CRITICAL SWIMMING SPEED OF SETTLEMENT-STAGE CORAL REEF FISHES FROM THE CARIBBEAN: A METHODOLOGICAL AND GEOGRAPHICAL COMPARISON

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ABSTRACT

We measured the critical swimming abilities (U_{crit}) of late-stage larvae of 46 species from 21 families of marine fishes from Belize, Central America, and we tested the robustness of the U_{crit} technique to variations in methodology. We found no significant effect of sampling method, or experimental method (i.e., varying the length of the time interval and varying the number of fish in the chamber), and conclude that U_{crit} is relatively robust to variations in methodology. Furthermore, we compared the U_{crit} estimates of six species to previously published U_{crit} estimates from the same species collected in the Turks and Caicos Islands. In all cases fishes from the Turks and Caicos Islands swam faster than fishes from Belize, and these differences were not due to differences in size of the fishes between the two locations. We conclude that differences in U_{crit} between fishes from the Turks and Caicos Islands and Belize are real and could be due to either geographic isolation between the two locations or some temporal effect of sampling. Spatial-temporal variation in U_{crit} must be considered when comparing or combining intra-specific data from different studies, and may play a role in the spatial-temporal variability in the ecology of settlement-stage coral reef fishes.

Much is known of the swimming capabilities of coral reef fish larvae. Experiments have shown that late-stage larvae can sustain swimming at ambient current speeds for hundreds of hours (Stobutzki and Bellwood, 1997). They can also demonstrate short-term sustained swimming speeds of up to 50 body lengths (bl) per second (Bellwood and Fisher, 2001). Larval swimming speeds increase throughout ontogeny (Fisher et al., 2000) with a marked increase in undisturbed swimming speeds around the time of settlement (Fisher and Bellwood, 2003). In situ, larvae have been shown to swim at approximately 50% of the speed measured in swimming chamber experiments (Leis and Fisher, 2006), which is also the same speed that larvae are capable of sustaining for periods of at least 24 hrs (Fisher and Bellwood, 2002; Fisher and Wilson, 2004). This speed also corresponds roughly to the speed that larvae will swim at when given the behavioral freedom to choose their swimming speed (Hogan and Mora, 2005). This wealth of knowledge has been used not only to surmise that reef fish larvae may be able to influence their settlement and dispersal, but also to estimate to what extent this may be possible. Although not yet definitively determined, swimming abilities have been recognized as an important component of dispersal. In fact, many recent dispersal models have included a fish-swimming component (Wolanski et al., 1997; Armsworth, 2001, Paris et al., 2005).

One common technique used to measure fish swimming is the U_{crit} method (see Kolok, 1999). An easy means of measuring swimming performance, the U_{crit} method involves swimming fish at incrementally higher speeds until exhaustion. This technique is useful because the experiments are of short duration yet provide a measure of maximum aerobic swimming speed that can be sustained for short periods (Plaut, 2001). Because U_{crit} measures aerobic sustained swimming performance it can be

translated into terms of effective swimming abilities. Leis and Stobutzki (1999) define effective swimming as the ability of a fish to maintain swimming speeds at least as great as those of the ambient currents. Also, there are strong positive correlations between U_{crit} and in situ swimming speeds (Leis and Fisher, 2006), as well as strong correlations with speeds sustainable for 24-hr periods (Fisher and Wilson, 2004). Because U_{crit} can be related to sustainable swimming speeds it can be used to estimate the effectiveness of a species' swimming abilities. The U_{crit} method is also useful because the experiments are simple and can be replicated easily allowing for a comparison of swimming abilities from a breadth of taxonomic groups and geographic regions.

Numerous studies have used U_{crit} to examine the swimming abilities of fishes in relation to environmental factors (Brett and Glass, 1973; Green and Fisher, 2004), pollutants (Kovacs and Leduc, 1982; Kumaragaru and Beamish, 1983; Cripe et al., 1984), and growth rate (Kolok and Oris, 1995). Although many of these studies cite Brett (1964) as the source of the methodology, most have modified the original technique in some way. As a result, there exists no standard protocol in the literature for conducting U_{crit} experiments (Kolok, 1999) and such aspects as velocity increment size, interval length, and the number of fish per channel varies among studies. Furthermore, the technique used to collect fishes is not standardized among studies. Which could bias U_{crit} estimates if certain sampling methods select for fish of a particular condition or developmental stage or age. For example, light-traps may select for fish in good condition because the fish are required to actively move toward the trap to be captured. Alternatively, crest nets could bias U_{crit} by selecting for fish that are more advanced in development, possibly even those that have already settled. These variations in methodology could be important sources of variation potentially biasing comparative studies of U_{crit}, specifically for intraspecific comparisons (Kolok, 1999).

