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Ontogeny of larval swimming abilities in three species of coral reef fishes and a hypothesis for their impact on the spatial scale of dispersal

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Abstract

The late-stage larvae of many reef fishes possess strong swimming abilities that may allow them to influence their dispersal. However, due to the challenges associated with directly measuring patterns of larval dispersal, determining how swimming abilities relate to dispersal outcomes remains a critical gap in our knowledge of the mechanisms that shape dispersal patterns. In this study, we first investigated the ontogeny of swimming speed and endurance in lab-reared larvae of the clown anemonefish (*Amphiprion percula*), and neon gobies (*Elacatinus lori* and *E. colini*). In general, the swimming speed and endurance of larvae improved with age. The congeners, *E. lori* and *E. colini*, possessed similar swimming speed and endurance, while *A. percula* was capable of swimming nearly twice as fast and 322 times longer than either *Elacatinus*. Second, to relate swimming abilities and other larval traits with patterns of dispersal, we searched the literature for all species in which the dispersal kernel, swimming speed, larval body size and pelagic larval duration have been measured. We found complete datasets for three species: *A. percula*, *E. lori* and *Plectropomus leopardus*. For these species, maximum swimming speed was a better predictor of long-distance dispersal than other larval traits. Thus, we propose the testable hypothesis that swimming abilities may play an important role in determining the extent of long-distance dispersal. Testing this hypothesis, and the alternatives, will require measuring the dispersal kernel, swimming speed, and other dispersal-related larval traits of multiple species in the same seascape.

Introduction

A major question at the interface of marine ecology and biological oceanography is: to what extent does larval behavior influence patterns of dispersal and population connectivity? The larvae of many marine organisms develop in the pelagic environment before settling on benthic habitat. Early efforts to model patterns of dispersal (i.e., the distribution of dispersal distances) using physical oceanographic data and pelagic larval duration (PLD) assumed that larvae drift passively with currents for 100s to 1000s of kilometers before settling (Roberts 1997). However, coupled biological–oceanographic models (from here on "biophysical" models) that integrate oceanographic data with larval swimming behavior predict that dispersal occurs over smaller spatial scales, just 10s to 100s of kilometers (Paris et al. 2005; Cowen et al. 2006; Faillettaz et al. 2018; Bode et al. 2019). The dispersal patterns predicted by biophysical models are more restricted than those predicted by purely physical models, suggesting that larval swimming abilities play an important role in determining the spatial scale of dispersal (Paris et al. 2005,

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2007; Cowen et al. 2006; Faillettaz et al. 2018; Bode et al. 2019). However, how swimming abilities relate to dispersal outcomes in nature remains a critical gap in our knowledge of the mechanisms that influence patterns of larval dispersal.

The swimming abilities of fish larvae are typically evaluated by measuring their speed and endurance in a swimming flume. Critical swimming speed (U_{crit}; from here on "swimming speed") measures the maximum flow velocity against which a larva maintains position in the flume, whereas swimming endurance tests the maximum duration that a larva swims against a fixed flow velocity and is often represented as the equivalent distance that the larva swam while in the flume. During flume trials, late-stage reef fish larvae often swim faster than the mean current speeds recorded around reefs, and the larvae of several species can swim continuously at moderate speeds for > 24 h with the potential to cover distances of up to 140 km (Stobutzki and Bellwood 1994, 1997; Stobutzki 1997, 1998; Fisher and Bellwood 2001, 2002; Fisher 2005). Some reef fish species develop these abilities shortly after hatching, suggesting that they may be able to influence their dispersal for the majority of their larval duration (Fisher et al. 2000; Fisher 2005; Leis et al. 2007, 2009; Leis 2010; Faria and Gonçalves 2010; Kashef et al. 2014).

Efforts to relate swimming abilities with the dispersal outcomes of larvae in situ have primarily focused on a larva's ability to offset horizontal displacement by currents (Stobutzki and Bellwood 1997; Fisher 2005). However, in addition to swimming against currents, larvae may use their swimming abilities to migrate vertically in the water column and may orient their movement with respect to environmental cues (Leis et al. 1996; Leis and Carson-Ewart 1999; Leis and Fisher 2006; Irisson et al. 2010; Mouritsen et al. 2013). These behaviors could retain larvae near their natal reef (Atema et al. 2002; Gerlach et al. 2007), or alternatively, they could disperse larvae over long distances. Indeed, a recent meta-analysis by Nanninga and Manica (2018) indicated that the swimming speed of late-stage reef fish larvae is negatively associated with genetic differentiation between populations, and by inference, swimming speeds may be positively associated with long-distance dispersal (LDD). A more direct test of this hypothesis would involve comparing larval swimming speeds, and other dispersal-related larval traits, to LDD inferred from dispersal kernels measured using genetic parentage analysis.

The first objective of this study was to investigate the ontogeny of swimming abilities in the larvae of two reef fishes for which genetic parentage techniques have been used to measure the pattern of larval dispersal: the clown anemonefish (*Amphiprion percula*) and the sponge-dwelling neon goby (*Elacatinus lori*). In both species, demersal embryos develop for 7–8 days before hatching at approximately 3–4 mm in notochord length. *Amphiprion percula* larvae spend 7–11 days developing in the plankton before settling to anemones at around 6–8 mm standard length (SL; Thresher et al. 1989; Almany et al. 2007), whereas *E. lori* spend 15–41 days developing before settling to sponges at around 8–9 mm SL (D'Aloia et al. 2015; Majoris et al. 2018). Considering PLDs alone, one might expect *E. lori* larvae to disperse farther than *A. percula* larvae (Shanks 2009). However, genetic parentage analyses have revealed that for both *A. percula* and *E. lori*, modal dispersal occurred within 0–1 km, and long-distance dispersal of *A. percula* was about six times farther than *E. lori* (D'Aloia et al. 2015; Almany et al. 2017). The second objective of this study was to relate the larval traits of these species, and data regarding the larval traits of other reef fishes gathered from the literature, with characteristics of the empirically measured dispersal kernel for each species.

Methods

Larval rearing for tests of swimming speed

We investigated the ontogeny of swimming speed and endurance in lab-reared *A. percula* and *E. lori* larvae at several ages from hatching through settlement. This is the first study to measure the swimming abilities of any member of the genus *Elacatinus*, so we included a third species, *Elacatinus colini*, to provide a congeneric comparison for *E. lori*. To investigate the ontogeny of swimming speed, larvae were obtained from breeding pairs of *A. percula*, *E. lori,* and *E. colini* in August 2014 through May 2015 and reared in separate tanks in a recirculating seawater system at Boston University (Boston, USA). Spawning shelters were checked each morning for clutches of eggs. For each species, clutches typically hatched 7–8 days after being observed in the spawning shelter. On the night prior to hatching an individual clutch was transferred to a black, cylindrical 76-L rearing bin. To oxygenate the eggs and stimulate hatching, a gentle stream of air was directed over the eggs using an air diffuser positioned underneath the clutch. Upon hatching, larvae were fed *HUFA*-enriched-rotifer *Brachionus rotundiformis* (15 rotifers ml^{-1}), decapsulated *Artemia* nauplii (3 *Artemia* ml^{-1}) and the water was tinted with *Nannochloropsis* algae paste (Rotigreen Nanno, Reed Mariculture, USA). The water quality of the rearing bins was maintained at a salinity of 33–35 ppt, with a temperature of 27–28 °C, pH of 8.0–8.3, NH_3 levels of 0–0.25 ppm, NO_2 levels of 0 ppm, and NO_3 levels of 0 ppm.

