Behavioral ontogeny in larvae and early juveniles of the giant trevally (*Caranx ignobilis*) (Pisces: Carangidae)

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Abstract—Behavior of young (8–18 mm SL) giant trevally (*Caranx ignobilis*), a large coral-reef–associated predator, was observed in the laboratory and the ocean. Size was a better predictor of swimming speed and endurance than was age. Critical speed increased with size from 12 to 40 cm/s at 2.7 cm/s for each mm increase in size. Mean scaled critical speed was 19 body lengths/s and was not size related. Swimming speed in the ocean was 4 to 20 cm/s (about half of critical speed) and varied among areas, but within each area, it increased at 2 cm/s for each mm increase in size. Swimming endurance in the laboratory increased from 5 to 40 km at 5 km for each mm increase in size. Vertical distribution changed ontogenetically: larvae swam shallower, but more variably, and then deeper with growth. Two-thirds of individuals swam directionally with no ontogenetic increase in orientation precision. Larvae swam offshore off open coasts, but not in a bay. *In situ* observations of *C. ignobilis* feeding, interacting with pelagic animals, and reacting to reefs are reported.

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The giant trevally (known as ulua aukea in Hawaii) (*Caranx ignobilis* (Forsskål)), is the largest species in the commercially important family Carangidae. It has a wide tropical Indo-Pacific distribution ranging from Japan to Australia and from East Africa to the Hawaiian and Marquesas Islands (Randall et al., 1997; Smith-Vaniz, 1999; Hoese et al., in press). Adults of this reef-associated pelagic species may be solitary or form schools on inner reefs, inshore on sand flats, or in reef channels, but primarily on seaward reefs to depths of 80 m (Kuiter, 1993; Myers, 1999; Hoese et al., in press). *Caranx ignobilis* is an important top-level carnivore in reef systems: adults and juveniles feed during the day primarily on demersal and pelagic fishes and to a lesser extent on cephalopods and crustaceans (Blaber et al., 1983; Sudekum et al., 1991; Myers, 1999). Adult coloration varies from silver grey to almost black above and fins are usually dark grey to black, but in small juveniles the body is barred (pale to dark gray) and the anal and caudal fins are yellow (Kuiter, 1993; Randall et al., 1997). *Caranx ignobilis* is important to commercial and recreational fisheries and to aquaculture because of its size (maximum of 1.7 m and 62 kg), abundance, palatability, and reputation as an excellent game fish (Smith-Vaniz, 1999; Yu, 2002). The species can, however, be ciguatoxic (Myers, 1999).

Little is known of the early life history of *C. ignobilis*. Adults, which reach maturity at about 60 cm in length and 3–4 years of age, have been reported to gather on shallow seaward reefs and offshore banks to spawn (von Westernhagen, 1974; Johannes, 1981; Sudekum et al., 1991; Myers, 1999). Neither eggs nor larvae have been described, and nothing is known of the distribution or behavior of the larvae or early juveniles. Juveniles are found in small schools over sandy inshore bottoms (Myers, 1999), but also in turbid estuaries, where they are "uncommon" (Blaber et al., 1983). Juveniles and subadults have wide tolerances for salinity and turbidity (Blaber et al., 1983). In Kaneohe Bay, Hawaii (a coral-reef lagoon with estuarine features), *C. ignobilis* juveniles less than 20 cm (<1 year old) were found on the "murky" lagoon floor (Wetherbee et al., 2004). Juveniles were associated with lagoonal patch reefs when they were between 25 and 40 cm in length, and appar-

ently moved out of the bay when larger than 40 cm. In South African estuaries, individuals larger than 55 cm were absent (Blaber et al., 1983). The high abundance of *C. ignobilis* in the NW islands of Hawaii (Sudekum et al., 1991), where estuaries are absent, shows that presence of juveniles in estuaries is facultative.

Recently, Taiwanese aquaculturists have developed culture methods for *C. ignobilis* (Yu, 2002), and this enabled us to obtain larvae and small juveniles that we used for laboratory and field observations of behavior. Behavior of early-life history stages of marine fishes can strongly influence both the survival and distribution of these small fishes (Leis and McCormick, 2002). Therefore, an understanding of the behavioral capabilities of these early-life history stages is essential to intelligent management, and to comprehend the demographics and ecology of any marine teleost fish.

Aside from field studies of the behavior of wild larvae in vertical distribution (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001), behavior has been studied in the early-life history stages of only a few carangid fishes. There has been extensive research on cannibalism, aggressive interactions, and schooling behaviour by using reared larvae and juveniles of Japanese amberjack (*Seriola quinqueradiata*) and white trevally (*Pseudocaranx dentex*) in the laboratory (e.g., Masuda and Tsukamoto 1996, 1998, 1999; Sakakura and Tsukamoto 1996, 1999). We report in the present study the first observations of the development of swimming abilities, orientation abilities, and vertical distribution for *C. ignobilis,* using both *in situ* methods (Leis et al., 1996) and laboratory swimming chambers (Fisher et al., 2000). These behaviors are important to dispersal, feeding, predator interactions, and survival generally during the early life history of *C. ignobilis*.

Materials and methods

Larvae and juveniles

Young *C. ignobilis* were obtained from a commercial aquaculture farm near Kaohsiung, Taiwan. They were identified as *C. ignobilis* by the farmer with reference to photographs, and the identification was subsequently confirmed by examination of preserved specimens. *Caranx ignobilis* eggs from an induced spawn were placed in a large outdoor earth pond (approximately 20×20×1m), and thus hatched under "natural" conditions. Larvae were provided with a "natural" food source (phytoplankton and zooplankton that were resident in the pond). Surface water temperature in the outdoor pond was 32°C when the larvae were collected in May 2004. Fish were obtained on two occasions at the same pond from a single cohort and from an unknown number of females; the first collection was at 20 days after hatching (dah) and the second at 24 dah.

The young fish were placed in oxygenated plastic bags in an insulated box and transported to the laboratory at the National Museum of Marine Biology and Aquarium (NMMBA), Kenting, Taiwan, about 1 hour by road. In the laboratory the larvae were acclimated in a 40-liter aquarium filled with water from the seawater system at NMMBA. Each aquarium was fitted with an aerator, and kept ca 25°C. Twice daily, the larvae were fed with live, newly hatched brine shrimp (*Artemia*) nauplii and 50% of the total volume of water exchanged with fresh seawater. The aquaria were cleaned daily by suctioning debris off the bottom.

Reported sizes of larvae are given in standard length (SL, in mm). Ages are reported as days after hatching (dah) and are based on the age reported by the aquaculturist when the larvae were obtained. The nomenclature for early life history stages of fishes is complex; there are many different systems of terminology and no consensus on which is the most appropriate. Depending on the nomenclature used, the *C. ignobilis* individuals we studied (Fig. 1) would be considered larvae, or juveniles, or as a mixture of both. In our *C. ignobilis*, all fin-rays were present in the smallest specimens (8 mm), and scales were present from about 14 mm, yet the preopercular spines that characterizes most carangid larvae (Leis and Carson-Ewart, 2004) were still present at 19 mm. Unlike the pelagic stages of demersal fishes, *C. ignobilis* does not undergo a clear ecological transition from pelagic to demersal habitat upon which one might base life history stages. We do not attempt to distinguish between larvae and juveniles, and to avoid awkward phrasing and for simplicity, we refer to the young fish that we studied as larvae on the basis that the largest individuals retained some head spines. We acknowledge that in some taxonomic systems they may be referred by other terms.

Laboratory observations

Multilane swimming chambers were used to measure swimming abilities (Stobutzki and Bellwood, 1994). One chamber was used to measure critical speed and a second identical chamber was used for measurements of endurance (Fisher et al., 2000). Both chambers were made of clear plexiglass and had 6 lane-ways, each 30 mm wide, 50 mm high, and 180 mm long. A black line across the lid of the chamber provided the larvae with a point of reference for orientation. Aside from the fine mesh (0.5-mm) ends, the chamber design was identical to that of Stobutzki and Bellwood (1994, 1997).