In this study we measured the U_{crit} swimming speeds of settlement-stage Caribbean reef fishes in Belize and made intra-specific comparisons to those from a previous study (Fisher et al., 2005) at the Turks and Caicos Islands. We investigated the validity of comparing U_{crit} estimates as measured by different observers by investigating the potential confounding effects of three aspects of methodology on U_{crit}. We also compared fish captured using different sampling methods, fish swum over long (15 min) and short (2 min) time intervals, and fish swum in schools or singly within the chamber.

Methods

Data from the Turks and Caicos Islands were obtained from specimens collected using light traps. All fish were swum on the day of collection using a three-channel swimming flume (for more details see Fisher et al., 2005). Experiments conducted in Belize were done using settlement-stage fishes from a range of species occurring at Calabash Caye, Turneffe Islands Atoll, Belize (17°16.414′N, 87°48.674′W), during the summer months (May through September) of 2003, 2004, and 2005. Specimens were collected using a variety of techniques including crest nets, channel nets, light traps, and night-light lift nets, although most specimens were collected using light traps and crest nets. Some specimens of *Abudefduf saxatilis* were collected with hand nets from a fish-attracting device that had been deployed over a seagrass bed near a dock. All specimens of *Clepticus parrae* were collected with hand nets from deep fore-reefs. Although they had already settled to the fore-reef, these individuals had yet to undergo complete metamorphosis and we assumed that they swam similarly to the larval stages.

After capture, individuals were held in fresh seawater, with an aeration stone, in 24-L buckets to reduce stress prior to swimming trials. All individuals were swum within 24 hrs of capture, usually within 6 hrs of collection from nets or traps. Settlement-stage individuals were swum in either a single-lane swimming chamber (internal dimensions of swimming area: 185 mm × 50 mm × 50 mm) or a three-lane swimming chamber similar in design to that used by Stobutzki and Bellwood (1997); both were constructed from Plexiglass™. A removable lid, sealed with an O-ring was used to introduce fish to, and remove them from both chambers. One section of flow straighteners, 45-mm long, was placed just after the inflow in order to reduce turbulence within the chamber. Fish were forced to swim within the swimming area by two 4.0 mm mesh metal retaining fences, which were covered with a finer mesh when required for very small larvae. All experiments were conducted at ambient seawater temperatures, which ranged between 28.5 °C and 31 °C in Belize and 28 °C and 30 °C in the Turks and Caicos Islands.

U_{crit} was measured by incrementally increasing water velocity until the individual could no longer maintain position in front of the metal retaining fence for the full interval. Water velocity was increased by a rate of 3 bl s^{-1} for each increment, following the methods of Bellwood and Fisher (2001). U_{crit} swimming speed was calculated following Brett (1964):

$$U_{crit} = U + (t/t_i \times U_i)$$

where U is the speed during the penultimate interval, U_i is the velocity increment, t is the time swum during the final velocity increment, and t_i is the duration in seconds for each interval. Four swimming protocols were used which varied either in the length of the time interval or in the number of individuals in a single lane of the chamber, they were: (1) single individuals for 2 min intervals; (2) single individuals for 15 min intervals; (3) two individuals for 2 min intervals; (4) three individuals for 2 min intervals. One-way ANOVAs were used to test for differences in swimming speed across all species as well as across species within individual families. The coefficient of variation (CV) of U_{crit} and total length (TL) was calculated at the within species level and the within families level for all species and families with more than one replicate.

Total lengths were measured either pre-trial using calipers (2003 and 2004), or post-trial from photographic analysis (2005). Photographs were taken using a Minolta XG9 SLR camera with a 50 mm lens and scanned from film into digital format. A ruler was included in all photos of larvae to provide scale. Image Tool© software (University of Texas Health Sciences Center in San Antonio) was used for image analysis. Specimens were preserved in 95% ethanol and each individual was identified to the lowest taxonomic level possible by either keying out preserved individuals, identifying individuals at the time of capture based on distinct colorations, or by rearing individuals in aquaria until their juvenile colorations revealed their identity. In those cases where it was not possible to identify all individuals to species level, individuals were identified to genus or family level.

