4 species. No overall metric, e.g. *X*% of Ucrit = ISS, was appropriate for conversion of Ucrit to ISS. Conversion of Ucrit to ISS is not straightforward. Ucrit measures swimming potential, not what larvae do in the ocean, whereas ISS directly measures larvae swimming in the ocean. Ucrit ontogeny is less variable, but ISS ontogeny is more relevant to dispersal. Ucrit may be useful for other purposes.

KEY WORDS: Critical speed · *In situ* speed · Swimming ontogeny · Larval dispersal · Dispersal models · Larval behaviour

1. INTRODUCTION

It is clear that larvae of many perciform fish species have swimming performance great enough to influence dispersal outcomes. This realization has come about via comparison of measured swimming performance of larvae at ambient current speeds (Leis & Carson-Ewart 1997, Fisher 2005, Leis 2006), and by modelling studies showing that assuming larvae drift passively provides substantially different predictions of dispersal outcomes than assuming that larvae swim at empirically determined speeds (Faillettaz et al. 2018b, Bode et al. 2019). As a result, much interest has been focussed on obtaining data on larval-fish swimming that are relevant to questions of dispersal and can be used in parameterizing dispersal models. Swimming performance of larval fishes can be measured in several ways, but only a few are potentially relevant to questions of dispersal, and there is no agreement on which swimming measures should be

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used for which purpose (Fisher & Leis 2009, Downie et al. 2020). Here, I will contrast these measures and discuss how they are being used, and the appropriateness of this use, with a focus on dispersal.

The measure of swimming performance in larval fishes most available in the literature is critical speed (Ucrit), a laboratory value obtained from larvae placed in a flume, wherein the speed is incrementally increased until the larvae can no longer maintain their position (Brett 1964). This is a convenient measure, because large numbers of individuals of any size can be measured quickly and efficiently. In studies of Ucrit in larval fishes, the time between speed increases is usually a few minutes, with a full measure complete in at most a few 10s of minutes.

As a forced measure of swimming performance, originally developed for physiological purposes (Brett 1964, Plaut 2001), Ucrit has been criticized from a variety of perspectives (Tudorache et al. 2013), and just what Ucrit measures is unclear. Few consider Ucrit to be a measure of sustainable swimming speed. Rather, it is best regarded as a measure of prolonged speed (Fisher & Leis 2009), in contrast to measures such as burst speed, which can be maintained only for seconds. In addition, attempts have been made to predict Ucrit of settlement-stage larvae from their morphology (Fisher & Hogan 2007, Rossi et al. 2019), with variable success. Using methodology akin to that used to measure swimming endurance (see below), Fisher & Wilson (2004) estimated a 'sustainable speed' in settlement-stage larvae of 9 species of 3 families by using a flume and several fixed speeds, arbitrarily defining the speed at which 90% of larvae could swim for 24 h as the 'maximum sustainable speed'. Fisher & Wilson (2004, p. 171) concluded that '50% U-crit is a good approximation of the speed able to be maintained […] for 24 hours'. Again, this is a forced measure, and as such, not a speed at which larvae would be swimming in the ocean. Only a few studies have used this measure, even indirectly in modelling (Kobayashi 2006, Chang et al. 2018).

An extensive review concluded that Ucrit 'is at least a rough estimate of the ability of a fish to conduct activities in which swimming is involved' (Plaut 2001, p. 47). A review of swimming in fish larvae concluded that 'critical speed is not directly applicable to dispersal and the control of spatial location on large scales' (Fisher & Leis 2009, p. 346). In spite of this caveat, Ucrit is the speed metric most often used in considerations of larval dispersal, with Ucrit recently being described as a 'valuable', or 'good', proxy for ecologically important swimming capabilities of pre-settlement fish larvae (Nanninga & Manica 2018, Majoris et al. 2019) or, combined with pelagic larval duration, as a measure of 'larval dispersal capabilities' (Wilson et al. 2018).

Most Ucrit data come from studies of settlement-stage larvae captured with light traps (Fisher et al. 2005, Faillettaz et al. 2018a, Rossi et al. 2019), crest nets (Leis et al. 2011a) or beach seines (Pattrick & Strydom 2009). A number of researchers have used Ucrit in studies of dispersal or range size, and these have most often used only Ucrit measures from settlement-stage larvae (e.g. Nanninga & Manica 2018, Wilson et al. 2018). Given that dispersal takes place across the full extent of a larva's pelagic larval dispersal (PLD) stage, it is important to use the ontogeny of swimming performance when considering questions of dispersal. Leis (2010) reviewed the few available studies of Ucrit swimming ontogeny available at that time, but a growing number of studies have documented the ontogeny of Ucrit, most often by using larvae of a range of sizes from laboratory or aquacultural rearings, but occasionally by using wild larvae, thereby increasing taxonomic coverage. Some species from these more recent studies are tropical (Leis et al. 2012b, Majoris et al. 2019), but the majority are warm to cool temperate in distribution, including perciform species (Koumoundouros et al. 2009, Leis et al. 2012a, Baptista et al. 2019), pleuronectiform species (Faria et al. 2011, Silva et al. 2015), schooling species such as atherinids and clupeids (Faria et al. 2014, Silva et al. 2014, Moyano et al. 2016) and gobiesocids (Faria & Gonçalves 2010). In general, Ucrit was found to increase in a linear manner with increasing size, but the rate of increase varied with species, generally being greater in tropical and warm-temperate perciform species than in species from other orders (Leis 2010, Leis et al. 2013; but for a different view, see Downie et al. 2020). This emphasizes the importance of the phylogeny and distribution of the species of interest in considerations of dispersal.