Larval rearing for tests of swimming endurance

To investigate the ontogeny of swimming endurance, *A. percula, E. lori*, and *E. colini* larvae were obtained from breeding pairs and reared in August 2014 through May 2015 at Boston University as described above. We also conducted swimming trials with *E. lori* and *E. colini* larvae in May through August 2015 at the International Zoological Expeditions (IZE) field station on South Water Caye, Belize (16°48′92″ N, 88°04′89″W). In brief, *E. colini* larvae were obtained from breeding pairs maintained in a flow-through seawater lab at IZE; *E. lori* larvae were collected by SCUBA divers on the day prior to hatching and transferred to the lab at IZE. Once established in rearing bins, larvae were cultured using enriched *B. rotundiformis* (15 rotifers ml^{-1}), decapsulated *Artemia* nauplii (3 *Artemia* ml^{-1}), wild-caught plankton, and *Nannochloropsis* algae paste. Water quality of the rearing bins was maintained at a salinity of 33–35 ppt, with a temperature of 27–29 °C, pH of 8.0–8.3, NH_3 levels of 0–0.25 ppm, NO_2 levels of 0 ppm, and NO_3 levels of 0 ppm. For additional details regarding rearing methods, see Majoris et al. (2018).

Swimming flume design

We tested the swimming speed and endurance of lab-reared *A. percula, E. lori* and *E. colini* in a single-channel swimming flume modified from the design by Stobutzki and Bellwood (1997). In this flume, the weir was removed from the outflow end and replaced with flow straighteners to improve laminar flow within the test chamber (Fig. 1). The flume was partially submerged in a water bath filled with saltwater that matched the temperature, salinity and pH of the rearing bin from which larvae were being sampled. The water velocity within the flume was regulated between 0.8 and 40 cm^{-s} using a submersible pump connected to a volumetrically calibrated flow meter (King Instruments, USA). Dye tests were conducted to verify unidirectional pipe flow was achieved along the length of the test chamber.

Larvae were sampled from rearing bins just prior to use in swimming trials and then introduced into the flume using a large-bore pipette. Recently hatched larvae were attracted toward overhead room lighting. To encourage young larvae to remain in the center of the water column and swim toward the front of the flume, the use of overhead lighting was minimized during trials and a circular bank of six LED lights was installed upstream from the in-flow straighteners.

Ontogeny of swimming speed

During preliminary rearing trials, *A. percula* larvae began settling to the bottom and side of the rearing bin at 8 dph (days post-hatch), while *E. lori* and *E. colini* began settling at 30 dph. Thus, to determine the effect of fish age on the swimming speed of larvae, we evaluated the swimming speed of *A. percula* at 0, 4, and 8 dph, and of *E. lori* and *E. colini* at 0, 10, 20, and 30 dph (Table 1). At the start of each trial, an individual larva was acclimated to the flume for 2 min with water flowing at a velocity of < 1 cm s^{-1}. If the larva displayed normal orientation and swimming behavior during acclimation, then the velocity was increased 2 cm s^{-1} every 2 min until the larva could no longer maintain position and was either expelled from the flume or collected on the downstream mesh. To determine the effect of fish size on swimming speed, larvae recollected following swimming trials were photographed using a dissection microscope, and photos were measured for total length (TL) using ImageJ (NIH, USA; Table 2). Due to difficulty re-collecting larvae

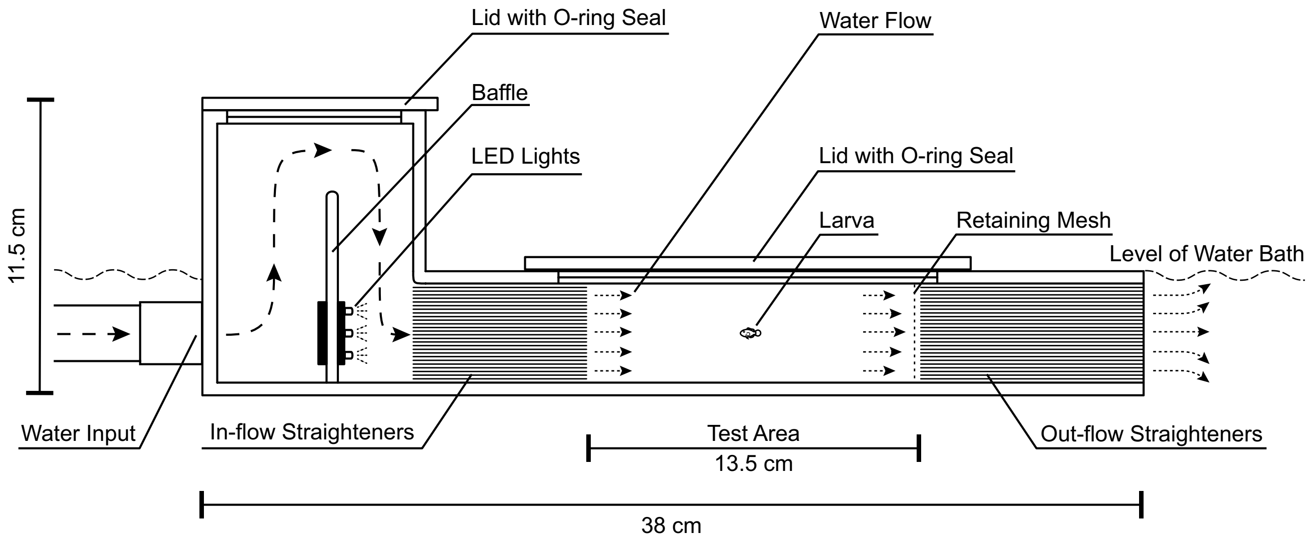

Fig. 1 Lateral view of a single-channel swimming flume used to test the swimming abilities of reef fish larvae, modified from the design used by Stobutzki and Bellwood (1997)

Table 1 Total number of individuals tested in swimming speed and endurance trials by age group and flow velocity for *Amphiprion percula*, *Elacatinus lori*, and *E. colini*