When comparing U_{crit} estimates between studies there are some potential sources of variation that must be accounted for, such as differences in fish collection methods and differences in U_{crit} estimation methods (i.e., length of time intervals, number of fish per lane in the swimming channel). To test for any bias in U_{crit} estimates between fish captured from different sampling devices we compared the U_{crit} values of individuals of one species, *Chaetodon capistratus*, caught in Belize during the 2005 field season using the two most commonly used sampling devices (light traps and crest nets). A paired t-test was used to test for differences in the U_{crit} estimates of fishes caught using the different techniques.

One-way analysis of variance was used to test for differences in U_{crit} between fish swum singly in the swimming chamber and those swum in schools, using an unknown gerreid (sp. 1). This species was chosen for this analysis because fish of this species tended to school in the wild and were repeatedly caught in large numbers in light traps and crest nets. We tested the effects for three experimental treatments: one, two, or three fish per lane.

Another source of variation in U_{crit} estimates could arise from differences in the length of the time interval between each incremental increase in current speed, because this will greatly increase the length of time the fish is forced to swim. Fish swum for five intervals at an interval length of 2 min would swim for only 10 min, whereas a fish swum for the same number of intervals at an interval length of 15 min would swim for 75 min. The length of time spent swimming could potentially affect the estimate of swimming speed if U_{crit} estimates are sensitive to energetic resource exhaustion. We experimentally examined the effect on U_{crit} estimates of swimming fish at interval lengths of 2 min and 15 min, using six common species in Belize including *Stegastes partitus*, *Stegastes diencaeus*, unknown Gerreid (sp 1), *C. capistratus*, *Astrapogon puncticulatus*, and *Apogon quadrisquamatus*. A two-way mixed model ANOVA was used to test the effects of varying the time interval in U_{crit} experiments.

We compared the swimming speed estimates of fish caught in two locations within the Caribbean Sea, Belize (BLZ), and the Turks and Caicos Islands (TCI). This comparison was possible for only six species from three families for which there were at least two individuals swum from each location (Table 1). U_{crit} was regressed against total length and the residual U_{crit} used for further analysis. Nested ANOVAs were used to test for significant differences between species for each location in both total length and residual U_{crit} measures. Sequential Bonferroni post hoc tests were used to determine which species showed differences between locations in both total length and residual U_{crit}.

Results

We measured the U_{crit} swimming speeds for 378 individuals from 46 species and 21 families (Table 2). There were significant differences in the mean U_{crit} among the species examined (ANOVA: $P < 0.001$). The fastest swimming species was the holocentrid *Sargocentron coruscum*, with a mean U_{crit} of 72.07 cm s^{-1}, while the ogcocephalid *Ogcocephalus nasutus*, was the slowest swimmer at only 0.29 cm s^{-1} (Table 2). The average variation in U_{crit} at the individual level was 27% of the mean. On average, total length only explained 14% of the variation in swimming ability within species (Table 3), but variation in length within species was only 17% of the mean length.

The level of variation across species (within families) was 29% of the mean (for n = 11 families). Variation across families was even higher than within families (CV = 63%), reflecting the large range in U_{crit} speeds at the family level. Thirty-six percent of the variation in U_{crit} among families was explained by body length ($P = 0.005$; Fig. 1). The family with the fastest swimming species was the Holocentridae, followed by the Acanthuridae (Table 2). The slowest swimming family was the Ogcocephalidae. The Syngnathidae were the next slowest swimming family despite the fact that this family was the largest in terms of body size (Fig. 1; Table 2).

Methodological Effects on U_{crit} Estimates.—We tested for any bias in U_{crit} estimates associated with method of specimen collection. We found no significant differences in the swimming speeds of fish caught using light traps or crest nets: (t-test: $t = 0.73$; $df = 24$; $P = 0.47$), there was also no difference in the size of fish caught by the different devices: (t-test: $t = -0.42$; $df = 24$; $P = 0.68$). We also tested for any possible effects of schooling (i.e., putting more than one fish per lane in the swimming chamber) on our estimates of U_{crit}. There was no significant difference in the U_{crit} estimates between fish swum singly or in a school of either two or three fish (ANOVA: $P = 0.13$). A two-way mixed model ANOVA revealed that the interaction between species and time interval (t_i) was not significant (ANOVA: $P = 0.09$). Therefore, there was no effect of varying the length of the time interval in terms of

Table 1. Summary of sample sizes for cross-regional, intra-specific comparison of U_{crit} estimates for coral reef fish larvae measured at Belize (BLZ) and the Turks and Caicos Islands (TCI).

