RESEARCH ARTICLE

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In situ ontogeny of behaviour in pelagic larvae of three temperate, marine, demersal fishes

Abstract The ontogeny of behaviour relevant to dispersal was studied in situ with reared pelagic larvae of three warm temperate, marine, demersal fishes: *Argyrosomus japonicus* (Sciaenidae), *Acanthopagrus australis* and *Pagrus auratus* (both Sparidae). Larvae of 5–14 mm SL were released in the sea, and their swimming speed, depth and direction were observed by divers. Behaviour differed among species, and to some extent, among locations. Swimming speed increased linearly at 0.4–2.0 cm s^{-1} per mm size, depending on species. The sciaenid was slower than the sparids by 2–6 cm s^{-1} at any size, but uniquely, it swam faster in a sheltered bay than in the ocean. Mean speeds were 4–10 body lengths s^{-1}. At settlement size, mean speed was 5–10 cm s^{-1}, and the best performing individuals swam up to twice the mean speed. In situ swimming speed was linearly correlated ($R^2 = 0.72$) with a laboratory measure of swimming speed (critical speed): the slope of the relationship was 0.32, but due to a non-zero intercept, overall, in situ speed was 25% of critical speed. Ontogenetic vertical migrations of several metres were found in all three species: the sciaenid and one sparid descended, whereas the other sparid ascended to the surface. Overall, 74–84% of individual larvae swam in a non-random way, and the frequency of directional individuals did not change ontogenetically. Indications of ontogenetic change in orientated swimming (i.e. the direction of non-random swimming) were found in all three species, with orientated swimming having developed in the sparids by about 8 mm. One sparid swam W (towards shore) when < 10 mm, and changed direction towards NE (parallel to shore) when > 10 mm. These results are consistent with limited in situ observations of settlement-stage wild larvae of the two sparids. In situ, larvae of these three species have swimming, depth determination and orientation behaviour sufficiently well developed to substantially influence dispersal trajectories for most of their pelagic period.

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Introduction

Upon hatching from a pelagic egg, the larvae of the vast majority of demersal teleost fishes are very small (1–3 mm) and poorly developed, often little more than a yolk sac with a tail, and with very limited behavioural abilities. With respect to currents, they are probably correctly regarded as being close to passive. In contrast, by the time the larvae settle from the pelagic environment into benthic habitats, they are clearly able to influence their dispersal trajectories: they are morphologically well developed with good swimming abilities, strong control over vertical distribution and the capacity to orientate rather than swim randomly (Leis and McCormick 2002; Leis and Carson-Ewart 2003; Leis, in press).

How and when these behaviours develop during the pelagic larval period is largely unknown. Behaviours that are important from the point of view of dispersal and retention such as swimming and orientation are difficult to study in the laboratory and the results of laboratory studies cannot realistically be applied directly to field situations (von Westernhagen and Rosenthal 1979; Theilacker and Dorsey 1980). On the other hand, it is logistically challenging to study the behaviour of such small, often transparent animals in the ocean, and most attempts to study behaviour of fish larvae in situ have concentrated on larger larvae near the end of their pelagic period (Leis, in press).

This dearth of knowledge about the ontogeny of behaviour in larval fishes inhibits the development of realistic dispersal models. Most modellers are yet to recognize the need to incorporate behaviour into

dispersal models (Armsworth 2000), and the laudable attempts to do this so far have been forced to use assumptions of behavioural capabilities, questionable application of laboratory measures of behaviour in unrelated, morphologically very different taxa, or rather crude 'on-off' applications of behavioural capabilities during the settlement stage (Werner et al. 1993; Wolanski et al. 1997; Porch 1998; Hare et al. 1999; Armsworth 2000; Armsworth et al. 2001). We have some understanding of the end points: planktonic start and nektonic finish. What is needed now is an understanding of when during the pelagic stage swimming and orientation abilities develop, and a quantitative description of the increase in capabilities in relation to morphological development of the larvae.

For larval fish behaviour, size is usually a better ontogenetic proxy than age because 'a given ontogenetic state is usually reached at a uniform size for a species, regardless of how long it takes to achieve it' (Fuiman and Higgs 1997). This conclusion has been reinforced in more recent work on the ontogeny of larval-fish behaviour (Clark et al. 2005; Leis et al., in press). As poikilotherms with indeterminate growth, growth rates in fish species can vary widely among individuals, and this combined with the developmental processes that take place during the larval phase ensure that size-at-age will vary, as will morphological development and behavioural capabilities (Fuiman et al. 2005).

Obtaining larvae from a wide variety of sizes and states of development suitable for study of behavioural ontogeny presents challenges. Settlement-stage wild larvae of some species can be captured in good condition in light traps (Doherty 1987) or fixed nets (Dufour and Galzin 1993; Dufour 1994) that take advantage of stage-specific behaviours (e.g. phototaxis or onshore settlement movements). Such settlement-stage larvae have been the basis for much of what is known about behaviour of fish larvae. Younger, wild larvae are usually more fragile, and can usually be captured only with plankton nets that are highly likely to kill or injure them in the process.