Age (dph)	Speed (*n*)	Endurance (*n*) by flow velocity (cm s^{-1})				
		2	4	6	8	10
A. percula						
0	10	6	6	6	6	6
	(2)	(2)	(2)	(2)	(2)	(1)
4	10	6	6	6	6	6
	(2)	(2)	(2)	(2)	(2)	(2)
8	10	1	4	5	–	7
	(2)	(1)	(2)	(1)		(2)
E. lori						
0	30	22	22	21	21	21
	(5)	(5)	(5)	(5)	(4)	(4)
10	25	20	20	20	20	20
	(4)	(9)	(10)	(11)	(10)	(7)
20	15	9	7	9	8	7
	(3)	(5)	(4)	(5)	(5)	(4)
30	10	11	11	11	11	11
	(3)	(2)	(2)	(2)	(2)	(2)
E. colini						
0	25	19	20	20	20	20
	(6)	(5)	(5)	(5)	(5)	(5)
10	20	19	19	19	19	19
	(5)	(7)	(7)	(7)	(6)	(7)
20	15	18	18	18	18	18
	(2)	(4)	(4)	(4)	(4)	(4)
30	15	15	17	17	17	17
	(2)	(5)	(5)	(5)	(5)	(5)

Numbers in parentheses indicate total number of clutches tested

following swimming trials, some size measurements were obtained by determining the mean TL of five siblings randomly sampled from the same clutch at the start of swimming trials. A larva's maximum swimming speed (U_{crit}) was then calculated following the equation from Brett (1964):

$$U_{\text{crit}} = U + \left(\frac{t}{t_i} \times U_i\right),$$

where U is equal to the penultimate speed, t is the time spent swimming at the final speed, t_i is the time increment (2 min), and U_i is the velocity increment in cm s^{-1}.

Ontogeny of swimming endurance

To determine the effect of ontogeny on the endurance of larvae between hatch and settlement, we evaluated the swimming duration of *A. percula*, *E. lori* and *E. colini* using the same ages of larvae and acclimation protocol as described above. Following acclimation, flow velocity was increased to a fixed setting of 2, 4, 6, 8 or 10 cm s^{-1} (Table 1). Swimming duration was recorded as the total time that a larva swam before being expelled from the flume or collected on the downstream mesh, minus the 2 min acclimation period. At slower flow velocities (2–4 cm s^{-1}), some larvae near settlement (i.e., *A. percula*: 8 dph; *Elacatinus* spp.: 30 dph) chose to rest on the bottom of the flume rather than swim in the water column and were, therefore, removed from the dataset.

Preliminary trials revealed that 8 dph *A. percula* larvae were capable of swimming continuously for several days. This extended swimming duration limited the number of trials that could be accomplished within the study period using single-channel swimming flumes. Therefore, to increase sample size, groups of three *A. percula* larvae were tested simultaneously in each endurance trial (Fisher and Bellwood 2002). Larvae were observed continuously for the first 12 h. After this observation period, cameras were used to observe the swimming behavior of the larvae and record the exact time when each trial ended. The larvae and cameras were checked twice daily, once in the morning and again in the evening. No behaviors were observed that suggested that swimming abilities of the larvae were influenced by the presence of the other fish. *Amphiprion percula* trials ended when the third larva stopped swimming and was collected on the

Table 2 Mean (± SE) and range of swimming speed, endurance, and the calculated equivalent swimming distance reported at hatch and settlement for *Amphiprion percula* (8 days post-hatch), *Elacatinus lori* and *E. colini* (30 days post-hatch)

	Swimming speed				Swimming endurance					
	Size (mm)		Speed (cm s^{-1})		Size (mm)		Duration (min)		Equivalent distance (m)	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Hatch										
A. percula	4.7 ± 0.03	4.5–4.8	6.2 ± 0.38	4.3–8.3	4.7 ± 0.02*	4.6–4.9*	9.4 ± 11.0	0.17–43.4	18.3 ± 14.7	1.0–52.5
E. lori	3.5 ± 0.03	3.3–3.7	2.7 ± 0.35	0.1–7.8	3.4 ± 0.07	3.0–3.8	1.1 ± 1.6	0.1–10.0	2.3 ± 2.0	0.2–12.0
E. colini	3.7 ± 0.06*	3.1–4.0*	4.1 ± 0.29	2.1–7.1	3.6 ± 0.05	3.2–3.8	1.5 ± 4.5	0.02–32.6	2.8 ± 5.6	0.1–39.1
Settlement										
A. percula	7.7 ± 0.13	6.9–8.3	15.8 ± 0.81	10.2–18.5	7.5 ± 0.13*	6.7–8.0*	5504 ± 5655	133–15,141	23,818 ± 25,375	638.4–64,116
E. lori	9.5 ± 0.31	8.4–10.9	7.2 ± 0.89	4.0–13.6	10.2 ± 0.23	7.7–11.6	17.1 ± 39.8	0.23–272.2	34.3 ± 55.5	1.1–326.7
E. colini	9.9 ± 0.15*	9.4–10.5*	8.6 ± 0.55	4.8–11.8	10.1 ± 0.13	7.9–11.9	13.2 ± 26.6	0.27–232.7	37.5 ± 45.6	1.6–279.2

Size measurements of larvae are provided for individuals used in swimming speed and endurance trials

*When size measurements were obtained from the mean of siblings sampled from the same clutch

downstream mesh. Measurements were obtained from larvae that completed swim trials or the mean of 5 siblings sampled randomly from the same rearing bin on the first day of trials (Table 2). Because larvae were not fed during trials, and most trials lasted < 24 h, we made the assumption that larvae did not grow significantly during trials.

Larval traits and observed patterns of dispersal

To determine the influence of larval traits on patterns of dispersal, we surveyed our colleagues and the published literature to locate reef fish species for which the pattern of dispersal had been measure directly using genetic parentage analyses and for which there were published values for dispersal-related larval traits: swimming speed, body size, and pelagic larval duration. Complete datasets were available for three species: *E. lori* (this study; D'Aloia et al. 2015), *A. percula* (this study; Almany et al. 2017), and the leopard coral-grouper *Plectropomus leopardus* (Fisher et al. 2005; Williamson et al. 2016). For consistency among species, we used only the population means reported for *A. percula* and *E. lori* rather than using the values for each year and location sampled (D'Aloia et al. 2015; Almany et al. 2017). Further, we excluded data for *Chaetodon vagabundus* because of the large confidence intervals around the fitted dispersal kernel (Almany et al. 2017) and the lack of published swimming speed data.

Statistical analyses

To investigate differences among species in the ontogeny of swimming abilities, we used analysis of covariance (ANCOVA) to determine whether the relationship between swimming abilities and age varied among species, with swimming speed or endurance as the response variable, and species and age as covariates. For analyses of swimming endurance, flow velocity was included as an additional covariate. ANCOVA's were also used to determine whether the relationship between swimming abilities and size varied among species.