Critical speed can be useful in comparing relative swimming performance of different developmental stages or species. However, swimming flume design can influence the Ucrit measure (Tudorache et al. 2013). For example, flume dimensions (Tudorache et al. 2007) or whether the flume is covered or not (Shi et al. 2014) both affect the measured Ucrit. Therefore, it is essential that comparisons between Ucrit values be based on measurements with similar flume design, or at least with the different flume types cross-calibrated. Ucrit is also useful for the study of the effects of environmental factors such as parasites or temperature on physiological performance (Grutter et al. 2011, Moyano et al. 2016).

In contrast to Ucrit, *in situ* speed (ISS) is a field-based measure of swimming performance, in which larvae released in the sea are followed by divers who measure speed with a modified plankton-net flowmeter (Leis & Carson-Ewart 1997), swimming direction with a compass and depth with a depth gauge (Leis et al. 1996). In other words, the larvae select the speed at which they swim within their natural environment, which can be regarded as a measure of preferred speed, as advocated by some researchers (Tudorache et al. 2013). In larval coral-reef fishes, Fisher & Leis (2009) regarded ISS to be relevant for studies of long-distance migration, large-scale movements and foraging. As with Ucrit, most ISS data come from studies of wild settlement-stage larvae captured with light traps or crest nets (e.g. see Leis & Carson-Ewart 1997, Trnski 2002, Leis & Fisher 2006, Fisher & Leis 2009 for available data on ISS of settlement-stage larval reef fishes). *In situ* studies have the advantage of including other behavioural data, and, of particular relevance to swimming, information on orientation in the sea. However, if they cover only the last portion of the PLD, they are of limited relevance to studies of dispersal. Further, ISS data are logistically more difficult to obtain, particularly if water clarity in the study area is not high, and larvae are small. Although there are questions about the influence of the observer divers, these have been addressed (Leis & Carson-Ewart 1997, Leis 2006). Information on the ontogeny of ISS is limited, and all data are derived from warmer waters. The few studies on the ontogeny of ISS have been reviewed (Leis 2010). As with Ucrit, increase in ISS with increase in size is generally linear, with rates of increase variable among species, but with the rate of speed increase with size generally smaller and more variable than in Ucrit.

Another potential measure of swimming speed made *in situ* involves the use of the Drifting *In Situ* Chamber (DISC) (Paris et al. 2008, Irisson et al. 2009), a disc-shaped chamber of 38 cm diameter into which larvae can be placed and filmed to record their behaviour while the DISC drifts in the ocean. The DISC has been used primarily to study orientation, but it is also possible to record the swimming speed of the larvae in the DISC and use this metric in the context of dispersal, although there seem to be no published attempts to do so. Whether the swimming speeds of larvae in such a small chamber represent a valid indication of what unconstrained larvae are doing is questionable. Indeed, the developers of the DISC have written that the DISC 'may allow measurements of in situ swimming speeds of the earlier stages, when swimming behavior might not be affected by the enclosure' (Paris et al. 2008, p. 62), but 'it is obvious that larvae cannot maintain a sustained swim speed in a relatively small behavioral arena of 38 cm' (Paris et al. 2013a, p. 67).

Some researchers attempting to study dispersal or parameterize dispersal models have recognized the limitations of using Ucrit for these purposes, and have attempted to derive more relevant measures either from or independent of Ucrit data. Fisher & Leis (2009) estimated that ISS was probably equal to 20 to 50% of Ucrit in larval coral-reef fishes. Other methods include the entirely laboratory-based maximum sustainable speed (Fisher & Wilson 2004), ratios of ISS to Ucrit (Leis & Fisher 2006), or correlations of one measure against the other. The last is difficult to do directly, as it is rarely possible to measure both Ucrit and ISS in the same individual. If data on ontogeny of swimming are available, an alternative is to use speeds from each method from larvae pooled by size increments, and then calculate a Model II regression (Leis et al. 2009a,b, Leis 2010). For the 10 species where this was possible, only half had a significant linear relationship between the Ucrit and ISS. Even in the 5 species with a significant relationship, the ISS:Ucrit slope ranged from 0.26 to 2.28, with widely varying 95% CIs, indicating that there was not a simple 'one size fits all' relationship between the 2 swimming measures (Leis 2010). Assertions that in larvae, mean levels of Ucrit 'strongly correlate with other measures of swimming performance including…*in situ* swimming speed' (Nanninga & Manica 2018, p. 8), or that Ucrit is a 'realistic laboratory estimate of *in situ* swimming speed' that has been verified in the field or is an 'adaptable and transferable metric' (Rossi et al. 2019, p. 349), are somewhat overstated, either being based only on settlement-stage larvae or ignoring results such as those in the previous sentences. Most often, attempts at correlation of swimming performance between measures use mean values at either the species or a higher taxonomic level, thus underestimating the frequently large variation in swimming performance among individuals and species.

A sound comparison between Ucrit and ISS is best achieved by use of an ontogeny-based comparison that includes among-individual variation. The main obstacle to achieving this is the few species for which both swimming measures are available over a range of sizes.

A third measure of swimming performance relevant to dispersal is endurance (also termed, somewhat confusingly, 'sustained swimming perform-

ance'), wherein larvae placed in a laboratory flume are forced to swim at a constant speed without rest or food until exhaustion (Stobutzki & Bellwood 1997). Endurance values are typically reported as equivalent distance swum (= flow speed × time to exhaustion), and these are very high (10s of km). Indeed, endurance runs take so long to complete that there are relatively few endurance values in the literature (summarized for settlement-stage larvae by Stobutzki & Bellwood 1994, 1997, Stobutzki 1998, Leis & Stobutzki 1999, and from an ontogenetic perspective by Leis 2010, Majoris et al. 2019). Although not directly useful in parameterizing dispersal models (but see Downie et al. 2020), measurement of endurance is important in providing some indication of how long larvae might be able to swim at empirically determined Ucrit or ISS, which are measured over only brief periods (i.e. minutes) in the laboratory or field, respectively. Larvae in the ocean are unlikely to swim at a fixed speed until exhaustion. Further, endurance experiments wherein the flume flow is stopped for brief periods 2 or 4 times per day and larvae are provided with planktonic food demonstrate that in such conditions, larvae continue to swim for greatly increased periods, and that they grow and begin to metamorphose (Fisher & Bellwood 2001, Leis & Clark 2005, Faria et al. 2011). Endurance values are inversely proportional to the swimming speed (Fisher & Bellwood 2002), which is further indication that larvae are able to maintain speeds that are meaningful in the context of dispersal for major portions of their PLD.