Family/Species	Location	n
Acanthuridae		
Acanthurus bahianus	BLZ	10
	TCI	20
Acanthurus coeruleus	BLZ	4
	TCI	8
Lutjanidae		
Lutjanus apodus	BLZ	14
	TCI	2
Ocyurus chrysurus	BLZ	6
	TCI	2
Pomacentridae		
Stegastes partitus	BLZ	20
	TCI	12
Stegastes diencaeus	BLZ	14
	TCI	6

swimming speed between fish swum at 2 min intervals and those swum at 15 min intervals for any of the six species tested (Table 4).

Regional Comparison of U_{crit} Estimates.—There were significant differences in the total length of fishes from TCI and those from Belize ($F_{6, 106} = 5.15$; $P < 0.001$). Total lengths of two species (*Acanthurus bahianus* and *S. diencaeus*) were significantly larger at TCI than at Belize (Fig. 2A). Regression analysis was used to remove the effect of length and obtain residual U_{crit} values. There were significant differences in the residual swimming speeds between fish from TCI and those from Belize (ANOVA: $P < 0.001$). Post hoc tests revealed that for five out of six species both U_{crit} and residual U_{crit} were higher for fish from the Turks and Caicos Islands (Fig. 2B).

Discussion

Late-stage larvae of Caribbean reef fishes show the same strong swimming abilities as those from the Pacific (Fisher et al., 2005), with mean critical speeds of some species exceeding 70 cm s^{-1}. Indeed, there is a large range of swimming abilities across families and species, emphasizing that swimming abilities may play a widely varying role in the ecology of the settlement stages of different taxa. We report here the slowest mean U_{crit} value for any species so far reported, the ogcocephalid *O. nasutus* (0.29 cm s^{-1}). It has been suggested that late-stage larvae can sustain swimming speeds roughly equivalent to 50% of their U_{crit} for 24 hrs, which can be considered a measure of sustained swimming speed (Fisher and Bellwood, 2002; Fisher and Wilson, 2004). In terms of what has been considered an effective swimming speed, 71% of species reported here can sustain swimming speeds greater than the average minimum current speed around Turneffe Atoll (7.7 cm s^{-1}) but only 2% can sustain speeds greater than the average mean current speed (28.4 cm s^{-1}) in the same area (current speed data from Tang et al., 2006).

Mean variation in U_{crit} within species was 27% and only a small percentage was explained by length (Table 2), most likely because within species variation in length

Table 2. U_{crit} for late-stage larvae of 46 species from 21 families of fishes caught at Calabash Caye, Turneffe Atoll, and Belize.