To facilitate interspecific comparison, analyses were based on developmental age (O_{Age}) expressed as the ratio of an individual's age (Age) in dph and its expected age at settlement (Age_{set}; Fuiman et al. 1998; Fisher et al. 2000; Job and Bellwood 2000):

$$O_{\text{Age}} = \frac{\text{Age}}{\text{Age}_{\text{set}}} \times 100.$$

Age_{set} was estimated based on our observations of the onset of settlement in lab-reared larvae: 8 dph for *A. percula* and 30 dph for *E. lori* and *E. colini.*

Because total length measurements were obtained from either larvae that completed swim trials or the mean of five siblings sampled randomly from the same rearing bin, we used the mean swimming performance and mean total length of each clutch in analyses. The swimming durations of larvae reared in Boston were similar to those reared in Belize, so the data were pooled (SI Table 1). Also, the swimming durations of *A. percula* tested as individuals were no different from *A. percula* tested as trios, so the data were also pooled (SI Table 1). Finally, the equivalent distance swum by larvae during endurance trials was calculated by multiplying the swimming duration by the flow velocity during each trial (Stobutzki and Bellwood 1997).

To investigate the relationship between larval traits and empirically measured patterns of dispersal, we used the published dispersal kernel (i.e., probability density function) for each species to calculate modal, median (50th percentile) and long-distance dispersal (LDD, 99th percentile; Table 3). We then used simple linear regressions to relate these metrics of dispersal distance with the mean swimming speed, maximum swimming speed, body size, and pelagic larval duration of late-stage larvae gathered from the literature (Table 3).

The assumptions of all regression analyses were tested graphically using diagnostic plots. For analyses of swimming duration, the data were log-transformed to improve approximation to normality. The regression analyses were then back-transformed from the log-scale for use in swimming duration figures. All analyses were completed in R version 3.5.2 (R Core Team 2013).

Results

Ontogeny of swimming speed

At hatch, the mean swimming speed of larvae ranged from 2.7 cm s^{-1} for *E. lori* and 4.1 cm s^{-1} for *E. colini*, to 6.2 cm s^{-1} for *A. percula* (Table 2). This disparity continued through settlement, with the mean swimming speed of larvae ranging from 7.2 cm s^{-1} for *E. lori* and 8.6 cm s^{-1} for *E. colini* (30 dph), to 15.8 cm s^{-1} for *A. percula* (8 dph, Table 2). To determine the effect of ontogeny on larval swimming abilities, we tested the effect of age on swimming speed. An ANCOVA analysis revealed that there was an effect of developmental age ($F_{1,30} = 100.6$, $p < 0.0001$), species ($F_{2,30} = 30.9$, $p < 0.0001$) and their interaction (Developmental age * Species: $F_{2,30} = 5.5$, $p = 0.009$) on larval swimming speeds (Fig. 2). The main effects indicated that swimming speed increased with developmental age, and that *A. percula* swam faster than either *Elacatinus*. The two-way interaction indicated that the slope of the relationship between swimming speed and developmental age varied among species (Fig. 2). Post hoc tests showed that there was no significant difference in the slopes of the relationship of swimming speed and age between *E. lori* and *E. colini* ($p = 0.998$), but that swimming speed increased more rapidly with age in *A. percula* than either *Elacatinus* spp. ($p < 0.015$).

Similarly, we used an ANCOVA analysis to investigate the effect of larval size on swimming speed. We found that there was an effect of size ($F_{1,27} = 143.7$, $p < 0.0001$), species ($F_{2,27} = 136.1$, $p < 0.0001$), and their interaction (Size * Species: $F_{2,27} = 59.0$, $p < 0.0001$) on larval swimming speed (Fig. 3). The main effects indicated that swimming speed increased with size, and that *A. percula* swam faster than either *Elacatinus*. The two-way interaction indicated that the slope of the relationship between swimming speed and size varied among species. Post hoc tests indicated that there was no significant difference in the slopes of the relationship of size with swimming speed between *E. lori* and *E. colini* ($p = 0.887$), but that the swimming speed increased more rapidly in *A. percula* than either *Elacatinus* ($p < 0.0001$). Ultimately, the ANCOVA analysis including size as a covariate explained more of the variance in larval swimming speeds ($R^2 = 0.91$) than the model including

Table 3 Traits of late-stage larvae and estimates of modal, median (50th percentile) and long-distance dispersal (LDD, 99th percentile) derived by integrating the area under the published dispersal kernel for each species

Species	Mean speed (cm s^{-1})	Max speed (cm s^{-1})	TL (mm)	PLD (days)	Dispersal distance (Km)			Sources
	Mean ± SE	Max	Mean ± SE	Mean ± SD	Mode	Median	LDD	
Elacatinus lori	7.2 ± 0.89	13.6	9.5 ± 0.31	26 ± 3.6	0–1	2.0	13.0	D'Aloia et al. (2015), This study
Amphiprion percula	15.8 ± 0.81	18.5	7.7 ± 0.13	11	0–1	11.1	74.0	Thresher et al. (1989), Almany et al. (2007, 2017), This study
Plectropomus leopardus	31.5 ± 3.2	43.4	21.4 ± 0.6	26 ± 2	0–1	187.8	1248.0	Williamson et al. (2016), Fisher et al. (2005)

TL, total length; PLD, pelagic larval duration

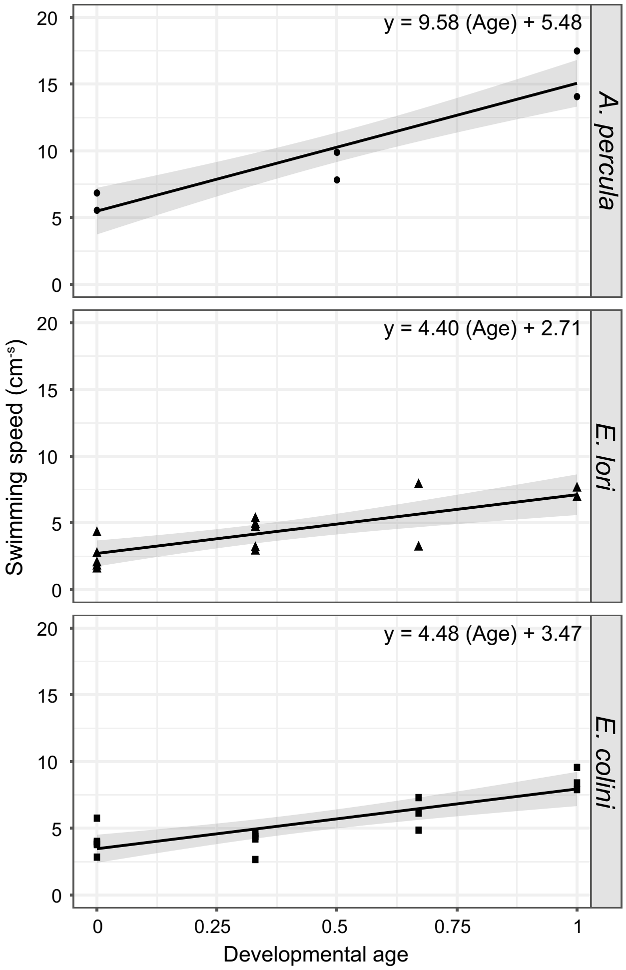

Fig. 2 Swimming speed by developmental age recorded for lab-reared *Amphiprion percula, Elacatinus lori,* and *E. colini* from hatching through settlement. Developmental age is the proportion of time to settlement