A fourth measure of swimming, i.e. routine speed, is a laboratory measure that returns very low estimates of swim speed. Routine speed is of most relevance to studies of foraging (Leis 2006, Fisher & Leis 2009), but can also be used to evaluate when larvae may emerge from a viscous hydrodynamic environment (low Reynolds number) into a more sustainable inertial environment (high Reynolds number). This is useful in attempting to estimate when swimming of sufficient speed and endurance to be relevant to dispersal can be expected.

When during ontogeny do the impressive swimming abilities shown by these methods of measuring swimming performance come into play? Work on the ontogeny of swimming endurance shows that smaller larvae, particularly those that have not yet formed a caudal fin, have very limited endurance (Leis 2010). This is probably because they are operating in a viscous hydrodynamic environment, and swimming more slowly would only aggravate this situation (Leis 2006). Similarly, Ucrit values for larvae before caudal-fin formation are very low, indicating that even in a forced swimming situation, these small larvae are swimming in a viscous hydrodynamic environment. There are very few data on ISS of larvae before caudal-fin formation because small larvae are very difficult to follow in the ocean, but the available values indicate that these preflexion larvae would also be operating in a viscous environment.

The objective of the present study was to compare the 2 measures of swimming performance that are most relevant to dispersal of marine fish larvae (Ucrit and ISS), and to do this in an ontogenetic context. A prime goal was to determine whether there is a strong relationship between the 2 measures, as has been generally assumed. In other words, is there a 'one size fits all' way to use Ucrit to predict ISS, regardless of species? This was done by calculating the relationship of speed to size for both Ucrit and ISS over common size ranges for each species, and testing for differences in regression statistics. Finally, for each of 10 species tested, equations were derived from the regressions that allow prediction of ISS from Ucrit, and these 10 different equations are contrasted.

2. METHODS

Data on swimming speed in larval fishes were required for species in which ontogeny of both Ucrit and ISS were available over a common size range of several mm. These were obtained from 7 previously published studies for 10 species in 8 families of warm-temperate and tropical, marine, western Pacific fishes, and consisted of 469 Ucrit measurements and 277 ISS measurements (Table 1). For 9 species, the number of measurements for both Ucrit and ISS was at least 14, ranging up to at least 44 for both; for *Platax teira*, only 11 ISS measurements were available over the common size range, and this small number increased the possibility of type II error in the regression analysis for this species. The study species belong to families traditionally classified as members of the Perciformes, and are demersal as adults (with the possible exception of *Caranx ignobilis*, which, although a member of a family that is normally considered pelagic, is closely associated with coastal habitats, including estuaries and coral reefs). Adults range from small to medium in size, and are of commercial value both in wild fisheries and in culture. All spawn pelagic eggs. Although Ucrit data on larvae too small to be measured *in situ* were available for most species, Ucrit data on these

Table 1. Sources for larval fish swim speed data used in the present study, the water temperatures at which measurements were made and the settlement habitats. Ucrit: critical speed; ISS: *in situ* speed; WTEC: warm, temperate, estuarine, coastal; TR: tropical reef; TNR: tropical, non-reef. Note that *Chrysophrys auratus* is frequently referred to as *Pagrus auratus* in the scientific literature

Species - Family	Ucrit source (temperature, °C)	ISS source (temperature, °C)	Habitat
Acanthopagrus australis - Sparidae	Clark et al. (2005) (19–24°)	Leis et al. (2006b) (19–20°)	WTEC
Argyrosomus japonicus - Sciaenidae	Clark et al. (2005) (19–24°)	Leis et al. (2006b) (20–24°)	WTEC
Caranx ignobilis - Carangidae	Leis et al. (2006a) (27–29°)	Leis et al. (2006a) (26–29°)	TR
Chrysophrys auratus - Sparidae	Clark et al. (2005) (19–24°)	Leis et al. (2006b) (20–24°)	WTEC
Eleutheronema tetradactylum - Polynemidae	Leis et al. (2007) (27–29°)	Leis et al. (2009b) (26–29°)	TNR
Epinephelus coioides - Serranidae	Leis et al. (2007) (27–31°)	Leis et al. (2009a) (26–29°)	TR
Epinephelus fuscoguttatus - Serranidae	Leis et al. (2007) (27–31°)	Leis et al. (2009a) (26–29°)	TR
Leiognathus equulus - Leiognathidae	Leis et al. (2007) (27–29°)	Leis et al. (2009b) (26–29°)	TNR
Lutjanus malabaricus - Lutjanidae	Leis et al. (2007) (27–31°)	Leis et al. (2009a) (26–29°)	TR
Platax teira - Ephippidae	Leis et al. (2007) (27–31°)	Leis et al. (2009a) (26–29°)	TR

small larvae were not used so as to maintain a common size range with ISS data within each species. In 8 species, the smallest individuals included were at the lower end of the post-flexion stage. Exceptions were *Epinephelus fuscoguttatus* and *Lutjanus malabaricus*, for which smaller larvae were not available at the time of the ISS study. In all of the study species, except *P. teira*, the largest larvae included were at or near size at settlement. The major limitation to the inclusion of species was the relatively small number of ISS ontogeny studies of larval stages.

All Ucrit measurements were taken using the 6-lane, covered swimming chamber design developed by Stobutzki & Bellwood (1997), so they are directly comparable. All ISS measurements were taken by the same research team. Reared larvae from aquaculture suppliers were obtained, and for each species, the supplier was the same for both Ucrit and ISS. More details are provided in the original publications cited in Table 1. For each species, water temperatures at which Ucrit and ISS were measured were similar (Table 1).