Family/Genus/Species	n	Mean U_{crit} (cm s^{-1}) ± SD	Max U_{crit} (cm s^{-1})	TL (mm) ± SD
Acanthuridae	16	38.09 ± 6.66	52.53	32.56 ± 7.95
Acanthurus bahianus Castelnau, 1855	11	36.3 ± 5.76	43.42	31.27 ± 9.42
Acanthurus chirurgus (Bloch, 1787)	1	42.00	42.00	33.98
Acanthurus coeruleus Bloch and Schneider, 1801	4	42.03 ± 8.57	52.53	35.77 ± 0.54
Antennariidae	3	6.23 ± 6.37	13.54	10.40 ±2.95
Unknown sp. 1	1	1.90	1.9	7.20
Unknown sp. 2	2	8.39 ± 7.28	13.54	12 ± 1.40
Apogonidae	58	19.94 ± 5.26	32.62	17.31 ± 4.28
Apogon maculatus (Poey, 1860)	11	19.85 ± 3.93	22.59	17.59 ± 3.25
Apogon planifrons Longley and Hildebrand, 1940	4	20.34 ± 4.45	22.62	19.16 ± 3.99
Apogon quadrisquamatus Longley, 1934	24	20.96 ± 6.45	32.62	20.29 ± 3.03
Astrapogon puncticulatus (Poey, 1867)	19	18.54 ± 4.83	22.54	13.33 ± 3.81
Carangidae	7	20.61 ± 5.51	30.04	11.93 ± 4.26
Unknown sp. 1	2	26.23 + 5.29	30.04	17.86 ± 1.62
Unknown sp. 2	5	18.33 ± 4.16	22.58	9.55 ± 1.37
Chaetodontidae	37	32.31 ± 6.27	55.22	17.96 ± 3.48
Chaetodon capistratus Linnaeus, 1758	36	31.67 ± 5.01	55.22	17.88 ± 3.52
Chaetodon striatus Linnaeus, 1758	1	55.22	55.22	20.00
Diodontidae	1	6.67	6.67	11.93
Chilomycterus antennatus (Cuvier, 1816)	1	6.67	6.67	11.93
Gerreidae	32	28.72 ± 6.67	47.92	12.04 ± 3.02
Unknown sp. 1	32	28.72 ± 6.67	47.92	12.04 ± 3.02
Haemulidae	2	33.84 ± 9.48	40.55	16.15 ± 0.09
Haemulon flavolineatum (Desmarest, 1823)	2	33.84 ± 9.48	40.55	16.15 ± 0.09
Holocentridae	3	72.07 ± 16.05	90.60	36.19 ± 8.75
Sargocentron coruscum (Poey, 1860)	3	72.07 ± 16.05	90.60	36.19 ± 8.75
Labridae	12	26.97 ± 10.60	50.16	13.56 ± 4.14
Clepticus parrae (Bloch and Schneider, 1801)	6	27.85 ± 1.78	31.51	16.88 ± 1.32
Doratonotus megalepis Günther, 1862	3	36.14 ± 13.50	50.16	8.16 ± 0.28
Xyrichtys sp. A	1	25.07	25.07	17.00
Unknown sp. 1	2	11.53 ± 4.63	14.81	10.00 ± 0.00
Lutjanidae	29	32.37 ± 4.44	45.06	21.77 ± 4.26
Lutjanus apodus (Walbaum, 1792)	16	32.22 ± 3.23	37.59	20.28 ± 3.10
Lutjanus mahogoni (Cuvier, 1828)	7	35.02 ± 6.18	45.06	25.99 ± 5.25
Ocyurus chrysurus (Bloch, 1791)	6	29.66 ± 3.72	33.63	20.59 ± 2.16
Monacanthidae	13	22.88 ± 10.86	42.52	14.80 ± 7.79
Monacanthus ciliatus (Mitchill, 1818)	5	15.14 ± 3.36	20.30	10.52 ± 1.89
Monacanthus tuckeri Bean, 1906	4	19.30 ± 8.67	30.02	19.02 ± 9.47
Stephanolepis setifer (Bennett, 1831)	4	36.14 ± 5.50	42.52	15.94 ± 9.59
Ogcocephalidae	3	0.29 ± 0.13	0.43	6.37 ± 0.55
Ogcocephalus nasutus (Cuvier, 1829)	3	0.29 ± 0.13	0.43	6.37 ± 0.55
Ostraciidae	13	14.03 ± 2.85	18.04	8.06 ± 0.82
Lactophrys bicaudalis (Linnaeus, 1758)	12	14.07 ± 2.98	18.04	8.14 ± 0.81
Lactophrys triqueter (Linnaeus, 1758)	1	13.52	13.53	7.21
Pomacanthidae	2	29.30 ± 11.62	37.52	23.36 ± 2.6
Holocanthus ciliaris (Linnaeus, 1758)	2	29.30 ± 11.62	37.52	23.36 ± 2.6

Table 2. Continued.

Family/Genus/Species	n	Mean U_{crit} (cm s^{-1}) ± SD	Max U_{crit} (cm s^{-1})	TL (mm) ± SD
Pomacentridae	105	34.18 ± 10.79	62.60	14.28 ± 2.46
Abudefduf saxatilis (Linnaeus, 1758)	22	30.86 ± 13.32	59.52	15.02 ± 2.22
Microspathodon chrysurus (Cuvier, 1830)	1	31.62	31.62	16.80
Stegastes diencaeus (Jordan and Rutter, 1897)	39	37.49 ± 12.12	62.60	12.01 ± 0.99
Stegastes adustus (Troschel, 1865)	1	31.52	31.52	14.97
Stegastes leucostictus (Müller and Troschel, 1848)	2	31.53 ± 0.01	31.54	14.21
Stegastes partitus (Poey, 1868)	40	33.03 ± 7.22	50.89	16.06 ± 1.96
Scaridae	1	6.00	6.00	9.00
Unknown sp. 1	1	6.00	6.00	9.00
Serranidae	10	24.15 ± 16.43	59.73	11.36 ± 2.26
Epinephelus mystacinus (Poey, 1852)	4	13.61 ± 3.74	18.21	10.15 ± 1.26
Epinephelus sp. A	4	40.77 ± 13.42	59.73	13.75 ± 0.5
Unknown sp. 1	2	12.00 ± 2.12	13.50	9.00 ± 0.76
Sphyraenidae	11	18.38 ± 3.12	22.64	18.55 ± 1.99
Sphyraena barracuda (Edwards, 1771)	11	18.38 ± 3.12	22.64	18.55 ± 1.99
Syngnathidae	7	4.03 ± 2.78	7.50	30.42 ± 9.94
Cosmocampus elucens (Poey, 1868)	7	4.03 ± 2.78	7.50	30.42 ± 9.94
Tetraodontidae	13	19.22 ± 4.82	27.56	16.14 ± 5.91
Canthigaster rostrata (Bloch, 1786)	4	20.00 ± 5.18	25.55	18.36 ± 0.86
Sphoeroides testudineus (Linnaeus, 1758)	4	20.38 ± 2.53	22.62	21.26 ± 5.50
Sphoeroides sp. A	5	17.65 ± 6.29	27.56	10.26 ± 2.72