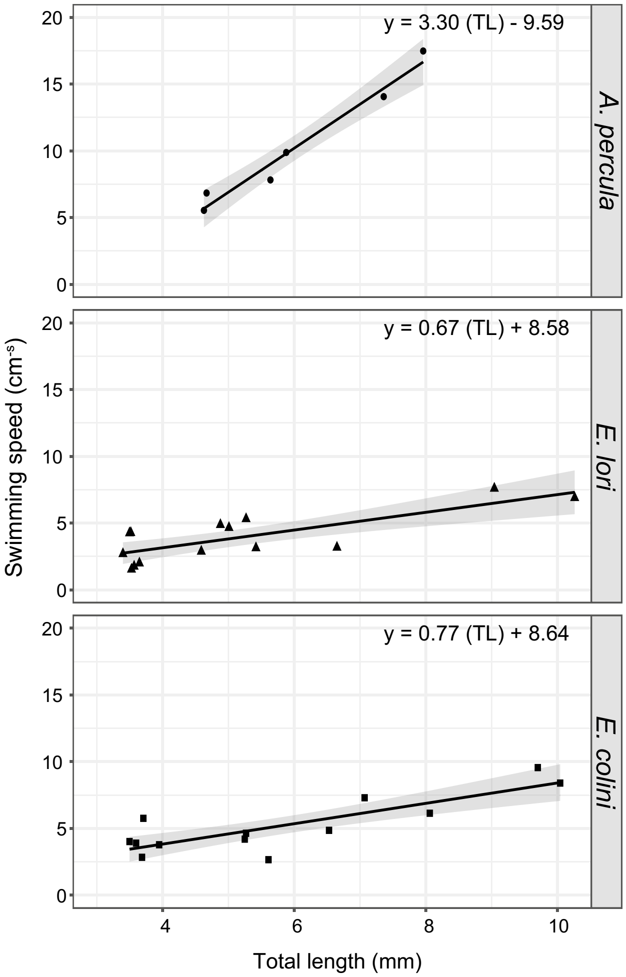

Fig. 3 Swimming speed by size (total length) recorded for lab-reared *Amphiprion percula, Elacatinus lori,* and *E. colini* from hatching through settlement

age ($R^2 = 0.85$), indicating that size was a better predictor of swimming speed than age.

Ontogeny of swimming endurance

The mean swimming duration of *A. percula* larvae was 8.5 times longer than that of *E. lori* and *E. colini* at hatch and 322 times longer at settlement (Table 2). For larvae tested near settlement, this converts to a mean distance traveled ranging from a low of 34.3 m for *E. lori* and 37.5 m for *E. colini*, to 23,818 m for *A. percula* (Table 2). An ANCOVA analysis revealed that there were effects of developmental age ($F_{1,202} = 479.5$, $p < 0.0001$), species ($F_{2,202} = 2.29.5$, $p < 0.0001$), flow velocity ($F_{4,202} = 102.1$, $p < 0.0001$) and their interaction (Developmental age * Species * Flow velocity: $F_{8,202} = 3.7$, $p = 0.0005$) on swimming duration (Fig. 3). The main effects indicated that swimming duration increased with developmental age, was higher in *A. percula* than either *Elacatinus*, and decreased at higher flow velocities. The three-way interaction effect is most readily interpreted by considering each of the two-way interactions. The slope of the relationship between swimming duration and age varied significantly among species (Developmental age * Species: $F_{2,202} = 44.3$, $p < 0.0001$). Post hoc tests indicated that swimming duration increased more rapidly with age in *A. percula* than either *Elacatinus* (post hoc test: $p < 0.0001$), but swimming duration increased at the same rate with age in *E. lori* and *E. colini* (post hoc test: $p = 0.118$). The slope of the relationship between swimming duration and age also varied among flow velocities, but the relationship was only marginally significant (Developmental age * Flow velocity: $F_{4,202} = 2.1$, $p = 0.079$). The trend suggests that swimming duration increases more rapidly with age at low flow velocities than at high flow velocities. Finally, the effect of flow velocity varied by species (Species * Flow velocity:

$F_{8,202} = 2.7$, $p = 0.007$). While older *A. percula* larvae were capable of swimming against higher flow velocities (e.g., 8 and 10 cm S^{-1}), *Elacatinus* larvae were either incapable of swimming against these flow velocities, or swam for negligible durations at each age (Fig. 3).

Similarly, we used an ANCOVA analysis to investigate the relationship between swimming endurance and larva size. We found that there were significant effects of size ($F_{1,202} = 349.2$, $p < 0.0001$), species ($F_{2,202} = 235.2$, $p < 0.0001$) and flow velocity ($F_{4,202} = 58.1$, $p < 0.0001$) and their interaction (Size * Species * Flow velocity: $F_{8,202} = 3.7$, $p < 0.0005$) on swimming duration. The main effects indicated that swimming duration increased with size, was higher in *A. percula* than either *Elacatinus spp.*, and decreased at higher flow velocities (Fig. 4). The slope of the relationship between swimming duration and size varied among species (Size * Species: $F_{2,202} = 85.1$, $p < 0.0001$). Post hoc tests revealed that swimming duration increased more rapidly with size in *A. percula* than either *Elacatinus* spp. (post hoc test: $p < 0.0001$), but *E. lori* and *E. colini* were not different from each other (post hoc test: $p = 0.978$). The slope of the relationship between swimming duration and size also varied among flow velocities (Size * Flow velocity: $F_{4,202} = 2.8$, $p = 0.025$). Swimming duration increased more rapidly with size at low flow velocities than at high flow velocities. The effect of flow velocity varied by species (Species * Flow velocity: $F_{8,202} = 2.7$, $p = 0.007$). While larger *A. percula* larvae were capable of swimming against higher flow velocities (e.g., 8 and 10 cm S^{-1}), *Elacatinus* larvae were either incapable of swimming against these flow velocities, or swam for negligible durations regardless of their body size (Fig. 4). Ultimately, the ANCOVA analysis including size as a covariate explained more of the variation in swimming duration ($R^2 = 0.901$) than the analysis