Even distribution of flow was achieved by a T-piece diffuser in the header portion of the chamber. Turbulence in the chamber was minimized by a 40-mm-long section of flow straighteners at the start of each lane. These straighteners also minimized possible boundary layers. Previous measurements have shown that water velocity in the 5 mm area closest to the wall was not significantly different from that in the center of the chamber (Stobutzki and Bellwood, 1997; Stobutzki, 1998; Fisher et al., 2000). Water flow speed was controlled by turning a calibrated ball valve. Flow rates were calibrated by recording the time taken for water

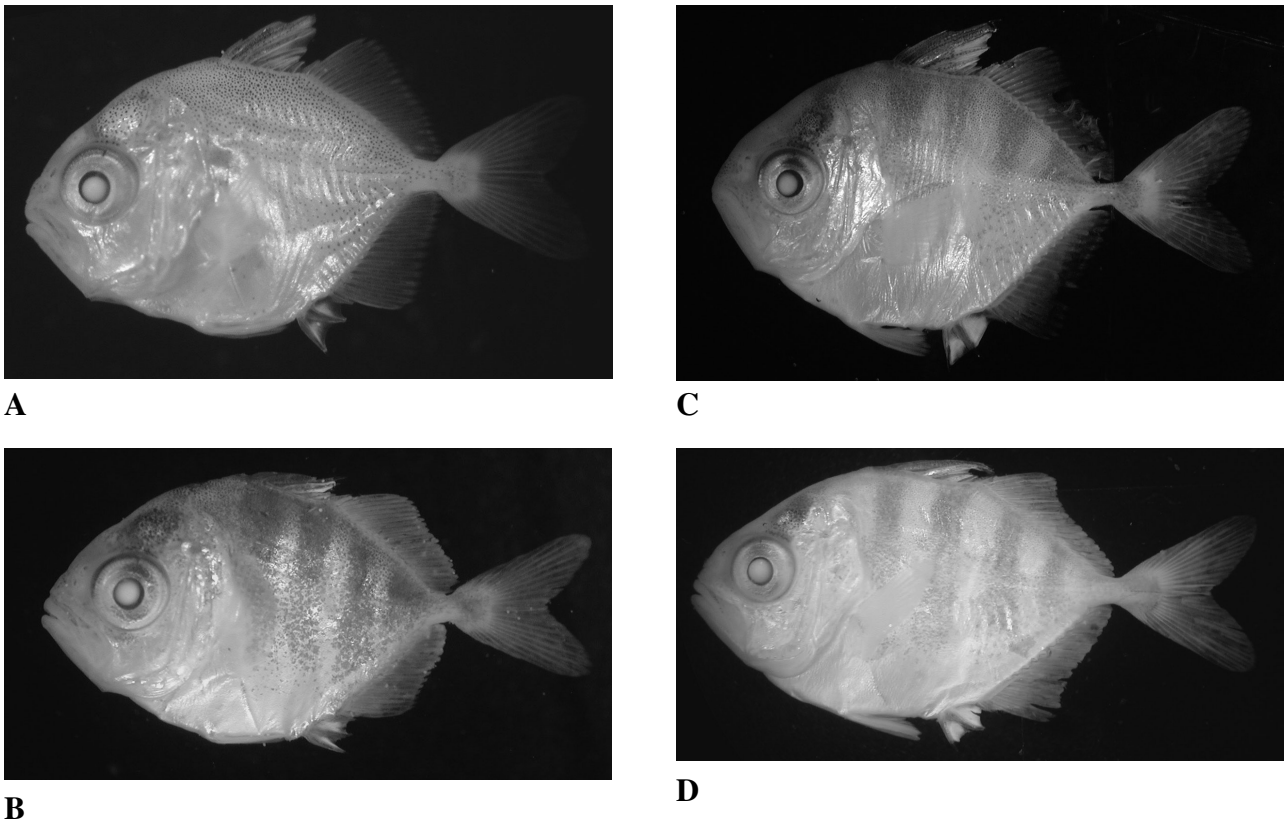

Figure 1

Preserved larvae of giant trevally (*Caranx ignobilis*) representing the range of sizes and developmental stages included in the present study. Preopercular spination was present in all specimens. The smallest specimen had a few scutes on the peduncle, the 14.5-mm specimen had scales forming elsewhere, and the largest specimen was largely scaled. Sizes are SL (Australian Museum catalogue numbers are provided). (**A**) 9.6 mm (I.43435-004); (**B**) 11.7 mm (I.43435-003); (**C**) 14.5 mm (I. 43435-004); (**D**) 18.5 mm (I.43435-002).

flowing over the outlet weir to fill a container of known volume, divided by the cross-sectional area of the chamber. The average of five calibrations was used as the flow speed for a given valve angle. The chambers were calibrated each time they were set up. Flow speeds in excess of 50 cm/s could be achieved with this system. The chambers were plumbed into the seawater system of the NMMBA aquaria and laboratory, which provided a continual flow of "fresh" seawater.

Before measurements of swimming speed and endurance were recorded, the larvae were acclimated to any differences in water quality between the holding tank and swimming chamber by gradual addition of seawater from the swimming chamber system. Larvae were placed in a chamber lane and allowed to acclimate for 5 minutes at 1 cm/s. Any larva showing signs of stress during the acclimation period was removed from the experiment and replaced with another individual. Water temperature in the swimming chamber ranged from 27° to 29°C. Two swimming parameters were measured: critical speed (U_{crit}), which measures maximum swimming speed over periods of minutes, and endurance, which measures how long larvae can swim without food or rest.

For U_{crit} tests, starting at 1.5 cm/s flow speed was increased by approximately 2 cm/s every 5 minutes until the larvae were unable to swim against the flow. The elapsed time when each larva drifted to the downstream mesh was recorded. Critical speed (U_{crit}) of larvae was calculated with the equation of Brett (1964):

$$U_{crit} = U + (t/t_i \; x \; U_i),$$

where U = penultimate speed;
U_i = speed increment (ca. 2 cm/s in the present study);
t = time swum in the final speed increment; and
t_i = the time interval for each velocity increment (5 min).

The total time for a critical speed measurement was proportional to the U_{crit} achieved, and varied from 15

Table 1

Location-specific relationships between *in situ* speed (cm/s) and size (mm SL) in *Caranx ignobilis* larvae. NA=not applicable.

Location	*n*	Regression	r^2	*P*
Wan Li Tong	7	$Spd = 1.69SL - 6.2$	0.83	<0.002
Her Chen	3	$Spd = 2.55SL - 12.2$	0.97	0.11
Nan Wan Bay South	2	$Spd = 0.12SL + 4.9$	NA	NA
Nan Wan Bay North	6	$Spd = 2.05SL - 17.9$	0.72	0.03

minutes for the slowest individual to 82 minutes for the fastest. Given the endurance of which these larvae are capable (see "Results" section), it is unlikely that the larvae would have become fatigued over such time intervals.

For endurance tests, a constant speed of 10 cm/s was used. Larvae were swum until they fatigued, which was defined as the time when a larva could no longer hold its position against the current and drifted onto the downstream mesh. During daylight hours, larvae were observed regularly and the exact time of fatigue (=swimming duration) was recorded. If a larva fatigued when it was not being observed, the time at fatigue was estimated as the midpoint between the time when the larva was last seen swimming and the time when it was found no longer swimming. Chambers were set up under cover so that they were shaded throughout the day, and a fluorescent light was used for illumination at night. The actual endurance measurements of time swum were converted to distance swum, by using the flow speed data, and were reported as kilometres swum.

Fatigued larvae from both experiments were removed from the chamber, euthanized and fixed in Bouin's solution for one hour, then placed in 70% alcohol and stored. All preserved larvae were later examined under a dissection microscope to determine standard length (SL) and state of notochord flexion. Total lateral area (TA) and propulsive area (PA) of larvae (Fisher et al., 2000) were measured by using Scion Image for Windows (Beta 4.02, Scion Corporation, Frederick, MD). PA is TA minus the head and gut.

In situ observations

Four sites were used for *in situ* observations of *C. ignobilis* in the South China Sea, at the southern tip of Taiwan (ca. 22°N, 121°E). Two study sites were used in Nan Wan Bay (21 May 2004) where the depth range was 14–23 m and another two were used on the west coast just off the peninsula that delineates the west side of Nan Wan Bay in the vicinity of Wan Li Tong and Her Chen (14 May 2004) at a depth range of 17–31 m (Table 1). At each site, observations were made at least 50 m offshore, and all observations were conducted in the morning.

Larvae were transported from the laboratory to the release sites in covered buckets fitted with a battery-operated aerator. Ambient seawater was gradually added to the buckets to allow the larvae to acclimatize to the surrounding water conditions. Then, 50% of the water in the bucket was exchanged for "fresh" seawater every hour. The behavior of the larvae was observed following the procedures of Leis et al. (1996) and Leis and Carson-Ewart (1997, 1998). Two scuba divers descended to a depth of 5 m where the observer diver released a larva from a small container. Once the larva chose its initial trajectory, the two divers followed. The observer diver's sole job was to follow the larva while the second diver, following the observer, recorded data. The direction the observer diver was facing when he or she released the larva was chosen at random. Each larva was used only once and, where possible, was recaptured at the end of the observation period and preserved. The size of each larva was estimated, with the aid of a ruler, before release. For recaptured larvae, the estimated and actual sizes were regressed, and this relationship was used to calculate the actual size of the five individuals that were not recaptured of the 24 released. Water column depth was measured by the depth sounder on the support boat at the start of each larval release.