Table 3. Summary statistics for regressions between U_{crit} and total length of coral reef fish larvae measured at Belize, analyzed at the individual level for 14 species. Bold text indicates significant associations.

Species	n	r^2	Slope	P-value
Acanthurus bahianus	11	0.01	–0.41	0.74
Apogon maculatus	11	0.05	0.26	0.51
Apogon quadrisquamatus	24	0.13	0.8	0.81
Astrapogon puncticulatus	**19**	**0.66**	**1.04**	**0.001**
Chaetodon capistratus	36	0.01	–0.12	0.66
Clepticus parrae	6	0.00	0.04	0.95
Lutjanus apodus	16	0.09	0.33	0.26
Lutjanus mahogani	**7**	**0.67**	**0.96**	**0.02**
Ocyurus chrysurus	6	0.01	0.20	0.82
Lactophrys bicaudalis	12	0.18	1.55	0.19
Abudefduf saxatilis	22	0.06	1.47	0.30
Stegastes diencaeus	39	0.02	–1.9	0.42
Stegastes partitus	40	0.01	0.75	0.70
Gerreidae sp 1	32	0.11	0.48	0.14

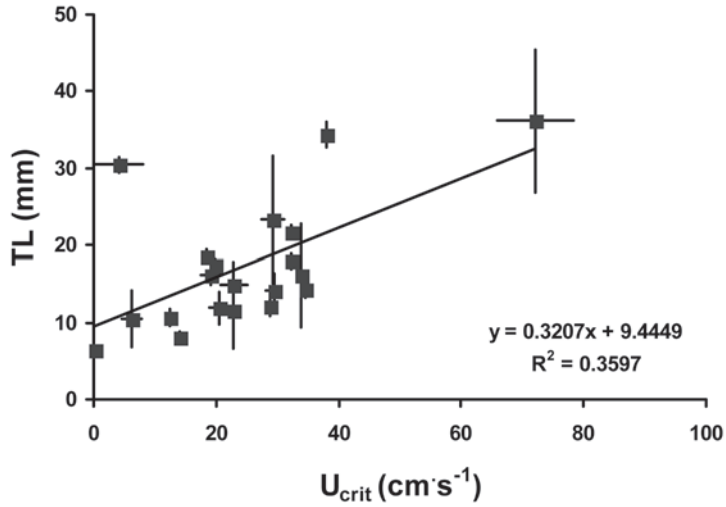

Figure 1. Relationship between mean total length and mean U_{crit} of each fish family with more than one individual. Error bars are standard errors.

at settlement was very small (17%). Variation in U_{crit} within families was similar to within species variation (29%). This value is higher than CV values previously reported at this taxonomic level on the Great Barrier Reef (CV = 14%, Fisher et al., 2005), and may reflect a greater degree of within family variation in size and/or body morphology in the present study. Variation across families was 63% of the mean, much higher than previously reported values (Fisher et al., 2005). In addition, body length explained 36% of the variation in swimming speeds among families. The relationship between swimming ability and length has been demonstrated repeatedly in the reef fish literature (Leis and Carson-Ewart, 1997; Stobutzki and Bellwood, 1997; Fisher and Wilson, 2004, Fisher et al., 2005), as well as the non-reef fish literature (Bainbridge, 1960) although length often explains only a modest portion of the variation in swimming abilities. Other morphometric measures (or a combination thereof) are proving to be better predictors of swimming ability than simply length alone (Fisher et al., 2005).

Methodological Effects on U_{crit} Estimates.—We found that there was no difference in the U_{crit} estimates for individuals of the butterflyfish *C. capistratus* that were collected by either light traps or crest nets despite the potential for differential selection by the different techniques. We also found no difference in the size of *C. capistratus* collected by the different devices suggesting that, at least for this species, individuals caught by the two methods are at the same developmental stage. One noticeable difference between the two collection techniques was the species composition of the catches. Crest nets collected a greater breadth of taxa than did light traps, perhaps because light traps require active behavior (swimming and photokinesis) on the part of larvae, whereas crest nets sample passively.