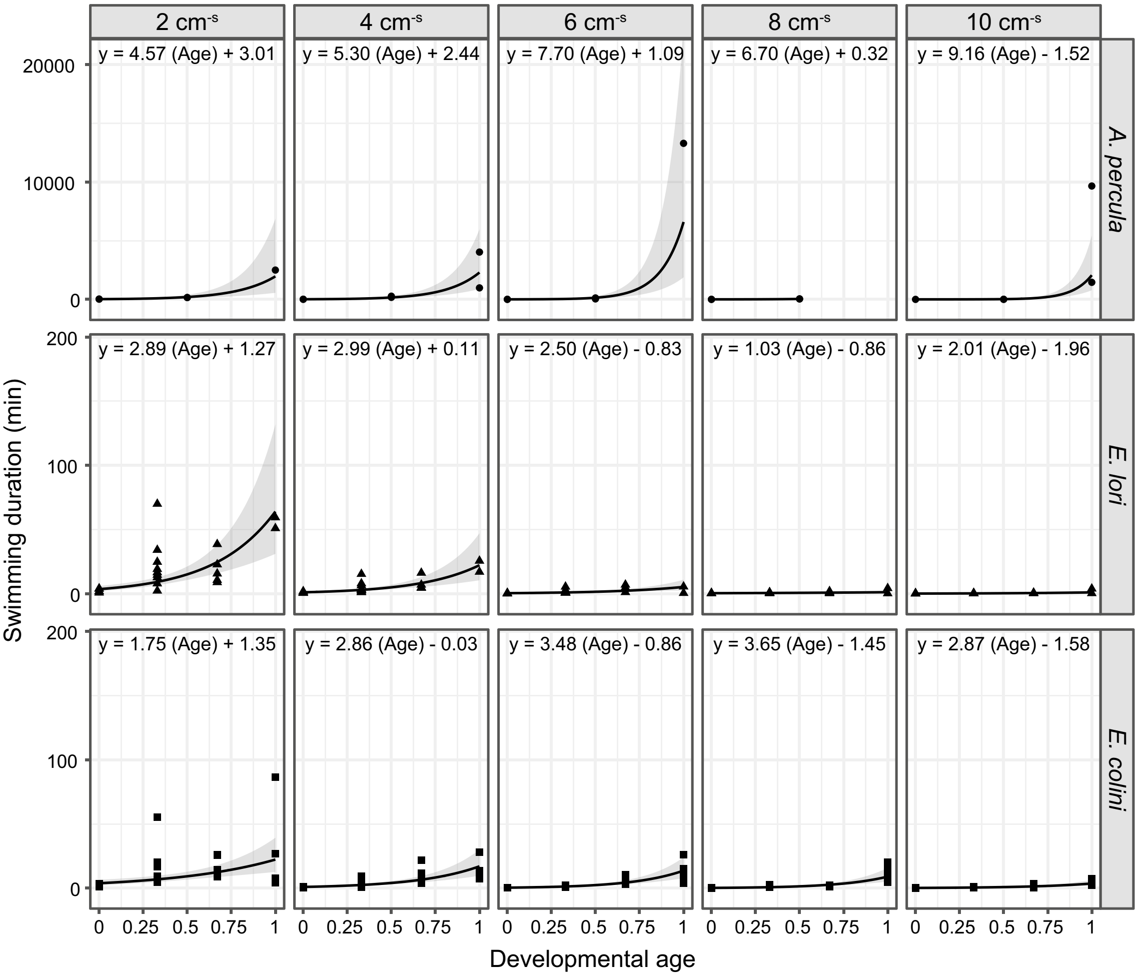

Fig. 4 Endurance (swimming duration) by developmental age and flow velocity recorded for lab-reared *Amphiprion percula, Elacatinus lori,* and *E. colini* from hatching through settlement. Following regression analyses, swimming durations were back-transformed from the $\log_{10}$-scale for plotting. Developmental age is the proportion of time to settlement

including age as a covariate ($R^2 = 0.881$), suggesting that size was a slightly better predictor of swimming duration.

Larval traits and observed patterns of dispersal

There were obvious similarities and differences among species in the patterns of dispersal that have been estimated empirically from genetic parentage analyses (Table 3; D'Aloia et al. 2015; Williamson et al. 2016; Almany et al. 2017). For each species, the modal dispersal class was 0–1 km and the probability of successful dispersal declined exponentially with increasing distance from the natal source. However, when comparing estimates of median (50th percentile) and long (99th percentile) distance dispersal, *A. percula* larvae disperse approximately six times farther than *E. lori,* and *P. leopardus* disperse nearly an order of magnitude farther than *E. lori* (Table 3). Considering the traits of late-stage larvae, the swimming speed, body size, and pelagic larval duration vary substantially among these species (Table 3). Linear regressions indicated that there was no relationship between the modal dispersal distance and dispersal-related larval traits (Fig. 6). However, both mean and long-distance dispersal increased with maximum swimming speed, mean body size, and pelagic larval duration (Fig. 6). Though similar, maximum swimming speed was a better predictor of dispersal distance than mean swimming speed. Further, maximum swimming speed and mean body size were both better predictors of dispersal distances than PLD (Fig. 6).

Discussion

In this study, we investigated the ontogeny of swimming abilities in lab-reared larvae of *A. percula, E. lori* and *E. colini* from hatching through settlement. The results showed that the swimming abilities of each species improved with both age and body size. But, size was ultimately a better predictor of both swimming speed and endurance. The congeners, *E. lori* and *E. colini*, possessed similar swimming speed and endurance abilities. However, *A. percula* were capable of swimming nearly twice as fast and 322 times longer than *E. lori*. Taken together, interspecific differences in swimming abilities suggest that these species have different capacities to influence their dispersal.

Ontogeny of swimming speed

In one of only a few studies that have investigated the swimming abilities of reef fish larvae from hatching through settlement, Fisher (2005) found that the recently hatched larvae of ten reef fish species (1.5–4.5 mm TL) were capable of swimming at mean speeds of 0–4.6 cm s^{-1}. In the current study, the mean speed of recently hatched larvae ranged from 2.7 cm s^{-1} for *E. lori* to 6.2 cm s^{-1} for *A. percula*, while the maximum speed at hatch was 7.8 cm s^{-1} for *E. lori* and 8.3 cm s^{-1} for *A. percula*. These upper limits of performance were similar to the maximum speed reported for recently hatched *Amphiprion melanopus* larvae (8.2 cm s^{-1}), and exceeded the maximum speeds of recently hatched *Pomacentrus amboinensis* (6.4 cm s^{-1}) and *Sphaeramia nematoptera* (4.4 cm s^{-1}; Fisher et al. 2000). Previous studies of the ontogeny of swimming speed, synthesized by Leis (2010), report that larvae similar in size to late-stage *A. percula* and *E. lori* (8–10 mm SL) swim at mean speeds of 4–19 cm s^{-1} (Leis 2010). Relative to these species, late-stage *A. percula* were among the strongest swimmers (mean: 15.8 cm s^{-1}), while late-stage *E. lori* were among the weakest swimmers (mean: 7.2 cm s^{-1}; Fisher et al. 2005; Hogan et al. 2007; Leis 2010). Our results suggest that *A. percula* and *E. lori*, like many other reef fish larvae, can attain swimming speeds that could allow them to influence their dispersal from the moment they hatch (Leis 2010), and that *A. percula* may have a greater ability to do so than *E. lori*.