Swimming speed, depth, and swimming direction were measured *in situ*. We attempted to observe each larva for 10 minutes, taking measurements of swimming direction and depth, using a dive compass and computer, respectively, every 30 seconds. Speed was calculated from distance traveled as measured by a calibrated flowmeter over the full period of observation (Leis and Carson-Ewart, 1997). Larvae were not followed deeper than 15–18 m on some dives for safety reasons; therefore observations on some individuals were curtailed. Twenty-four larvae were observed, and observations on 18 of the larvae lasted the full 10 minutes. Five larvae swam monotonically downward to below our safety depth from 3 to 6 minutes, whereas one initially ascended, before descending after 5 minutes and exceeding the safety depth after 8 minutes.

Data analysis

To determine the best predictor of performance, values of critical swimming speed and endurance were regressed against SL, TA, and PA by using linear, logarithmic, power, and exponential models. The model with the greatest r^2 (coefficient of determination) was used as the best description.

All bearings are given as degrees magnetic. Cardinal directions are not abbreviated, but other directions are abbreviated (e.g., SE for southeast). From these bearings and the flowmeter data, we estimated swimming direction and speed in relation to the water (not the bottom).

Circular statistical procedures followed Batschelet (1981) and Zar (1996). Mean vector length (r), is a measure of angular dispersion ranging from 0 (maximum dispersion) to 1 (lack of dispersion). The Rayleigh test was used for single-sample hypotheses about directional swimming. Watson-Williams test was used for hypotheses about directional swimming involving more than one sample. Most of the circular statistical procedures were performed with Oriana software (vers. 2, Kovach Computing Services, Pentraeth, Wales, UK). For all statistical tests, we report actual P values whenever possible, but consider $P<0.05$ to constitute a "significant" result.

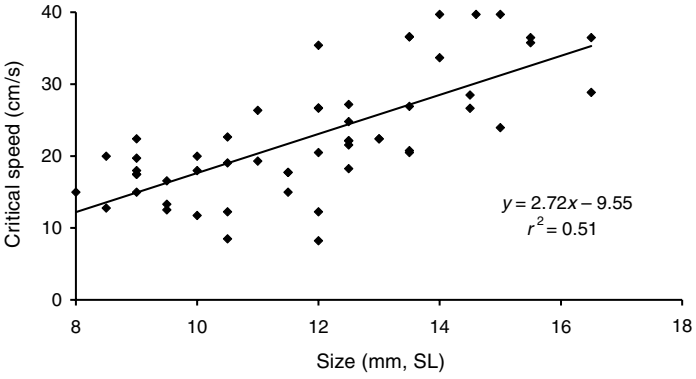

Figure 2

Critical speed of giant trevally (*Caranx ignobilis*) larvae of different sizes. At any size, variation in swimming speed was large.

Results

Larvae used in the critical speed trials were 21–30 days old, and ranged from 8.0 to 16.5 mm SL. Larvae up to 18 mm were used in the *in situ* observations. All fins were formed in the smallest individual and over the size range studied, the larvae were very deep bodied, primarily silver, and usually had six dark vertical bars laterally. Although the specimens used on any day did not constitute a random sample of the available sizes, they could be used to obtain a rough estimate of the growth rate over the experimental period. The range of size-at-age on any day was as much as 6.5 mm. Average growth over this period was 0.36 mm/d, and the slope of the size versus age line was significantly different from zero, but the relationship between size and age was weak (size=0.36 age + 2.87, $P<0.001$, $r^2=0.28$). Total lateral area increased approximately as the square of SL ($TA=0.51SL^{2.01}$, $r^2=0.93$), whereas propulsive area increased at a lower rate ($PA=0.34SL^{1.96}$, $r^2=0.94$).

Critical speed

Critical speed was measured in 54 individuals in eight batches of six over 10 days. Critical speed increased with size from about 12 cm/s in the smallest individuals (ca. 8 mm) to about 40 cm/s in the largest (16.5 mm, Fig. 2). For SL, a linear model provided the best fit for this relationship ($U_{crit}= 2.72SL-9.55$, $P<0.001$, $r^2=0.51$, $n=54$), but the difference between the linear model and the others was small (r^2 for the other models ranged from 0.43 to 0.49). Both TA and PA gave somewhat better fits than SL ($U_{crit}= 0.39TA + 5.25$, $r^2=0.58$; $U_{crit}= 0.22PA +5.73$, $r^2=0.55$). Size was a much better predictor of critical speed than was age ($U_{crit}=0.90age-0.22$, $P<0.01$, $r^2=0.13$, $n=54$).

The fastest individual within each 1-mm increment of size was considered the best performer, and these constituted 16.6% of all larvae. These nine best performing larvae swam at 20 to 40 cm/s. The nine best performing larvae had the same increase in performance with size (2.7 cm/s per each mm of growth) as the "all-individuals" line, but were 8 cm/s faster at all sizes ($U_{crit}=2.69SL-1.46$, $P<0.001$, $r^2=0.76$). Therefore, both average performers and "best performers" increased speed at 2.7 cm/s per each mm of growh in SL.

Scaled speed in terms of body lengths per second did not increase significantly with size ($P=0.07$, $r^2=0.06$), and the overall mean (±standard error) was 19 ±0.7 BL/s. The fastest 10% of individuals swam at a mean U_{crit} of 28.2 ±0.6 BL/s.

In situ speed

In situ speed was measured in 24 individuals ranging in size from 8.5 to 18 mm SL. Some individuals stopped and hovered at times during the observation period, but these pauses in swimming were incorporated into the speeds measured over the observation period. Observations were made a week apart when the larvae were 24 and 31 days old, respectively, and at a total of four locations that differed in depth, exposure, and bottom type. Observed *in situ* speeds ranged from 3 to 19 cm/s. The *in situ* speeds were less than the critical speed measurements (see below). Mean scaled *in situ* speed was 9.5 ±0.9 BL/s.

Overall, there was no significant increase in speed with size ($P=0.89$, $r^2=0.001$, $n=24$), but it was obvious that the larvae behaved differently in the different locations; therefore we examined the data for each location separately. Further, we eliminated observations on one larva that simply drifted without swimming and on four individuals that quickly swam to depths greater than 18 m and thus provided less than 5 minutes of observations, because short measurements of speed taken at steep angles of descent can be inaccurate. The *in situ* speed data on the 19 remaining individuals were used.

For each location, *in situ* speed increased with size, as expected, except, perhaps for the largest individual (Table 1, Fig. 3). For the three locations with three or more observations, *in situ* speed increased at 1.7–2.6 cm/s per each mm of growth depending on location (Table 1), and the 95% confidence interval for the three slopes overlapped broadly. However, because the height of the speed versus size lines varied (y intercept ranged from −6 to −18), the actual speed at any size differed among locations by as much as 10 cm/s. For the *in situ* speed data, PA provided fits with r^2 values that were very similar to those of SL. The r^2 for PA was 0.07 higher than that for SL for Nan Wan Bay North, equal for Her Chen, and 0.15 lower for Wan Li Tong.

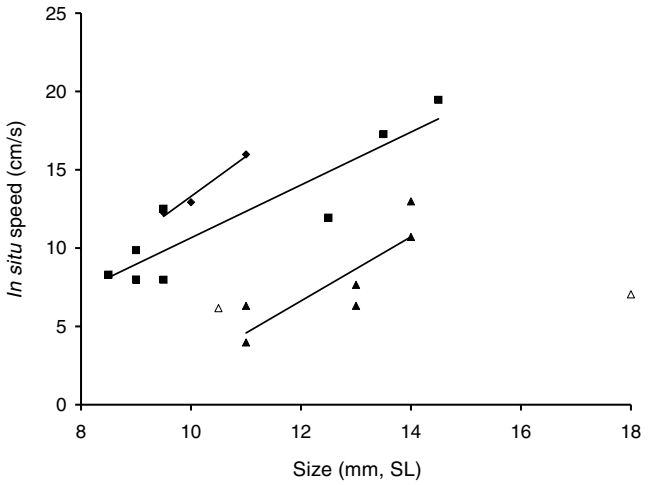

Figure 3

In situ speeds of giant trevally (*Caranx ignobilis*) larvae and juveniles of different sizes at different locations. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. See Table 1 for details of best-fitted regression lines for each area. No line was fitted to the two points from Nan Wan Bay South.

Table 2

Comparison of two measures of size-specific speed (cm/s) in *Caranx ignobilis* larvae. Dashes indicate that no data were available.