We found no significant effect of schooling on the U_{crit} estimates of individuals of one gerreid species, regardless of whether there was one, two, or three fish in the channel. Possible benefits of schooling include increased energy savings due to drafting and increased swimming performance caused by turbulent waves from schooling partners (Liao et al., 2003). As such, it seems possible that varying the number of fish

Table 4. Mean ± 1 SD U_{crit} measurements from fishes of six species swum using two time interval treatments (2 min and 15 min).

Species	Time Interval	n	Mean ± SD
Apogon quadrisquamatus	2	15	20.5 ± 8.1
	15	9	21.8 ± 2.5
Astrapogon puncticulatus	2	12	17.1 ± 5.5
	15	7	21.0 ± 2.2
Chaetodon capistratus	2	27	31.9 ± 5.6
	15	9	31.1 ± 2.4
Gerreid sp. 1	2	21	30.6 ± 7.2
	15	11	25.5 ± 3.6
Stegastes diencaeus	2	29	39.4 ± 13.6
	15	10	32.0 ± 1.4
Stegastes partitus	2	32	32.7 ± 8.0
	15	8	34.5 ± 2.3

in the swimming channels (as a way of increasing sample sizes) might inadvertently influence estimates of U_{crit} swimming speed. Despite the potential benefits, U_{crit} appears insensitive to possible advantages of schooling; perhaps due to the fact that U_{crit} measures maximum speed, and that fish do not reach metabolic exhaustion (Plaut, 2001). However, schooling may still provide energy savings during long term, sustained swimming experiments, potentially altering the results of such experiments.

U_{crit} estimates also appear to be relatively robust to the length of the time increments used during the experiments. We found no significant effect of varying the length of the time interval on U_{crit} estimates between 2 min and 15 min intervals. Fisher et al. (2005) also tested the effect of time interval lengths (2 and 5 min intervals in that study), however, their comparison was confounded by the fact that the sizes of the velocity increments were also different between treatments. In their experiment, the fish swum at 2 min intervals experienced velocity changes of three body lengths per second, where as fish swum at 5 min intervals experienced velocity changes of 1.6 cm s^{-1}. Although inconsistent methodology of Fisher et al. (2005) confounded the true effect of altering the time interval, their results were similar to ours. Our results suggest that U_{crit} estimates are fairly insensitive to changes in time increment length, and that experiments of varying length produce similar estimates of maximum speed at least up to a 15 min interval length. However, time intervals of > 30 min may lead to a decrease in U_{crit} estimates, because fish are subjected to trials that more closely resemble sustained swimming performances (Kolok, 1999).

Regional Comparison U_{crit} Estimates.—In conducting this study, careful attention was taken to ensure that the methods used here were as similar as possible to those used by Fisher et al. (2005), to minimize variability caused by differences in methodology. In both studies light traps and/or crest nets were deployed at dusk and retrieved at dawn. Collected fish were put into holding containers (kept in the shade) with no overcrowding, and most fishes were swum within 6 hrs of capture. Fishes were handled very carefully so as not to cause stress that could affect swimming performance. Prior to the start of swimming trials, all fishes were behaviorally assessed for signs of stress (coloration, lack of alertness, immobility), and any fishes that were deemed stressed were removed from the trials in both studies. We believe there was no meaningful difference in the way the fishes were collected or handled