For each species, linear regressions of Ucrit and of ISS against size (standard length) over the size range common to both measures were calculated (Zaiontz 2019), and the correlation coefficients and slopes of the regressions were compared (Wuensch 2019). For each species, the Ucrit on size regression equation was solved for size, and then substituted into the ISS on size regression equation and used to derive an equation to predict ISS from Ucrit. These resulting equations were used to examine whether there was a constant ratio of Ucrit to ISS, and whether the common assumption that ISS = *X*% of Ucrit was justified.

3. RESULTS

The ontogeny of Ucrit and ISS varied considerably among the 10 species examined (Fig. 1, Table 2). All 10 species had a significant increase in Ucrit with size, the slopes of which ranged from 1.3 to 3.6 cm s^{-1} per 1 mm increase in size (Fig. 1, Table 2). Seven of 10 species had a significant increase in ISS with size, with slopes ranging from 0.3 to 2.5 cm s^{-1} per 1 mm increase in size (Fig. 1, Table 2). The mean slope of the Ucrit relationship was greater than that of the ISS relationship in 8 species, with the difference being significant in 6 species (Table 3); *Epinephelus fuscoguttatus* and *Chrysophrys auratus* lacked significant differences. The remaining species, *Leiognathus equulus* and *Platax teira*, had mean ISS slopes greater than Ucrit, but the differences were not significant (Table 3). Only in *L. equulus* was the correlation coefficient (r) significantly greater for ISS than for Ucrit, whereas in 6 species, r of Ucrit was significantly greater than r of ISS (Table 3). Three species lacked a significant difference in r between Ucrit and ISS: *C. auratus*, *E. fuscoguttatus* and *P. teira*. The fact that the majority of species had a significantly greater r between size and speed for Ucrit than for ISS (Table 3) indicates that, in general, there is more variability in the relationship between size and ISS than in the Ucrit relationship.

The 3 species that lacked a significant increase in ISS with size were *Lutjanus malabaricus, Caranx ignobilis* and *P. teira* (Fig. 1A–C). These 3 had a reasonably strong increase in Ucrit with size, with Ucrit and ISS values overlapping broadly in smaller larvae, but diverging with size in the first 2 and overlapping throughout the size range in *P. teira*.

One species, *L. equulus*, had broadly overlapping Ucrit and ISS values (Fig. 1D), but although the ISS slope was double that of the Ucrit slope, the difference was not significant. Both Ucrit and ISS increased significantly with size, but the ISS relationship explained more of the variation than did the Ucrit relationship (R^2 = 0.63 vs. 0.15), which was unique.

The Ucrit slope was 2 to 3 times greater than the ISS slope in *Acanthopagrus australis, Epinephelus coioides, Argyrosomus japonicus* and *Eleutheronema tetradactylum* (Fig. 1E–H). In all 4 species, the Ucrit

Fig. 1. Comparisons of swim speed ontogeny over a common size range within each species as measured by critical speed (Ucrit, blue diamonds) and *in situ* speed (ISS, red squares) in larvae of 10 species of western Pacific marine fishes. Data are from studies listed in Table 1. All figures are plotted at the same scale to facilitate comparisons. A broken regression line indicates that the slope is not significantly different from zero. SL: standard length. (A) *Lutjanus malabaricus* (Lutjanidae), (B) *Caranx ignobilis* (Carangidae), (C) *Platax teira* (Ephippidae), (D) *Leiognathus equulus* (Leiognathidae), (E) *Epinephelus coioides* (Serranidae), (F) *Acanthopagrus australis* (Sparidae), (G) *Argyrosomus japonicus* (Sciaenidae), (H) *Eleutheronema tetradactylum* (Polynemidae), (I) *Epinephelus fuscoguttatus* (Serranidae), (J) *Chrysophrys auratus* (Sparidae)