Size interval (mm, SL)	Mean *in situ* speed (n)	Mean U_{crit} (n)	Ratio: *in situ*/U_{crit}
8.1–9.0	8.7 (3)	17.5 (3)	0.50
9.1–10.0	11.4 (4)	15.3 (12)	0.75
10.1–11.0	8.1 (4)	18.0 (6)	0.45
11.1–12.0	– (0)	20.2 (9)	—
12.1–13.0	8.6 (3)	24.5 (9)	0.35
13.1–14.0	13.7 (3)	30.7 (7)	0.45
14.1–15.0	19.5 (1)	29.7 (4)	0.66
15.1–16.0	– (0)	36.1 (2)	—
16.1–17.0	– (0)	32.7 (2)	—
17.1–18.0	7.0(1)	– (0)	—
Mean ±SE			0.52 ±0.15

Comparison between critical speed and *in situ* speed

For each 1-mm (SL) increment in size, we calculated a mean speed for both critical speed (54 individuals) and *in situ* speed (19 individuals). These size-specific speeds are summarized in Table 2 (both measurements were not available for every size increment). The ratio of the two size-specific measures (*in situ*/U_{crit}) ranged from 0.35 to 0.75, and had a mean value of 0.52 ±0.15. The size-specific speed measures were not significantly correlated (*in situ*=0.45U_{crit}+1.45, r^2=0.47, P=0.13, n=6). Scaled *in situ* speed (BL/s) was one-half scaled U_{crit}.

Endurance

Endurance data were available for 12 individuals ranging in size from 9 to 14 mm SL, and for two ages (21 and 24 days at the start of the endurance run) measured in two batches of six. The range in fish swimming times was 12.6 to 105 hours. Swimming endurance increased with size from about 5 km in the smallest individuals to about 40 km in the largest (Fig. 4). Again, a linear model provided the best fit for this relationship ($End.$=5.2SL−41.5, P<0.001, r^2=0.80, n=12), and the difference between the linear model and the others was small (r^2 for the other models ranged from 0.73 to 0.79). In contrast to critical speed, the fit of the relationship between size and performance was not improved by using TA or PA instead of SL (r^2=0.57 and 0.62, respectively). Endurance also increased with age, but endurance data were available only for larvae of two ages (21 and 24 days). Size was a better predictor of performance than was age ($End.$= 6.6age−128, P=0.001, r^2=0.66, n=12).

Vertical distribution

There was not a significant overall relationship between mean swimming depth and size (P=0.29, r^2=0.05). In spite of this, larvae of different sizes differed in their depth selection behavior. The smallest larvae (8–10 and 10–12 mm) swam primarily between 4 and 10–12 m (Fig. 5, A and B). One larva of each of these smallest size groups did, however, swim deep monotonically. If one ignore these two deep-swimming larvae, both smallest size groups reached an overall mean depth of about 9 m

at about 5 minutes. The smaller (8–10 mm) larvae then stayed at about 9 m, whereas the larger (10–12 mm) larvae gradually ascended, reaching a mean depth of about 6 m by the end of the 10-min observation period. In contrast, larvae of 12–14 mm were more varied in their depth ranges, some reaching the surface, whereas others remained within 2–3 m of the release depth (Fig. 5C). Larvae of 12–14 mm had no overall temporal trend in depth and maintained a mean depth of about 5–6 m throughout the study period. Several of the larvae of this group did oscillate over a depth range of several m during the 10-min observation period. The largest larvae (14–18 mm) had more varied vertical-distribution ranges, leading to high amplitudes (Fig. 5D). Three of the five largest larvae swam deep monotonically and the other two oscillated—one reaching the surface after an initial descent, whereas the other reached our lower dive limit (16 m), but only after first ascending above the release depth for the first 5 minutes.

We found a weak relationship between depth amplitude (difference between deepest and shallowest observations) and size ($amp.=0.44SL + 1.7$, $P=0.03$, $r^2=0.21$, $n=24$); larger individuals swam over a greater range of depths owing to the tendency of larger larvae to either oscillate or to swim deep monotonically. Water column depth did not influence either mean swimming depth ($P=0.11$, $r^2=0.11$) or amplitude ($P=0.06$, $r^2=0.15$).

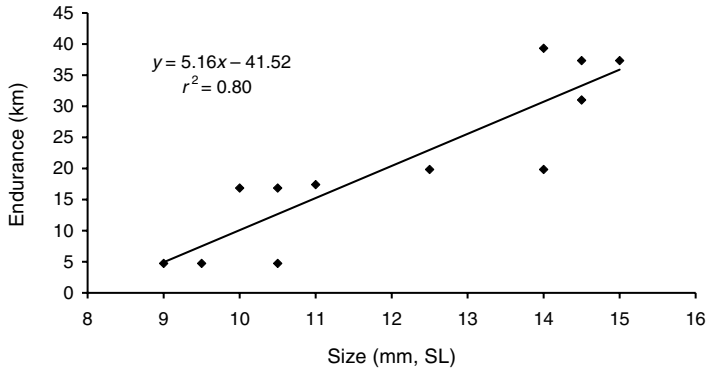

Figure 4

Endurance swimming of giant trevally (*Caranx ignobilis*) larvae of different sizes.

Table 3

Directionality of *in situ* swimming for *Caranx ignobilis* of different sizes. Only values from directional individuals are included for r (the length of the mean vector, which ranges from 0 to 1): the higher r, the more directional was the trajectory.

Size interval (mm SL)	*n*	*n* directional (Rayleigh test, $P<0.05$)	Range of r	Mean r
8–10	8	6	0.41–0.86	0.73
10–12	5	2	0.60–0.90	0.75
12–14	6	4	0.60–0.83	0.72
14–18	5	4	0.45–0.92	0.74

Orientation

Sixteen of the 24 larvae observed *in situ* had directional trajectories ($P<0.05$, Rayleigh test, Table 3). Figure 6 represents the direction frequency distribution of a *C. ignobilis* larva with average directionality. The remaining analyses included only the 16 individuals for which directional trajectories were found (termed "directional larvae" or "directional individuals" for the sake of brevity), but the same result was obtained when all 24 individuals were included. If all locations were considered together, the mean swimming directions of these 16 individuals had no overall directionality ($P>0.20$, Rayleigh test). In contrast, there was significant overall directionality off the west coast (Fig. 7A) where the larvae swam, on average, offshore or toward the west (269°, Rayleigh test, $P=0.024$). There was no indication of any overall directionality in mean swimming direction in Nan Wan Bay (Fig. 7B) (mean direction, 145°, $P=0.58$, Rayleigh test). Overall swimming direction, however, differed significantly between the west coast and Nan Wan Bay (Watson-Williams test, $P=0.028$).

We found only a limited indication that the directionality of the larvae changed with size (Table 3). There was no ontogenetic increase in precision of directionality (measured as r, the length of the mean vector) ($r^2=0.05$, $P>0.10$). Similarly, although the mean size of the eight nondirectional larvae was 11.6 mm, and that of the 16 directional larvae was 12.2 mm, this difference was not significant (*t*-test, $P=0.22$). In terms of overall orientation, larvae observed off the west coast were smaller by about 4 mm (*t*-test, $P=0.002$) and were studied a week earlier than those studied in Nan Wan Bay; therefore it is possible that the difference in overall swimming direction between locations was due to temporal or ontogenetic factors rather than to spatial factors. At the west coast location, the overall mean direction of the five small (8–9.5 mm) directional larvae was the same (268°) as the overall mean direction of the 4 large (10–14.5 mm) directional larvae, indicating there was no ontogenetic change in directionality.

Finally, within trajectories, there was no increase in directionality with time. The r value for the first half of the trajectories was not significantly different from the r value for the second half of the trajectory (Wilcoxon signed-rank test, $P>0.2$). Nor was there any indication that larger larvae had a greater difference in r between the first and second halves of their trajectories than did smaller larvae ($r^2=0.02$, $P>>0.20$).