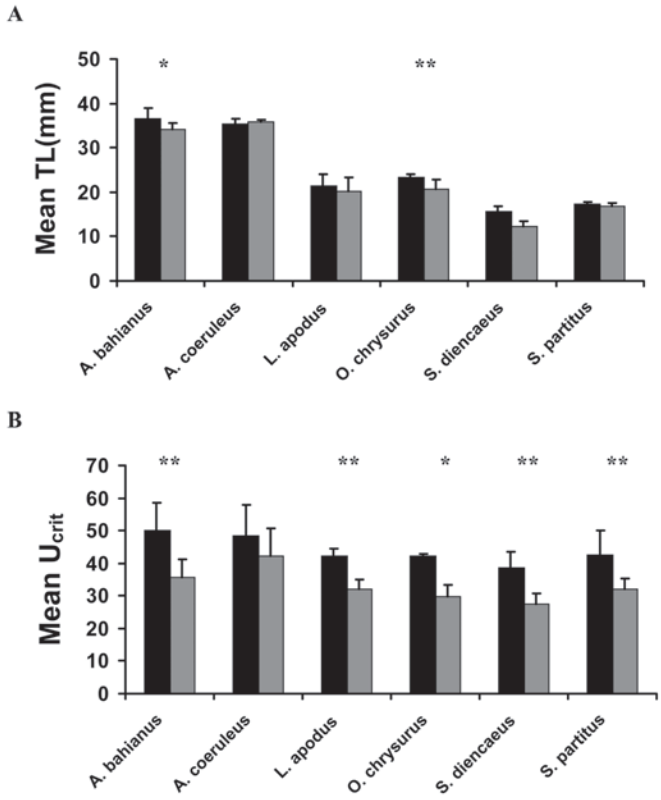

Figure 2. (A) Mean total lengths and (B) mean raw U_{crit} values for the larvae of six species of coral reef fish tested in both the Turks and Caicos Islands (black bars) and Belize (grey bars). Asterisks indicate significant differences between the two locations as determined by nested ANOVAs, * = $P < 0.05$ and ** = $P < 0.01$. In (B), nested ANOVA was performed using residual U_{crit} values. All error bars are standard deviations.

prior to swimming trials that could introduce systematic bias between the TCI and BLZ studies.

That said, residual U_{crit} swimming speeds were significantly higher in fishes swum at TCI than those from BLZ for five of six species. These differences in swimming ability were not due to differences in sizes of the fish between the two locations since residuals were used to remove the effect of length on these U_{crit} estimates. Furthermore, total length did not differ significantly between locations for four of the six species, and total length explained < 3% of the variation in the U_{crit} of those five species that showed regional differences in U_{crit}. It is possible that intra-specific differences in U_{crit} estimates can be explained by geographic distance/isolation between TCI and BLZ. Based on their geographic location (eastern vs western Caribbean) and associated oceanography, it is possible the populations of fishes from these two locations are genetically isolated (Cowen et al., 2006) and that region-specific selection and/or environmental conditions could explain differences in swimming performance.

It is important to note, however, that the U_{crit} estimates from the two locations may be temporally confounded, because the experiments were conducted in different seasons and years, consequently, difference in seasonal seawater temperature between the two locations could explain the differences in U_{crit} (Fuiman and Batty,

1997). Despite the fact that the studies were conducted in different seasons, seawater temperatures at the two locations were fairly constant and encompassed a very similar range (28–30 °C and 28.5–31 °C in TCI and BLZ, respectively). Thus, there is no evidence to suggest that fishes from the two locations experienced different thermal environments that could explain the systematically higher U_{crit} measured for larval fishes at TCI. However, because factors that affect larval condition, such as food availability (Alsop and Wood, 1997; Fisher and Bellwood, 2001) may have differed significantly between years and/or times of year, we cannot say definitively whether spatial or temporal factors are responsible for the observed differences in U_{crit} between conspecifics from these two locations.

It is becoming clear that swimming abilities play an important roll in the ecology of reef fishes. Studies have found a relationship between swimming abilities and post-settlement distribution and habitat use by labrids both in tropical and temperate regions (Fulton et al., 2001; Fulton and Bellwood, 2004). Swimming abilities have been suggested to play a role in habitat choice at settlement, ultimately affecting settlement patterns (Leis and Carson-Ewart, 1999; Montgomery et al., 2001; Leis and Carson-Ewart, 2002; Schmitt and Holbrook, 2002). Swimming abilities of larval and settlement-stage reef fishes may be strong enough in some species to affect dispersal trajectory and dispersal distance from the natal reef site either by horizontal swimming toward reefs (Leis and Carson-Ewart, 1997; Fisher and Bellwood, 2003) or through vertical migrations to take advantage of onshore currents (Cowen et al., 2000). There is a strong coherence in the swimming abilities of a few families of reef fish found in both the Caribbean and on the Great Barrier Reef, although some Caribbean fishes swim significantly slower than their familial relatives in the Pacific (Fisher et al., 2005), suggesting that differential selection for swimming abilities in the two oceans.

As the first intra-ocean comparison of U_{crit} swimming performance, our study highlights that the swimming abilities of fish can vary for a species both spatially and/or temporally. It appears that spatial-temporal differences in swimming performance must be considered when comparing or combining work done in different places, during different years, or at different times of the year. It would be beneficial for future studies to further investigate the temporal and spatial variability of intraspecific U_{crit} estimates, focusing in on smaller geographic distances and seasonal differences (winter vs summer months). It is well known that the replenishment of reef fish populations is spatially and temporally variable (Doherty and Williams, 1988). Variation in the magnitude of swimming abilities may contribute to this spatial-temporal variability.

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