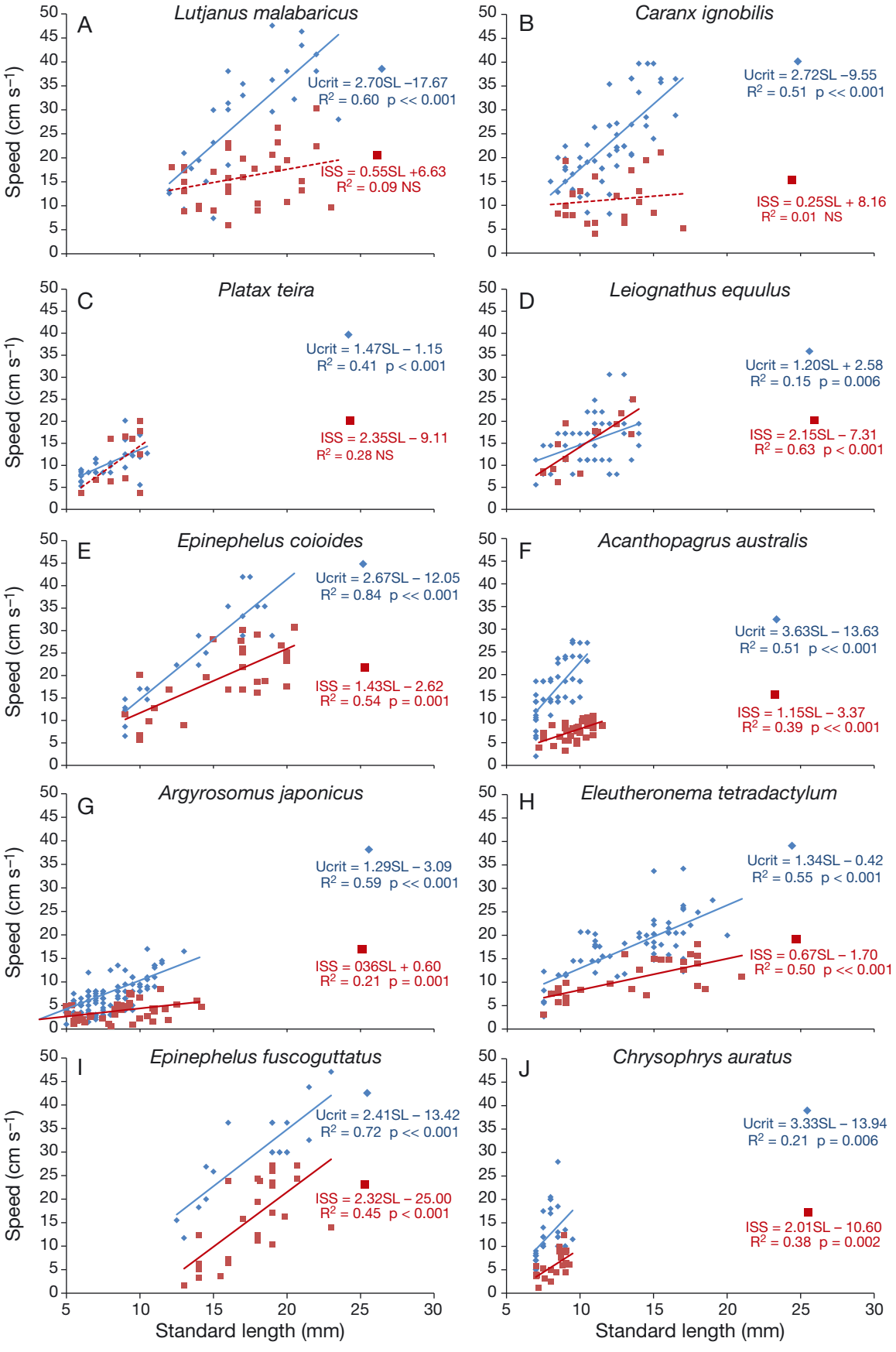
Table 2. Regression statistics for ontogeny of critical speed (Ucrit) and *in situ* speed (ISS) for the 10 study species. SL: standard length; NS: not significant (p > 0.05). Size at settlement is derived from references cited in Table 1; na: not applicable

Species	Size range [settlement size] (mm SL)	Ucrit slope (95% CI) [n]	p [R^2]	ISS slope (95% CI) [n]	p [R^2]
Acanthopagrus australis	7.0–12.0 [10–12]	3.63 (2.61–4.66) [48]	1.31×10^{-8} [0.51]	1.15 (0.65–1.66) [41]	6.8×10^{-6} [0.34]
Argyrosomus japonicus	5.0–14.2 [12–13]	1.29 (1.10–1.48) [124]	2.3×10^{-25} [0.59]	0.36 (0.18–0.54) [48]	0.001 [0.21]
Caranx ignobilis	8.0–17.0 [na][a]	2.71 (1.98–3.45) [54]	1×10^{-9} [0.51]	0.25 (–0.67–1.17) [22]	0.57 NS [0.02]
Chrysophrys auratus	7.0–9.5 [10–15]	3.33 (1.02–5.63) [34]	0.006 [0.21]	2.01 (0.82–3.19) [23]	0.002 [0.37]
Eleutheronema tetradactylum	7.5–21.0 [ca. 20]	1.34 (1.04–1.64) [67]	8.7×10^{-13} [0.55]	0.67 (0.40–0.93) [28]	2.5×10^{-5} [0.5]
Epinephelus coioides	9.0–20.0 [20–24]	2.67 (2.10–3.24) [20]	1.1×10^{-8} [0.84]	1.43 (0.91–1.95) [29]	6.1×10^{-6} [0.53]
Epinephelus fuscoguttatus	13.0–27.0 [20–24]	2.41 (1.69–3.13) [19]	5.09×10^{-6} [0.72]	2.32 (1.25–3.40) [26]	0.0002 [0.45]
Leiognathus equulus	7.5–13.5 [13–15]	1.20 (0.45–2.32) [49]	0.006 [0.15]	2.15 (1.12–3.17) [14]	0.0007 [0.63]
Lutjanus malabaricus	12.0–23.5 [25]	2.70 (1.80–3.60) [27]	1.9×10^{-6} [0.59]	0.55 (–0.11–1.21) [32]	0.10 NS [0.09]
Platax teira	6.0–10.5 [30]	1.47 (0.79–2.16) [30]	0.0001 [0.41]	2.35 (–0.50–5.20) [11]	0.09 NS [0.28]

[a]*Caranx ignobilis* is a neritic, pelagic species that does not settle

Table 3. Two-tailed tests of critical speed (Ucrit) vs. *in situ* speed (ISS) correlation coefficients (r) and regression slopes, and also equations to predict ISS from Ucrit derived from the 2 regression equations in Table 2 for each species. Tests of r using Fisher's *Z*. Tests of slope using *Z*-test for slopes. NS: not significant; ND: not significantly different