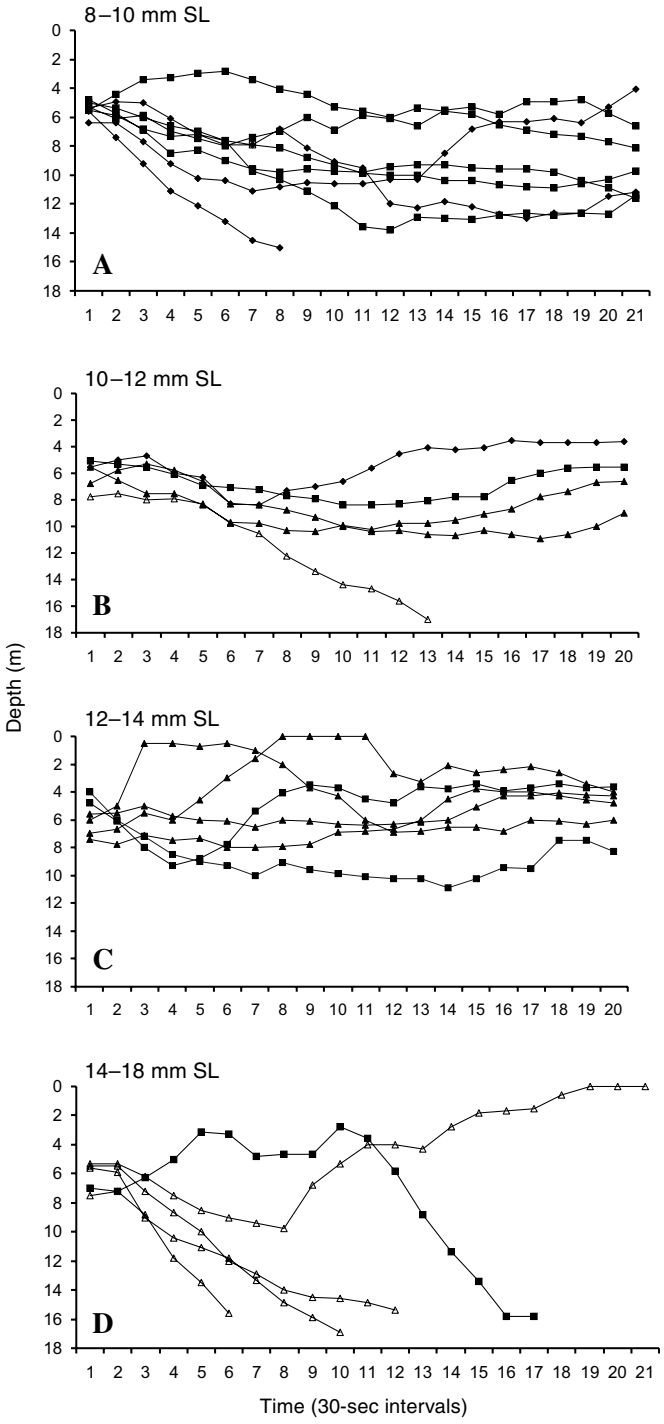

Figure 5

In situ vertical distribution trajectories for giant trevally (*Caranx ignobilis*) larvae and juveniles of four size groups. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. (**A**) 8–10 mm SL larvae; (**B**) 10–12 mm SL larvae; (**C**)12–14 mm SL larvae; (**D**) 14–18 mm SL larvae.

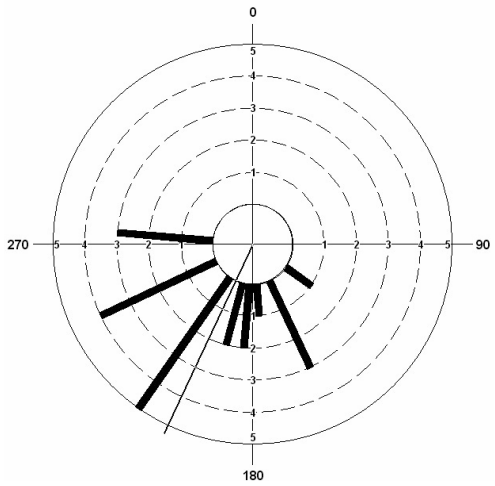

Figure 6

Frequency distribution of *in situ* swimming directions based on bearings taken every 30 seconds for an 18-mm-SL giant trevally (*Caranx ignobilis*,) at Nan Wan Bay South. Bearings are grouped into 10° intervals. The radius that penetrates the outer circle (thin line) is the mean direction. This significantly directional distribution (Rayleigh test, P=0.000001) has an r (length of the mean vector) of 0.76, which is close to the overall mean for the 16 directional individuals (Table 3). The numbers on dashed lines represent the number of times that bearing was recorded for a larva.

Other behaviors

Unplanned observations were made of feeding, interactions with other pelagic animals, and reactions with the bottom. At least nine of the 24 larvae were seen feeding, grabbing at, and apparently eating small zooplankton while swimming. One 12-mm larva encountered a large (ca. 30–40 cm) *Naso* sp. in open water and changed direction by 140° over the following minute. An 11-mm *C. ignobilis* encountered a jellyfish and briefly (<30 s) hovered under it. Five individuals (9–13.5 mm SL) came into visual contact with relatively high-relief coral reefs (at least the divers could clearly see the reefs) at Wan Li Tong and Her Chen. The larvae showed no particular interest in the reefs; two ascended slightly (0.5–1 m), two maintained a distance of 3–4 m from the reef surface as they swam over it, and one turned offshore. One 12.5-mm larva passed through a strong thermocline at 8 m that was very noticeable to the divers without slowing or giving any indication that the temperature change was sensed.

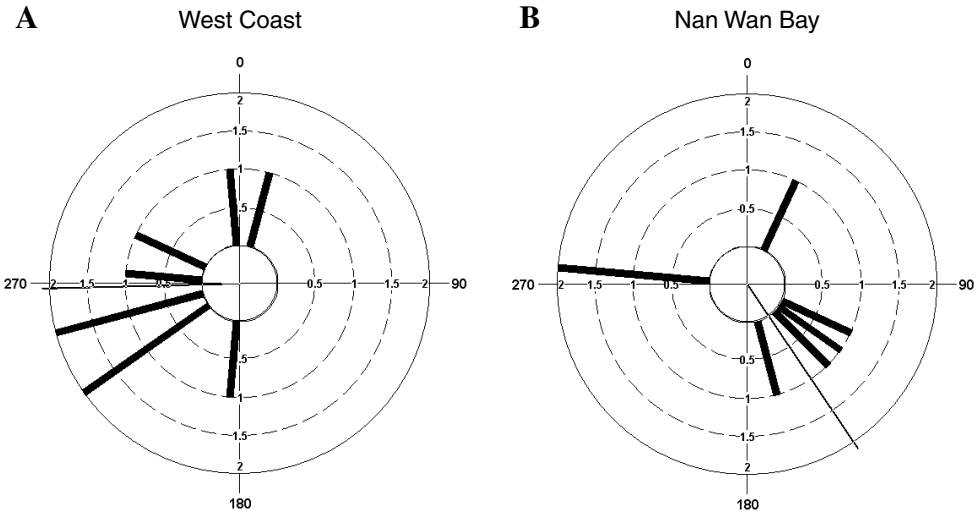

Figure 7

Frequency distributions of mean *in situ* swimming directions for giant trevally (*Caranx ignobilis*) larvae at two locations. Thick lines represent mean values for individuals, and the radius (thin line) that penetrates the outer circle represents the overall mean. The numbers on dashed lines represent the number of times that bearing was recorded for a larva. (**A**) West coast off Wan Li Tong and Her Chen, where larvae swam offshore: overall mean=268°, r=0.59, P=0.04. (**B**) Nan Wan Bay, where larvae had no overall swimming direction: overall mean=146°, r=0.29, P=0.58. "r" is the length of the mean vector, P is for the Rayleigh test.

Discussion

Previous studies of the behavior of larval carangids have focused primarily on their vertical distribution in the ocean and have been based on plankton net samples and on observations of the development of schooling-related behavior in the laboratory (see references at the beginning of this article). There have been no previous studies on the ontogeny of orientation or of vertical distribution determined from *in situ* observations, and only one article has considered the development of swimming abilities of carangid larvae.

Growth rates in *C. ignobilis* larvae of 0.36 mm/d in the laboratory and ca. 0.3–0.8 mm/d at the aquaculture farm at Kaohsiung, where we obtained larvae for our experiment, were comparable to the few reported field growth rates for larvae of other carangids. Small (<5 mm SL) larvae of Atlantic bumper (*Chloroscombrus chrysurus*) grew at 0.3–0.4 mm/d in the Gulf of Mexico (Leffler and Shaw, 1992), and larvae of two species of *Trachurus* grew at 0.2–0.7 mm/d (Hewett et al., 1985; Jordan, 1994). The *C. chrysurus* larvae were found at 26–30°C, whereas the two *Trachurus* spp. were living at about 15°C. In *T. declivis* (greenback horse mackerel), 8-mm larvae were about 17 days old and 12-mm larvae were about 22 days old (Jordan, 1994). In *T. symmetricus* (Pacific jack mackerel), a 10-mm larva was 40 days old and a 20-mm larva was about 57 days old (Hewitt, 1981). Growth rates for *C. ignobilis* in culture or in the laboratory are unlikely to be relevant to field situations, and the available field measurements of other species are either for much smaller larvae or for individuals in much cooler water and are unlikely to be applicable to *C. ignobilis*. Therefore, it is not possible to relate the size-based performance measures reported in our study to ages of larvae in the field. Further, for the laboratory-reared larvae that we used, size was a much better predictor of performance than was age, as is generally found to be the case (e.g., Fuiman and Higgs, 1997; Clark et al., 2005). We found that using PA instead of SL as a measure of size resulted in little or no improvement in the proportion of the variation in swimming performance that was explained by the linear relationships developed in our study. Other studies have had mixed results in this regard (Fisher et al., 2000; Clark et al., 2005).