Ontogeny of swimming endurance

Previous studies have shown that swimming endurance remains low (< 5 km) until larvae reach 9–10 mm in size, at which point they can improve rapidly. In swimming flumes, the late-stage larvae of several reef fish families often swim for durations equivalent to distances of 20 km or more (Stobutzki and Bellwood 1997; Leis 2010). Here, we found that swimming duration increased significantly with age in all three species. All larvae tested at hatch had minimal endurance abilities (equivalent distance: 0.001–0.05 km). Near settlement, however, late-stage *A. percula* larvae (mean: 7.5 mm TL) swam a mean distance of 23.8 km, which is more than 15 km farther than the mean distances reported for other reef fish larvae of similar body size (Fisher et al. 2000; Clark et al. 2005; Leis 2006, 2010). Remarkably, the best performing *A. percula* larva swam continuously for 10.5 days and had the potential to cover 64.1 km. In contrast, the best performing *E. lori* larva swam for only 4.6 h with the potential to cover 0.3 km, which is among the lowest swimming durations reported for larvae of similar body size (mean: 10.2 mm TL; Fisher et al. 2000; Clark et al. 2005; Leis 2006, 2010). While swimming durations improved dramatically throughout ontogeny for *A. percula*, *E. lori* had relatively low swimming durations throughout their entire larval phase. Our results suggest that *A. percula* can sustain swimming speeds that could allow them to influence their dispersal, whereas *E. lori* may be less competent to do so.

Not surprisingly, several studies have shown that the swimming durations of late-stage larvae decrease with increasing flow velocity (Fisher and Bellwood 2002; Fisher and Wilson 2004; de la Sabate et al. 2013). Fisher and Bellwood (2002) found that swimming durations did not improve during ontogeny until swimming speeds had reached approximately double the experimental flow velocity. In this study, swimming durations also began to improve when the swimming speed of larvae was greater than the experimental flow velocity (SI Fig. 1). The mean swimming duration decreased with increasing flow velocities, except for late-stage *A. percula* (Figs. 4, 5), which swam for similar durations across a range of flow velocities from 2 to 10 cm s^{-1}.

Swimming abilities and the potential to influence dispersal

Despite the limited availability of data for coral reef fishes, our analysis revealed several interesting trends regarding the relationship between dispersal-related larval traits and empirically measured patterns of dispersal. Though larval traits differ substantially among late-stage *E. lori*, *A. percula*, and *P. leopardus* larvae, the modal dispersal distance of each species occurred within 0–1 km of their natal origin. This observation challenges the prevailing paradigm that traits, such as strong swimming abilities and/or short PLDs, are generally necessary to help retain larvae near their natal reef (Jones et al. 1999; Sponaugle et al. 2002; Fisher 2005; Fig. 6). Though modal dispersal is the same among species, there are large differences in median and long-distance dispersal that correlate well with both the swimming speed and the body size of late-stage larvae. Maximum swimming speed and mean body size were also both better predictors of dispersal distances than PLD (Fig. 6). This trend is consistent with a growing body of evidence indicating that PLDs are poor predictors of dispersal distances (Bradbury et al. 2008; Shanks 2009; Berumen et al. 2010; D'Aloia et al. 2015), possibly because PLD oversimplifies both inter- and intraspecific variations

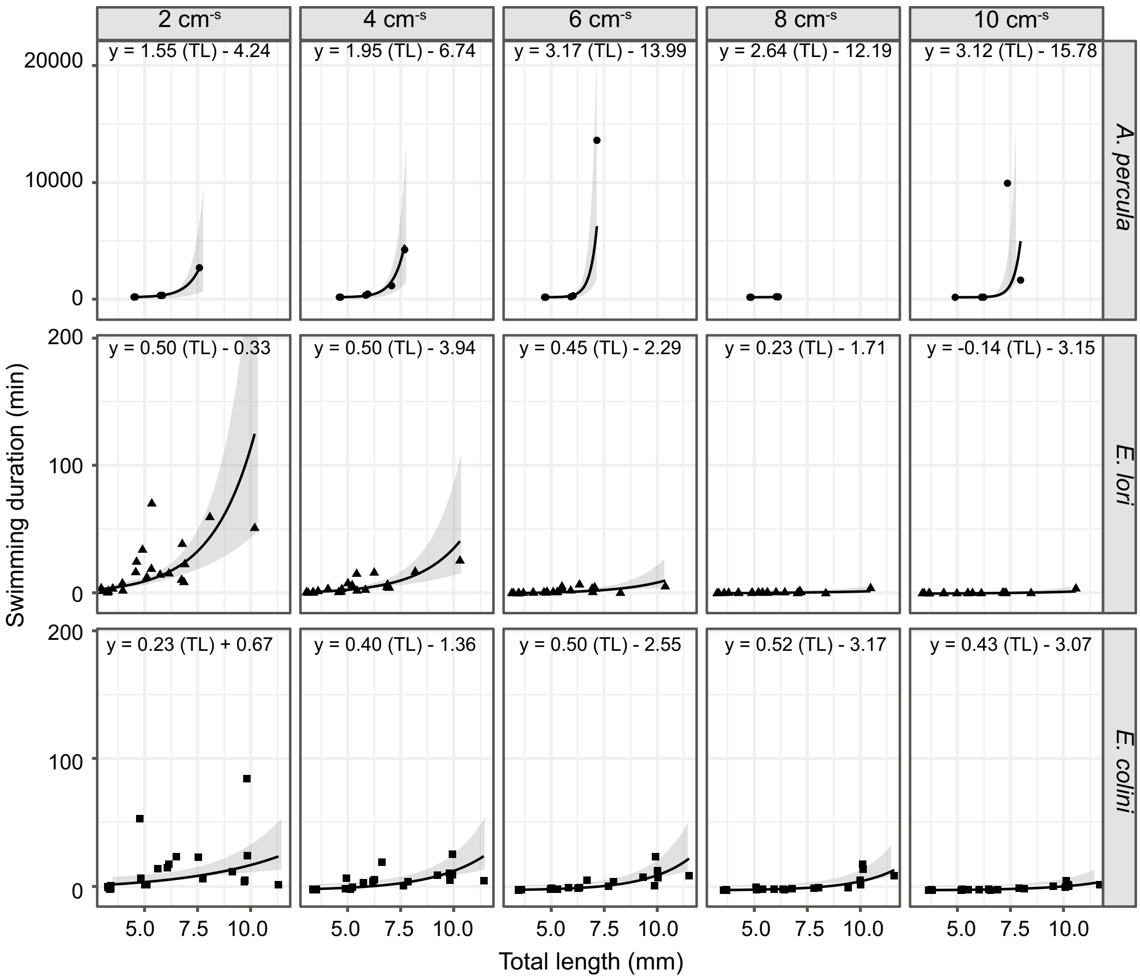

Fig. 5 Endurance (swimming duration) by size and flow velocity recorded for lab-reared *Amphiprion percula, Elacatinus lori,* and *E. colini* from hatching through settlement. Following regression analyses, swimming durations were back-transformed from the log$_{10}$-scale for plotting