Species	Correlation coefficient (r) test *Z* (p)	Test results for r	Slope test, *Z* (p)	Test results for slope	Prediction of ISS from Ucrit
Acanthopagrus australis	1.00 (>0.20 NS)	Ucrit ND ISS	4.36 (<0.001)	Ucrit > ISS	ISS = 0.32Ucrit + 0.99
Argyrosomus japonicus	3.01 (<0.01)	Ucrit > ISS	7.07 (<0.001)	Ucrit > ISS	ISS = 0.28Ucrit + 1.27
Caranx ignobilis	2.88 (<0.01)	Ucrit > ISS	4.23 (<0.001)	Ucrit > ISS	ISS = 0.09Ucrit + 9.02
Chrysophrys auratus	0.74 (>0.20 NS)	ISS ND Ucrit	1.07 (>0.10 NS)	Ucrit ND ISS	ISS = 0.60Ucrit – 2.19
Eleutheronema tetradactylum	0.29 (>0.10 NS)	Ucrit ND ISS	3.30 (<0.001)	Ucrit > ISS	ISS = 0.50Ucrit + 1.91
Epinephelus coioides	2.08 (<0.05)	Ucrit > ISS	3.19 (<0.01)	Ucrit > ISS	ISS = 0.54Ucrit – 3.89
Epinephelus fuscoguttatus	2.31 (<0.03)	Ucrit > ISS	0.12 (>0.20 NS)	Ucrit ND ISS	ISS = 0.96Ucrit – 12.08
Leiognathus equulus	2.02 (<0.05)	ISS > Ucrit	1.78 (>0.07 NS)	ISS ND Ucrit	ISS = 1.79Ucrit – 11.92
Lutjanus malabaricus	2.64 (<0.01)	Ucrit > ISS	3.76 (<0.001)	Ucrit > ISS	ISS = 0.20Ucrit + 10.22
Platax teira	0.42 (>0.20 NS)	Ucrit ND ISS	0.88 (>0.20 NS)	ISS ND Ucrit	ISS = 1.60Ucrit – 7.27


A
Lutjanus malabaricus
Ucrit = 2.70SL –17.67
R² = 0.60 p << 0.001
ISS = 0.55SL +6.63
R² = 0.09 NS
B
Caranx ignobilis
Ucrit = 2.72SL –9.55
R² = 0.51 p << 0.001
ISS = 0.25SL + 8.16
R² = 0.01 NS
C
Platax teira
Ucrit = 1.47SL – 1.15
R² = 0.41 p < 0.001
ISS = 2.35SL – 9.11
R² = 0.28 NS
D
Leiognathus equulus
Ucrit = 1.20SL + 2.58
R² = 0.15 p = 0.006
ISS = 2.15SL – 7.31
R² = 0.63 p < 0.001
E
Epinephelus coioides
Ucrit = 2.67SL – 12.05
R² = 0.84 p << 0.001
ISS = 1.43SL – 2.62
R² = 0.54 p = 0.001
F
Acanthopagrus australis
Ucrit = 3.63SL – 13.63
R² = 0.51 p << 0.001
ISS = 1.15SL – 3.37
R² = 0.39 p << 0.001
G
Argyrosomus japonicus
Ucrit = 1.29SL – 3.09
R² = 0.59 p << 0.001
ISS = 036SL + 0.60
R² = 0.21 p = 0.001
H
Eleutheronema tetradactylum
Ucrit = 1.34SL – 0.42
R² = 0.55 p < 0.001
ISS = 0.67SL – 1.70
R² = 0.50 p << 0.001
I
Epinephelus fuscoguttatus
Ucrit = 2.41SL – 13.42
R² = 0.72 p << 0.001
ISS = 2.32SL – 25.00
R² = 0.45 p < 0.001
J
Chrysophrys auratus
Ucrit = 3.33SL – 13.94
R² = 0.21 p = 0.006
ISS = 2.01SL – 10.60
R² = 0.38 p = 0.002
Speed (cm s⁻¹)
Standard length (mm)

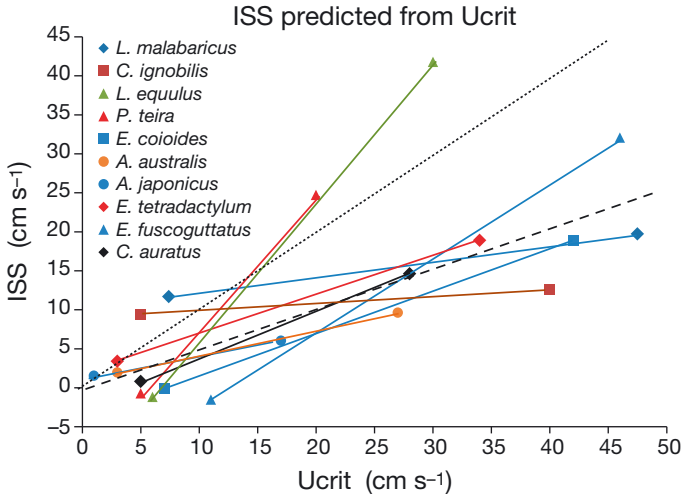


Fig. 2. *In situ* speed (ISS) predicted from critical speed (Ucrit) using the equations in Table 3. Symbols at the ends of each line represent the predicted ISS values for the slowest and fastest Ucrit values for each species over the size ranges considered in the present study. The dotted black line represents Ucrit = ISS, and the dashed black line is 50% Ucrit = ISS

relationship explained more of the variation in speed than did the ISS relationship (with the Ucrit R^2 up to 3 times the ISS R^2).

Two species, i.e. *Epinephelus fuscoguttatus* and *C. auratus*, had similar Ucrit and ISS slopes, but with Ucrit values about 12 and 3 cm s^{-1} greater than ISS, respectively (Fig. 1I,J). There was much less variation in the *E. fuscoguttatus* Ucrit and ISS relationships than in *C. auratus.*

For each species, the differences between the Ucrit and ISS relationships indicate that the ratios of the 2 measures differed ontogenetically: in other words, no single ratio applied overall. For example, within species there was a 4 to 36% difference in the Ucrit:ISS value between the largest larvae (usually settlement stage) and larvae in the middle of the common size range.

Although most species showed significant relationships between speed and size for both Ucrit and ISS, speed at any size varied considerably, particularly for ISS. Of the larvae considered here, all but a few small, slow individuals swam outside a viscous hydrodynamic environment.