Swimming speed of *C. ignobilis* increased rapidly with growth for both critical speed and *in situ* speed, although the rate of increase was greater for critical speed. Both in terms of actual speeds and rate of increase with growth, critical speeds of *C. ignobilis* are within the range of reported values for larvae of other warm water marine perciform fishes (Fisher et al., 2000; Clark et al., 2005). For larvae of benthic fishes about to settle (ca. 8–12 mm SL), pomacentrids have higher U_{crit} values than *C. ignobilis*, whereas apogonids, percichthyids, sciaenids, and sparids have similar U_{crit} values. *Seriola quinqueradiata* is the only other caran-

gid for which we could find information on ontogeny of swimming abilities (Sakakura and Tsukamoto, 1999), although the method of measuring swimming performance (so-called "routine speed") differed from those used in our study. Reared *S. quinqueradiata* larvae and juveniles of 5–40 mm TL were filmed swimming in small (30-cm diameter, 7-cm deep) laboratory tanks lacking currents and the speed was measured over 3-min intervals. Speed of *S. quinqueradiata* increased at about 0.4 cm/s per each mm of growth until about 10 mm TL, after which speed remained steady at about 2–2.5 cm/s. This is much slower, both in terms of rate of increase and absolute speed, than was found for either measure of swimming speed in *C. ignobilis*. Possibly, the slow speeds for *S. quinqueradiata* were due to the small containers in which the fish were confined and which lacked currents, as has been found for other species (Theilacker and Dorsey, 1980).

Although we did not study larvae smaller than 8 mm SL, it is safe to assume that smaller larvae have poorer swimming abilities. Previous investigations of swimming ontogeny have revealed that critical speed increases steadily with size (Fisher et al., 2000; Clark et al., 2005), as we did in our study; therefore it seems likely that a reasonable estimate of performance of smaller larvae can be obtained by extrapolating the linear relationship in Figure 2. Thus, a larva of 5 mm (about the size when the caudal fin is formed in carangids; Leis and Carson-Ewart, 2004) would be expected to have critical speeds of about 4–5 cm/s. We found that critical speeds for *C. ignobilis* were about twice *in situ* speeds, and similar relationships have been found for larvae of other species at other sizes (Fisher and Wilson, 2004; Leis and Fisher, in press). Therefore, a 5-mm *C. ignobilis* would be expected to be able to swim at about 2 cm/s (=72 m/h) in the ocean. This speed would have limited effectiveness for directly influencing horizontal position, but would be sufficient to determine vertical distribution at scales over which fish larvae are known to migrate vertically.

To put these swimming performances into an ecological context requires knowledge of ambient currents in the area of interest. If it is assumed that effective swimmers (those with swimming speed equal to or greater than average current speed [Leis and Stobutzki, 1999]) have the ability to control their dispersal by horizontal swimming, then the size at which larvae become effective swimmers is of interest to dispersal modelers. For example, at Lizard Island on the Great Barrier Reef, average current speeds are 10–15 cm/s (Frith et al., 1986). At Lizard Island, average performing *C. ignobilis* would become effective swimmers at about 7–9 mm SL on the basis of critical speed, and at about 11–14 mm based on *in situ* speed which is about half of critical speed (assuming the relationship between *in situ* and critical speeds found in the present study). The best performers would be able to reach these mean Lizard Island current speeds at about 4–6 mm SL, if based on critical speed (assuming the relationship in Fig. 2 applies to smaller larvae), and at 8–12 mm if based on *in situ* speed. Larvae that are too small to be effective swimmers may still readily influence their dispersal by other means, particularly by vertical swimming where current velocity is not uniform with depth (Sponaugle et al., 2002; Paris and Cowen, 2004). Speeds of only 1 cm/s (36 m/h) are sufficient for vertical migration, and this could be achieved by very small larvae. Indeed, vertical movements by small carangid larvae are well documented in studies where plankton nets were used (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001).

In situ speeds of *C. ignobilis* are within the range of those reported for other perciform species, although most of the available values are for settlement-stage larvae of demersal reef fishes (Trnski, 2002; Leis and Fisher, in press). Further, the rate of increase in speed at 1.6–2.6 cm/s per each mm of growth is similar to that found in the three other perciform species for which there are data (0.3–2.0 cm/s per each mm of growth; Leis et al., 2006). Differences in swimming speed among areas has been reported in a variety of reef fish larvae (Leis and McCormick, 2002); therefore finding a difference for *C. ignobilis* was not unexpected. This variation in behavior among areas and the fact that the rate of increase in speed with growth in the field was less than the increase of U_{crit} in the laboratory clearly demonstrates the complexities of applying laboratory measures to the field, and how behavior in the field can vary with location and situation. The cause for differences in behavior among locations was not clear in our study, but it is only through *in situ* observations that such differences can be discovered.

The approximately linear increase in swimming speed with growth found in *C. ignobilis* was similar to that reported in other species (Fisher et al., 2000; Clark et al., 2005). The ontogeny of endurance in *C. ignobilis* was also linear, in contrast to that of some other species, which are reported to have a strongly concave curvilinear increase in endurance with growth (Fisher et al., 2000; Clark et al., 2005). Perhaps this linearity was the result of studying *C. ignobilis* larger than 8 mm. In other species, preflexion and early postflexion larvae (which we did not study) have very low endurance, but endurance increases rapidly with growth in postflexion larvae.

All our speed measurements were made over periods of 10 minutes or less, but endurance measurements showed that speeds of 10 cm/s can be maintained from several to many hours, enabling distances of up to 40 km to be traversed. The ecological relevance of laboratory measurements of swimming endurance is difficult to assess because, on one hand, these are forced measures of performance, and it is unlikely that larval fishes would swim to exhaustion. On the other hand, endurance measurements are made without rest or food, and are therefore conservative because larvae of other species of the size studied in the present study can swim at least three times farther when fed (Fisher and Bellwood, 2001; Leis and Clark, 2005). In any case, it is clear that *C. ignobilis* larvae can swim for extended

periods at speeds that would make them effective swimmers in many situations. According to the relationship in Figure 4, *C. ignobilis* larvae of about 9 mm could swim without food or rest for about 13 hours (5 km at 10 cm/s) at a speed that is within their observed capabilities *in situ*: this ability increases markedly with growth. Clearly, *C. ignobilis* larvae from a size of 1 cm or less are capable of maintaining speeds of similar magnitude to mean ambient currents for periods of time long enough to strongly influence their dispersal.

Knowledge of vertical distribution of fishes is important because many things vary vertically in the ocean, including current velocity, food concentrations, and predators, all of which can strongly influence survival and dispersal. For these vertically varying factors, the conditions that larval and small juvenile fishes actually encounter are fully under their control because swimming abilities and sensory abilities capable of determining vertical position in the water column develop at a very small size. The *C. ignobilis* we observed in the ocean had considerable control over their vertical distribution, and the depths selected changed with size. Masuda and Tsukamoto (1996) noted ontogenetic changes in preferred light intensity in larvae of *P. dentex*, and it is possible that such changes influence the selection of depth in larval *C. ignobilis*. Two notes of caution are necessary in interpreting the depth-selection behavior and ontogenetic changes in this behavior. The largest larvae were primarily observed at one site, and, it is possible that vertical-distribution behavior varies among areas (Leis, 2004). Secondly, the largest larvae tended to swim to below our safety depth and we therefore do not know if they continued to descend, if they subsequently ascended (in accord with the oscillatory behavior observed in a number of larger individuals), or if they leveled off. In a similar experiment, much larger (60–140 mm) *Pseudocaranx dentex* juveniles initially descended several meters before ascending to a much shallower "preferred depth," usually within 60 seconds (Kuwada et al., 2000). We did not observe such ascents following an initial descent, but we cannot rule out the possibility that they occur for individuals that swam below our safe diving depth (Fig. 5D).

Orientation in the pelagic environment is difficult for fish larvae because of the movement of the water column and the scarcity of reference points in a moving pelagic environment. Orientation is, however, necessary for the arrival of late-stage larvae at nursery habitat and can greatly influence dispersal trajectories (Shanks, 1995; Leis and Carson-Ewart, 2003). Two-thirds of the *C. ignobilis* larvae that we observed swam directionally, as opposed to swimming randomly. This is a somewhat smaller percentage than the 80–100% for directional individuals at the settlement stage for demersal coral reef fishes of similar size (Leis and Carson-Ewart, 2003). Neither the proportion of individual *C. ignobilis* that swam directionally, nor the precision of their directional swimming, increased with growth. The lack of ontogenetic change in individual orientation—in contrast to speed, endurance, and vertical distribution—indicates that orientation ability develops early (at less than 8 mm SL) in *C. ignobilis* larvae. Of course, orientation may improve in individuals larger than those we studied.