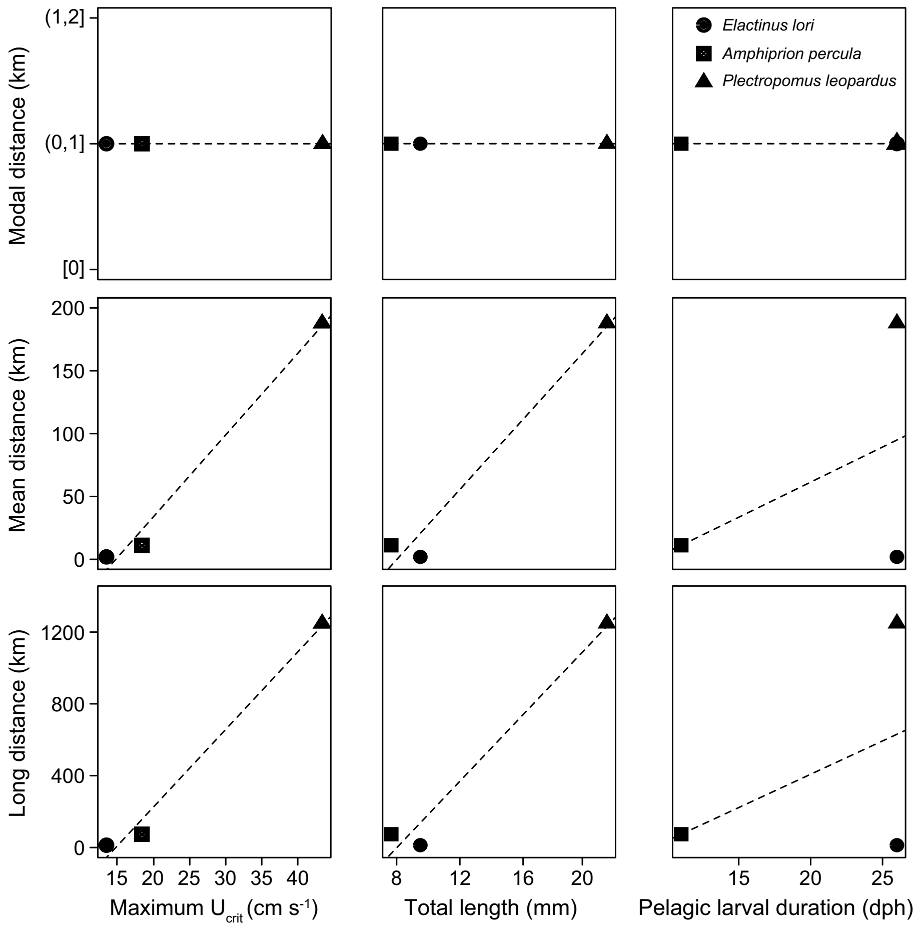

Fig. 6 Relationship between estimated dispersal distance and dispersal-related larval traits of *Elacatinus lori, Amphiprion percula,* and *Plectropomus leopardus*. Dashed line—trend line plotted from the results of a simple linear regression

in the dispersal behavior of reef fish larvae (Nanninga and Berumen 2014). Instead, this trend supports the hypothesis that larval swimming abilities may play an important role in determining the spatial scale of long-distance dispersal (Majoris 2017; Nanninga and Manica 2018). To more rigorously test this hypothesis, dispersal-related larval traits and dispersal kernels will need to be empirically measured for multiple species sampled from the same seascape and hydrodynamic regime.

Why might swimming speed be positively related with LDD?

The mechanism by which larval swimming abilities might facilitate long-distance dispersal can be considered from the larva's perspective or the parent's perspective (Shaw et al. 2019). From the larva's perspective, individuals with strong swimming abilities may simply be able to swim farther in search of suitable settlement habitat (Fig. 7a). While from the parent's perspective, larvae that have strong swimming abilities can be displaced farther from their natal origin without being lost to advection if the larvae can successfully orient and swim toward suitable habitats over greater distances (Fig. 7b). Additional work is needed to determine how inter- and intraspecific variation in larval traits influence patterns of dispersal and population connectivity.

This study represents a first attempt at relating the behavioral potential of reef fish larvae with empirically described patterns of dispersal. The emerging trend suggests that swimming abilities may play an important role in determining the spatial scale of long-distance dispersal, and is consistent with the results of Nanninga and Manica (2018), who showed that swimming abilities of demersal marine fishes were associated with genetic differentiation among populations (an indirect measure of dispersal). Taken together these studies suggest that swimming abilities may be a good proxy for the spatial scale of population connectivity, which has important implications for maximizing the evolutionary, ecological, and socioeconomic benefits of marine reserve networks (White 2015; Manel et al. 2019).

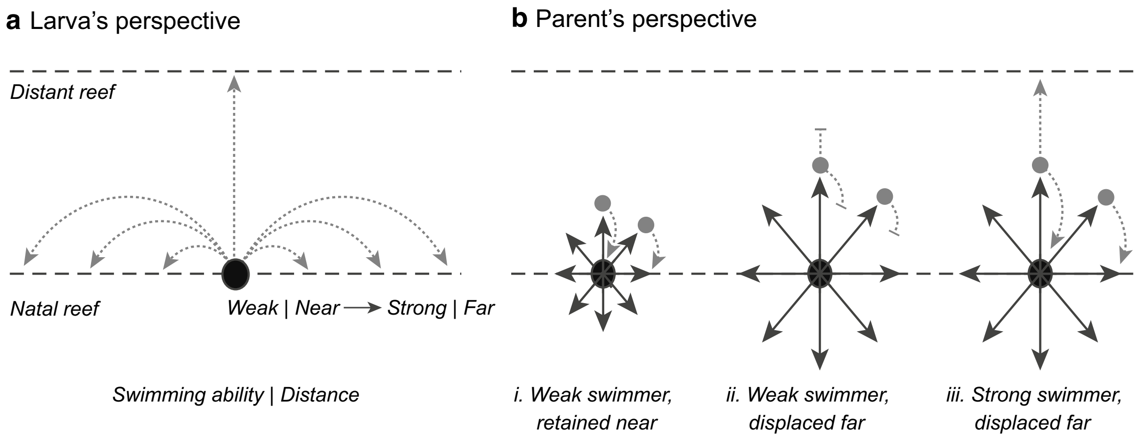

Fig. 7 Mechanisms by which strong swimming abilities could facilitate long-distance dispersal. **a** From the larva's perspective, larvae with strong swimming abilities may be able to swim farther in search of suitable settlement habitat. **b** From the parent's perspective, (1) larvae with weak swimming abilities, if retained close to their natal origin, may still locate suitable habitat. But, if displaced far from their natal origin, (2) larvae with weak swimming abilities will be less likely to locate suitable habitat and will perish, while (3) larvae with strong swimming abilities may be able to orient and swim toward suitable habitat over long distances and may also have the opportunity to colonize distant reefs. Symbol meanings: solid black circles—natal origin; dashed gray arrows—swimming abilities of larvae; solid black arrows—distance displaced from parents; | indicates larval mortality

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Data availability The datasets generated during and/or analyzed during the current study are available in the BCO-DMO repository, https://www.bco-dmo.org/dataset/739171 and https://www.bco-dmo.org/dataset/739149 (Buston and Majoris 2018a, b).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed involving animals were in accordance with the ethical standards of the Boston University IACUC (protocol #'s: 13-021 and 10-036) and were approved by the Belize Fisheries Department.

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