The regressions in Table 2 were used to derive equations that enable ISS to be predicted from Ucrit for each species (Table 3, last column). These equations vary considerably among species. The lines resulting from these predicted ISS values over the range of measured Ucrit values are shown in Fig. 2. Five species (*A. australis*, *A. japonicus*, *C. auratus*, *E. tetradactylum* and *E. coioides*) are close to paralleling the ISS = 50% Ucrit line, although the first 3 cross it, whereas the last 2 remain a few cm s^{-1} either above or below it. In 3 species (*E. fuscoguttatus*, *L. equulus* and *P. teira*), predicted ISS increases at a greater rate than 50% Ucrit, so larvae at the slower end of the Ucrit range have ISS less than 50% Ucrit, whereas in larval *E. fuscoguttatus* with Ucrit greater than about 27 cm s^{-1}, ISS is predicted to be greater than 50% Ucrit, and in *L. equulus* and *P. teira* with Ucrit greater than about 14 cm s^{-1}, predicted ISS is greater than Ucrit itself. Finally, in *C. ignobilis* and *L. malabaricus,* ISS increases at a slower rate than 50% Ucrit, so larvae with slower Ucrit have ISS that is greater than Ucrit, but at higher Ucrit speeds, the ISS is less than 50% Ucrit. Therefore, depending on the species and the Ucrit, ISS values predicted from Ucrit can range from much greater than Ucrit to much less, and in some cases, even negative ISS values are predicted.

4. DISCUSSION

Accurate predictions of where larvae travel during their pelagic dispersal stage are essential for understanding the ecology and evolution of populations and species of marine fishes, and for informed planning for their conservation and sustainable exploitation (e.g. Kough et al. 2013, Andrello et al. 2015). Coupled biological–oceanographic models are increasingly used to explore larval dispersal for these purposes (Swearer et al. 2019). Many developers of these models now recognize that dispersal of fish larvae is not passive, and that including behaviour of the larvae can make a major difference to the dispersal predictions of their models (Paris et al. 2013b, Faillettaz et al. 2018b). However, including incorrect behaviour in a model may result in predictions of dispersal that are worse than not including behaviour at all (Bode et al. 2019). Horizontal swimming by larvae has the potential to greatly and directly influence dispersal outcomes, but there are several ways of measuring swimming performance, and it varies among species and ontogenetically (Fisher & Leis 2009), thus making it a challenge to incorporate swimming into models appropriately. The present study comparing the 2 swimming measures most relevant to larval dispersal, Ucrit and ISS, in an ontogenetic context leads to several conclusions.

First, it is important to reiterate what Ucrit and ISS represent, and how the 2 measures are related (or not). Critical speed is an estimate of what larvae are capable of doing, based on forced swimming in the laboratory, whereas ISS is an estimate of what larvae

elect to do in the ocean, measured in the ocean, and the difference between the 2 varies with species. The present analysis shows that Ucrit vs. ISS relationships are not consistent: they vary among species and within families. Predicting ISS from Ucrit is not straightforward, and the 2 measures are not correlated in many species. Ratios of Ucrit to ISS are not consistent ontogenetically, and because the slope of the Ucrit vs. size relationship is greater than that of the ISS vs. size relationship in most species, overall, the ISS to Ucrit ratio vs. size is not constant, and often not linear. In species where the relationships between speed and size are known for both Ucrit and ISS, it is, of course, possible to predict ISS from Ucrit, as has been done here, but if only Ucrit data are available, accurate prediction of ISS is unlikely to be possible without more information.

It is commonly assumed that 50% of Ucrit provides a valid swimming speed for dispersal studies and modelling (e.g. Faillettaz et al. 2018b, Rossi et al. 2019). This assumption originates from early swimming studies on settlement-stage larvae of relatively few taxa, which produced a 50% conversion (Leis & Fisher 2006, Fisher & Leis 2009), and probably also the conclusion of Fisher & Wilson (2004) that their rather arbitrary 'maximum sustainable speed' is approximated by 50% Ucrit. However, this ignores the substantial among-individual and among-species variation associated with Ucrit, and the caveats of those studies (Fisher & Wilson 2004, Leis & Fisher 2006, Fisher & Leis 2009). For example: '[…] around 50% of […] Ucrit values provides an *upper limit* to the speeds likely to be used by larvae to influence dispersal patterns on relatively large scales' (Fisher & Leis 2009, p. 363) (emphasis added). Even the first publication to attempt a comparison of Ucrit to ISS in larval fishes noted that Ucrit was 3 to 5 times the ISS, although that result was based on only 3 species, with individuals at the settlement stage (Leis & Carson-Ewart 1997).

More recent attempts to find conversion factors between Ucrit and ISS based on larvae of a range of sizes produced varying values depending on family and habitat, and noted that 'the relationship between critical speed and in situ speed may differ between environments, temperatures, or taxa, and that tropical species may swim closer to their potential speed (i.e. Ucrit) in the ocean than do temperate species' and 'the wide range of values among individual species and within families suggests that caution should be applied when using the central value to predict in situ speed in taxa for which no data on in situ speed are available' (Leis 2010, p. 331).

The difference in variability between the speed at size relationships for Ucrit and ISS shown here is another obstacle for successful conversion between the 2 measures. Valid considerations of the effects of behaviour of larvae, including swimming, must include variability of the behaviour to avoid unrealistically constraining dispersal outcomes (Leis 2007, Bode et al. 2019). It should not be surprising that Ucrit speed at size is less variable, as it is a forced measure, in a laboratory flume, wherein larvae have little latitude to engage in other behaviours such as feeding or orientation. In contrast, when free to swim in the ocean, as is the case with ISS, larvae are subject to various sensory signals, and can engage in a range of behaviours that may slow or otherwise divert them from swimming rapidly or in a straight course. Measurements of ISS in open water include feeding behaviour by larvae, manoeuvring around clumps of marine snow, salps or jellies, stop-and-go swimming for no apparent reason and changes in depth and direction (Leis & Carson-Ewart 1997, 2003). Near settlement habitat such as reefs or seagrass beds, swimming becomes more complex, with changes in direction, including stops and returns to open water, alterations of depth and speed, reactions to potential predators and inspection and rejection of potential settlement sites before settling (Leis & Carson-Ewart 1998, 1999, 2002, Trnski 2002).