The offshore swimming direction of *C. ignobilis* larvae found off the west coast is similar to behavior reported for larvae of some other species at other locations (e.g., Leis et al., 1996; Leis and Carson-Ewart, 2003), but could, in fact, be orientation to the west, rather than offshore. Observations off the east coast would be required to separate the possibilities, and any such test would need to take into account the possibility of temporal factors. The lack of any directionality in Nan Wan Bay is possibly a result of the "U" shape of the bay. Such a bay, where "offshore" constitutes less than half of the possible swimming directions, and where west is onshore, may present challenges to orientation that are greater than those present off an open coast. Alternatively, a bay may offer characteristics that would induce larvae to remain, rather than swim away as they did off the more open coast. Or, older larvae may prefer inshore environments, whereas younger ones do not. The important points, however, are that larvae of 8–15 mm SL demonstrated orientated swimming in the field and that smaller larvae swam in the same direction as larger ones. We can offer only speculation as to the types of cues that *C. ignobilis* may use to orient their swimming, and refer the reader to other sources for this information (e.g., Kingsford et al., 2002; Leis and McCormick, 2002). Our observations on *C. ignobilis* support other research showing that orientation behavior in fish larvae can be location-dependent (Leis et al., 1996; Stobutzki and Bellwood, 1998; Leis and Carson-Ewart, 2003), and if so, this feature add a further complication for attempts to model dispersal.

Our unplanned *in situ* observations of behavior shed light on little-known aspects of the early life history of *C. ignobilis,* which are otherwise difficult to study. Feeding activity by 8–18 mm larvae of *C. ignobilis* was common while they were swimming, as has been found with other species (Leis and Carson-Ewart, 1998). The only larva to encounter a large pelagic fish reacted in the same way as that reported for other species, namely with the apparent goal of moving away from the potential large predator before the small fish could be readily detected (Leis and Carson-Ewart, 2001). Such behavior in a reared individual with no experience with piscivorous fishes indicates that the behavior is not learned. Many carangids associate with jellyfish medusae when small (Shojima, 1962); therefore the brief association we observed between a jellyfish and a 10-mm *C. ignobilis* was not unexpected. *Caranx ignobilis* is considered to be reef-associated during some periods of its life history, but individuals of 9–13 mm do not seem to be inclined to associate with coral reefs. Unlike the larvae of many demersal reef fishes (Leis and Carson-Ewart, 2002), the larval *C. ignobilis* that we observed made no attempt to settle and showed no interest in coral reefs. If anything, *C. ignobilis* moved away from the coral reefs they encountered, although this behavior is not uncom-

mon in larvae of other species (Leis and Carson-Ewart, 1999, 2002). We observed one individual penetrate a thermocline, indicating not only a tolerance for rapid temperature change, but also, that the thermocline is not a barrier to vertical movement for *C. ignobilis*, as has been proposed sometimes for larvae of other species (e.g., Gray and Kingsford, 2003).

We used reared larvae in our study and it is possible that the behavior we observed may have differed from that of wild individuals. Results of studies comparing wild and reared individuals have been inconsistent. Some studies have shown large differences in behavior of reared and wild fishes, the most marked of which involve learned interactions with predators (Brown and Laland, 2001). Differences in swimming performance (in both directions) have been documented in some studies, but not others, or have been present at some developmental stages but not others (e.g., Blaxter, 1975; Dunmall and Shreer, 2003; Smith and Fuiman, 2004). Even if differences in predator-related behavior exist, swimming and orientation are presumably less dependent on experience and learning, and there is less reason to expect them to differ as well. The possibility that reared larvae of *C. ignobilis* may behave differently from wild larvae cannot be entirely dismissed, but the fact that *C. ignobilis* larvae were reared in conditions approaching those found in the field (but with the absence of predators)—kept in large outside ponds at an aquaculture farm and fed a natural assemblage of zooplankton—would presumably make large differences in behavior with their wild counterparts less likely. Unfortunately, we did not have access to wild *C. ignobilis*, and therefore we could not make direct tests; moreover, little is known of behavior in other carangid larvae upon which we might base comparisons.

Caranx ignobilis apparently schools when young (Myers, 1999), and the size range of larvae we studied overlapped with that at which schooling begins in other carangid species (Masuda and Tsukamoto, 1998). We did not attempt to observe schooling in *C. ignobilis*, but it is conceivable that some of the aspects of behavior may differ between individuals that are schooling and those that are solitary.

We observed strong ontogenetic changes in behavior of *C. ignobilis* across a size range of 8 to 18 mm SL. At any size, there was usually a wide range of performances present, and the best performers were able to swim much better than average performers. Given the very high mortality rates experienced by marine fish larvae, the average larva at any given size is unlikely to survive (Cushing, 1990), and it may be only the exceptional performers that do survive. Therefore, it may be more appropriate to use values for the best performers than for average performers in models of dispersal or survival. Increases in swimming abilities with growth were most marked, and significant swimming abilities would probably be present, in larvae as small as 5 mm SL based on extrapolation of performance at size relationships. Ontogenetic changes in vertical distribution behavior were more complex and difficult to interpret, but depth selection seemed to be more variable (both within and among individuals) in larger larvae. We found that orientation behavior of small *C. ignobilis* was already developed and did not increase ontogenetically, although the direction they swam differed between locations. Behavior in small *C. ignobilis* was complex and swimming abilities were well developed. These behaviors are capable of strongly influencing survival and dispersal and show that the larvae of some pelagic fishes have behavioral capabilities similar to those recently documented for larvae of demersal reef fishes (Leis and McCormick, 2002).

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Literature cited

Ahlstrom, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull. 60:107–146.

Batschelet, E.
1981. Circular statistics in biology, 371 p. Academic Press, London.

Blaber, S. J. M., and D. P. Cyprus.
1983. The biology of the Carangidae (Teleostei) in Natal estuaries. J. Fish. Biol. 22:173–188.

Blaxter, J. H. S.
1975. Reared and wild fish—how do they compare? Proc. 10th Europ. Symp. Mar. Biol. 1:11–26.

Brett, J. R.
1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21:1183–1226.

Brown, C., and K. Laland.
2001. Social learning and life skills training for hatchery reared fish. J. Fish. Biol. 59:471–493.

Clark, D. L., J. M. Leis, A. C. Hay, and T. Trnski.
2005. Swimming ontogeny of larvae of four temperate marine fishes. Mar. Ecol. Prog. Ser. 292: 287–300.

Cushing, D. H.
1990. Plankton production and year class strength in

fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249–293.

Dunmall, K. M., and J. F. Schreer.
2003. A comparison of the swimming and cardiac performance of farmed and wild Atlantic salmon, *Salmo salar*, before and after gamete stripping. Aquaculture 220:869–882.

Fisher, R., and D. R. Bellwood.
2001. Effects of feeding on the sustained swimming abilities of late-stage larval *Amphiprion melanopus*. Coral Reefs 20:151–154.

Fisher, R., D. R. Bellwood, and S. D. Job.
2000. Development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. 202:163–173.

Fisher, R., and S. K. Wilson.
2004. Maximum sustainable swimming speeds of late-stage larvae of nine species of reef fishes. J. Exp. Mar. Biol. Ecol. 312:171–186.

Flores-Coto, C., R. Rivas-Vega, F. Zavala-Garcia, and J. Sanches-Robles.
2001. Vertical distribution of larval carangids in the southern Gulf of Mexico. Gulf Carib. Res. 13:1–8.

Frith, C. A., J. M. Leis, and B. Goldman.
1986. Currents in the Lizard Island region of the Great Barrier Reef Lagoon and their relevance to potential movements of larvae. Coral Reefs 5:81–92.

Fuiman, L. A., and D. M. Higgs.
1997. Ontogeny, growth and the recruitment process. *In* Early life history and recruitment in fish populations (R. C. Chamber, and E. Trippel, eds.), p. 225–249. Chapman and Hall, London.

Gray, C. A., and M. J. Kingsford.
2003. Variability in thermocline depths and strength, and relationships with vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. Mar. Ecol. Prog. Ser. 247:211–224.

Hewitt, R.
1981. The value of pattern in the distribution of young fish. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178: 229–236.

Hewitt, R. P., G. H. Theilacker, and N. C. H. Lo.
1985. Causes of mortality in young Jack mackerel. Mar. Ecol. Prog. Ser. 26: 1–10.