Although ISS is more difficult and time-consuming to measure than Ucrit, it is the best available measure of what larvae actually do in the ocean, and the method of measuring it also provides a measure of the variability in speed, orientation and depth selection that is necessary to understand larval dispersal and to model it. In contrast, Ucrit is a quick and easy measure of swimming capacity, and is less variable than ISS, but there is no straightforward way to convert it into a meaningful measure of swimming in the ocean, and it provides no information on other behaviours in the ocean. Even if ISS data are available, information on within-individual precision of swimming orientation is necessary to determine straight line speed through the water in the mean direction of travel (Leis 2007) if such a measure is desired for modelling or other purposes.

If only Ucrit data are available, and the acquisition of ISS is unlikely to be possible, researchers must proceed cautiously in obtaining a realistic measure of swimming ontogeny for their study species (Downie et al. 2020). Some possibilities should be explored. Swimming ontogeny measurement using the ISS methodology (Leis & Carson-Ewart 1997) could be tried in large mesocosms. The morphology-based modelling

approach of Fisher & Hogan (2007), which was developed only for settlement-stage larvae, might be able to be adapted to apply across the full post-flexion ontogeny. Ultimately, more data on ISS ontogeny for a wider variety of species and habitats are required to give a broader perspective on swimming abilities of fish larvae in the ocean to help us understand larval dispersal better and model it more accurately.

The exercise of deriving a formula for predicting ISS from a Ucrit value has limitations, and was engaged in here primarily for illustrative purposes (Fig. 2). The resulting equations are not necessarily recommended for use in modelling because they are species-specific and only apply over the limited size range used to derive them. Also, the fact that the result is a size-free equation, but is derived from regressions of speed on size, means that extending this approach to other species requires data on the ontogeny of Ucrit, information that is still only available for few species. Regardless of these limitations, applying the equations to hypothetical examples can be useful in examining the influence of using Ucrit (or some fixed percentage of it) instead of ISS for applications such as dispersal modelling. In the case of the 10 species studied here, depending on the species and its Ucrit, the ISS predicted from Ucrit can be as much as ca. 130% Ucrit (*Leiognathus equulus*) to predicted ISS values that are negative (*Epinephelus* spp.), with the predicted Ucrit percentages varying with ontogeny (Fig. 2).

An example of how using Ucrit vs. ISS will lead to very different results both within and among species can be demonstrated with 3 species using the equations for predicting ISS from Ucrit in Table 3. This assumes a situation where larvae of each of 3 species had a Ucrit of 10 or 30 cm s^{-1}, i.e. speeds that were achieved by each species (Fig. 1), and swam for 1 h. At Ucrit speed, distances swum would be 360 m for 10 cm s^{-1} and 1080 m for 30 cm s^{-1}. The common practice of assuming ISS equals 50% Ucrit would give 180 m and 540 m, respectively. An average *Acanthopagrus australis* larva with Ucrit of 10 cm s^{-1} would swim only 151 m at the predicted ISS for 1 h, and if it had a Ucrit of 30 cm s^{-1}, it would swim 381 m at the predicted ISS. The same values for *Epinephelus coioides* are 54 and 443 m, respectively, and for *L. equulus,* 215 and 1504 m, respectively. This set of examples raises 2 points: (1) no species had swum distances similar to a assumed constant value of 50% Ucrit, and (2) in all 3 species, the predicted swim distance did not increase in proportion to the increase in Ucrit from 10 to 30 cm s^{-1}. However, it must be reemphasized that the equations for predicting ISS from Ucrit are not valid outside the size range of the larvae tested (see Table 2).

The large species-specific differences between the Ucrit:standard length (SL) and ISS:SL relationships invite speculation about their origins. Most likely, much of this variation arises from differences among species in their morphological development and in their larval or adult habitats. For example, some species settle at about 10 mm, whereas others settle at 20+ mm (Table 2). Some species have direct development, with few morphological specializations to pelagic life (e.g. sparids, sciaenids), whereas others have many such specializations (e.g. serranids, lutjanids, ephippids). *Epinephelus* spp. settle at a large size, and are among the fastest settlement-stage larvae studied here, but are poor swimmers until they are nearly the same size as settlement-stage sparids and sciaenids. This is probably due to the very large spines of the dorsal and pelvic fins of *Epinephelus* species, which can be longer than their SL in smaller larvae (Baldwin et al. 2000). Three of the species studied here are temperate (Table 1), and their larvae are found over the continental shelf, but settle into estuaries. Two species are tropical, and spend their larval phase over, and settle onto, the shelf. Four are tropical, and settle onto reefs. The carangid is tropical, pelagic, and found in a variety of habitats following its larval phase, whereas adults are reef-associated. Different swimming abilities are required to survive in the ontogenetically changing habitats of larvae and settlers. For example, entering an estuary may be facilitated by selective tidal stream transport (Teodósio et al. 2016), and therefore might not require the same swimming abilities that were used to actually reach the vicinity of the estuary mouth. Reaching a reef-edge from rather large distances requires different swimming and sensory abilities than negotiating the 'wall of mouths' of the reef-residents and finding appropriate settlement microhabitat. One can imagine interactions between phylogeny, biogeography, ecology and physiology that would lead to differences among species in larval swimming abilities, and between 2 ways of measuring them, particularly as these differ in just what aspects of swimming they measure. Ucrit is a short-term, forced measure that includes both aerobic and anaerobic aspects of swimming (Tudorache et al. 2013), whereas ISS is a longer-term, volitional measure that probably measures aerobic swimming primarily, if not exclusively. Finally, the senses used by larvae to orientate while pelagic and to find settlement habitat can differ, both ontogenetically and among species (Leis et al. 2011b), and this will probably influence swimming speeds in the ocean (i.e. ISS).

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