Hoese, D. F., D. J. Bray, G. R. Allen, C. Allen, N. Cross, and J. R. Paxton.
In press. Pisces. Zoological catalogue of Australia. Australian Biological Resources Survey, Canberra, Australia.

Johannes, R. E.
1981. Words of the lagoon, 245 p. Univ. California Press, Berkeley, CA.

Jordan, A. R.
1994. Age, growth and back-calculated birthdate distributions of larval jack mackerel, *Trachurus declivis* (Pisces:Carangidae), from eastern Tasmanian coastal waters. Aust. J. Mar. Freshw. Res. 45:19–33.

Kingsford, M. J., J. M. Leis, A. Shanks, K. Lindeman, S. Morgan, and J. Pineda.
2002. Sensory environments, larval abilities and local self-recruitment. Bull. Mar. Sci. 70 (suppl. 1): 309–340.

Kuiter, R. H.
1993. Coastal fishes of south-eastern Australia, 437 p. Crawford House, Bathurst, New South Wales, Australia.

Kuwada, H., R. Masuda, S. Shiozawa, T. Kogane, K. Imaizumi, and K. Tsukamoto.
2000. Effect of fish size, handling stress and training procedure on the swimming behavior of hatchery-reared striped jack: implications for stock enhancement. Aquaculture 185:245–256.

Leffler, D. L., and R. F. Shaw.
1992. Age validation, growth, and mortality of larval Atlantic bumper (Carangidae: *Chloroscombrus chrysurus*) in the northern Gulf of Mexico. Fish. Bull. 90:711–719.

Leis, J. M.
2004. Vertical distribution behaviour and its spatial variation in late-stage larvae of coral-reef fishes during the day. Mar. Freshw. Behav. Physiol. 37:65–88.

Leis, J. M., and B. M. Carson-Ewart.
1997. Swimming speeds of the late larvae of some coral reef fishes. Mar. Ecol. Prog. Ser. 159:165–174.
1998. Complex behaviour by coral-reef fish larvae in open-water and near-reef pelagic environments. Environ. Biol. Fish. 53: 259–266.
1999. *In situ* swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the Coral Trout (Pisces, Serranidae, *Plectropomus leopardus*). Mar. Biol. 134:51–64.
2001. Behavioural differences in pelagic larvae of four species of coral-reef fishes between two environments: ocean and atoll lagoon. Coral Reefs 19:247–257.
2002. *In situ* settlement behaviour of damselfish larvae (Pisces: Pomacentridae). J. Fish. Biol. 61:325–346.
2003. Orientation of pelagic larvae of coral-reef fishes in the ocean. Mar. Ecol. Prog. Ser. 252:239–253.
2004. The larvae of Indo-Pacific coastal fishes, 870 p. Brill, Leiden, The Netherlands.

Leis, J. M., and D. L. Clark.
2005. Feeding greatly enhances endurance swimming of settlement-stage reef-fish larvae (Pomacentridae). Ichthyol. Res. 52:185–188.

Leis, J. M., and R. Fisher.
In press. Swimming speed of settlement-stage reef-fish larvae measured in the laboratory and in the field: a comparison of critical speed and *in situ* speed. Proc. 10th Internat. Coral Reef Symp., Okinawa, Japan.

Leis, J. M., A. C. Hay, and T. Tronski.
2006. *In situ* ontogeny of behaviour in pelagic larvae of three temperate, marine, demersal fishes. Mar. Biol. 148(3):655–669.

Leis, J. M., and M. I. McCormick.
2002. The biology, behaviour and ecology of the pelagic, larval stage of coral-reef fishes. *In* Coral reef fishes: new insights into their ecology (P. F. Sale, ed.), p. 171–199. Academic Press, San Diego, CA.

Leis, J. M., and I. C. Stobutzki.
1999. Swimming performance of late pelagic larvae of coral-reef fishes: *in situ* and laboratory-based measurements. *In* Proc. 5th Indo-Pacific Fish Conf., Noumea, 1997 (B. Séret, and J.-Y. Sire, eds.), p. 575–583. Société Francaise d'Ichtyologie & Institut de Recherche pour le Développment, Paris.

Leis, J. M., H. P. A. Sweatman, and S. E. Reader.
1996. What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behaviour. Mar. Freshw. Res. 47:401–411.

Masuda, R., and K. Tsukamoto.
1996. Morphological development in relation to photo-

taxis and rheotaxis in the striped jack, *Pseudocaranx dentex*. Mar. Freshw. Behav. Physiol. 28: 75–90.

1998. The ontogeny of schooling behaviour in the striped jack. J. Fish. Biol. 52:483–493.

1999. School formation and concurrent developmental changes in carangid fish with reference to dietary conditions. Environ. Biol. Fish. 56:243–252.

Myers, R. F.

1999. Mirconesian reef fishes. A comprehensive guide to the coral reef fishes of Micronesia, 330 p. Coral Graphics, Guam, U.S.A.

Olivar, M. P., and A. Sabatés.

1997. Vertical distribution of fish larvae in the northwest Mediterranean Sea in spring. Mar. Biol. 129: 289–300.

Paris, C. B., and R. K. Cowen.

2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol. Oceanogr. 49:1964–1979.

Randall, J. E., G. R. Allen, and R. C. Steene.

1997. Fishes of the Great Barrier Reef and Coral Sea, 557 p. Crawford House, Bathurst, New South Wales, Australia.

Sakakura, Y., and K. Tsukamoto.

1996. Onset and development of cannibalistic behaviour in early life stages of yellowtail. J. Fish. Biol. 48:16–29.

1999. Ontogeny of aggressive behaviour in schools of yellowtail, *Seriola quinqueradiata*. Environ. Biol. Fish. 56:231–242.

Shanks, A. L.

1995. Orientated swimming by megalopae of several eastern North Pacific crab species and its potential role in their onshore migration. J. Exp. Mar. Biol. Ecol. 186:1–16.

Shojima, Y.

1962. On the postlarvae and juveniles of carangid fishes collected together with the Jelly-fishes. Contrib. Seikai Regional Fish. Res. Lab. 147:49–58.

Smith, M. E., and L. A. Fuiman.

2004. Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. J. Exp. Mar. Biol. Ecol. 302:17–33.

Smith-Vaniz, W. F.

1999. Carangidae. *In* FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific., vol. 4, Bony fishes, part 2 (Mugilidae to Carangidae) (K. E. Carpenter, and V. H. Niem, eds.), p. 2659–2756. FAO, Rome.

Sponaugle, S., R. K. Cowen, A. Shanks, S. G. Morgan, J. M. Leis, J. Pineda, G. W. Boehlert, M. J. Kingsford, K. Lindeman, C. Grimes, and J. L. Munro.

2002. Predicting self-recruitment in marine populations: biophysical correlates. Bull. Mar. Sci. 70:341–376.

Stobutzki, I. C.

1998. Interspecific variation in sustained swimming ability of late pelagic stage reef fish from two families (Pomacentridae and Chaetodontidae). Coral Reefs 17:111–119.

Stobutzki, I. C., and D. R. Bellwood.

1994. An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. J. Exp. Mar. Biol. Ecol. 175:275–286.

1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Mar. Ecol. Prog. Ser. 149: 35–41.

1998. Nocturnal orientation to reefs by late pelagic stage coral reef fishes. Coral Reefs 17:103–110.

Sudekum, A. E., J. D. Parrish, R. L. Radtke, and S. Ralston.

1991. Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. Fish. Bull. 89:493–513.

Theilacker, G., and K. Dorsey.

1980. Larval fish diversity, a summary of laboratory and field research. UNESCO Intergov. Oceanogr. Comm. Workshop Rep. 28:105–142.

Trnski, T.

2002. Behaviour of settlement-stage larvae of fishes with an estuarine juvenile phase: *in situ* observations in a warm-temperate estuary. Mar. Ecol. Prog. Ser. 242:205–214.

von Westernhagen, H.

1974. Observations on the natural spawning of *Alectis indicus* (Rüppell) and *Caranx ignobilis* (Forsk.) (Carangidae). J. Fish. Biol. 6:513–516.

Wetherbee, B. M., K. N. Holland, C. G. Meyer, and C. G. Lowe.

2004. Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, *Caranx ignobilis*. Fish. Res. 67:253–263.

Yu, N.-H.

2002. New challenges: breeding species in Taiwan, VIII. Fish Breeding Assoc., Republic of China, Kaohsiung, Taiwan, 52 p. [In Chinese, but in English at www.fish.org.tw.]

Zar, J. H.

1996. Biostatistical analysis, 3rd ed., 662 p. Prentice Hall, Upper Saddle River, NJ.