Therefore, to study behaviour of younger larvae, researchers have turned to species that can be reared in captivity. This requires a major logistic effort, but has produced an important body of laboratory-based work on temperate taxa, particularly clupeiform and gadiform fishes, and a few perciform taxa (e.g. Theilacker and Dorsey 1980; Blaxter 1986; Burke et al. 1995; De Vries et al. 1995; Forward et al. 1996; Fuiman et al. 1999;

Fuiman and Cowan 2003; Smith and Fuiman 2004). Japanese workers have expanded this behavioural research effort, relying on larvae of warm temperate species that are reared for aquaculture purposes, rather than for research goals (e.g. Fukuhara 1985, 1987; Masuda and Tsukamoto 1996, 1998). Again, this research effort was based on laboratory observations. More recently, larvae reared for research purposes have been used in the laboratory to study the ontogeny of swimming in perciform coral reef fishes (e.g. Fisher et al. 2000; Fisher and Bellwood 2001; Fisher and Bellwood 2002; Fisher and Bellwood 2003; Fisher 2005).

The present study applies the method of using reared larvae of a range of sizes and developmental stages from aquaculture sources to the in situ approach to the study of larval-fish behaviour by divers (Leis et al. 1996). We studied the ontogeny of behaviours relevant to dispersal (swimming speed, vertical distribution and orientation) in three species of warm temperate, demersal, perciform fishes. We were also able to examine possible differences in behaviour among locations. Importantly, laboratory-based studies of the ontogeny of swimming performance in reared larvae of these species (Clark et al. 2005) and in situ observations on the settlement-stage larvae of two of them were available for comparison (Trnski 2002).

Methods

Three species of commercially important temperate marine fishes were studied: *Argyrosomus japonicus* (Sciaenidae), *Pagrus auratus* (Sparidae) and *Acanthopagrus australis* (Sparidae) (Table 1). All larvae were obtained from aquaculture facilities producing rearing stock for commercial culture. Larvae of *A. japonicus* and *P. auratus* were reared at New South Wales Fisheries, Port Stephens Research Centre (NSWF), in 2,000 l aquaria at 22.6–24°C, under a 14:10 h light:dark photoperiod. The larvae were fed rotifers (*Brachionus plicatilis*) from 4 days after hatching (dah) and brine shrimp (*Artemia*) nauplii from 15 dah (Fielder and Bardsley 1999). Larvae of *A. australis* were reared at Searle Aquaculture (SA), northern NSW in 2,500 l aquaria at 21–23°C, in a hothouse providing 70–80% ambient light. The larvae were fed rotifers and copepod nauplii from 3–4 dah and *Artemia* nauplii from 14 dah. These rearing protocols had been developed to optimize the growth and survival of each species. Illustrations and descriptions of the larval development of these three

Table 1 Details of larvae studied

Species	N (recaptured)	Size range (mm, SL)	Age range (dah)	Dates	Size at settlement (mm SL)
Argyrosomus japonicus	48 (39)	5.0–14.2	19–30	6 days in January–March 2002	12–13
Acanthopagrus australis	44 (29)	7.2–11.5	31–37	5 days in September 2002	8–11
Pagrus auratus	23 (18)	7.0–9.3	28–31	4 days in November 2001	9–12

Sizes are of specimens fixed and preserved in 70% ethanol. Settlement sizes are adapted from Clark et al. (2005)

species are available in Neira et al. ([1998](#)). All body sizes of larvae are given as standard length (SL) unless stated otherwise.

In situ observations of the larvae were made off the east coast of New South Wales, Australia. Larvae of *A. japonicus* and *P. auratus* were studied in the vicinity of Port Stephens (32°25′S, 152°12′E), both inside, near the entrance of the port at Shoal Bay and Jimmy's Beach, and outside the port in ocean conditions of the Tasman Sea, near Point Stephens. Port Stephens is a large, sheltered bay with a narrow mouth and a surface area of over 1,000 km^2. Within Port Stephens, observations were made 100–1,000 m offshore over bottom depths of 2.5–9.5 m, and off Point Stephens they were made 100–500 m offshore over depths of 10–20 m. Larvae of *A. australis* were studied in the Tasman Sea off Yamba (29°25′S, 153°22′E), at bottom depths of 20–25 m and distances of 500–1,500 m offshore, with the exception of observations on eight larvae made about 50 m off Turner's Beach in water 5–7 m deep. Water temperatures were 20–24°C in the Port Stephens vicinity and 19–20°C off Yamba. All observations were made over sandy bottoms. Because observations were made in both the ocean and the semi-enclosed port, we were able to determine if behaviour differed between locations.

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, until the larvae were used for observations within 6 h.

The behaviour of the larvae was observed following the standard in situ procedures (Leis et al. [1996](#); 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 divers followed. The observer diver's sole job was to follow the larva while the second diver, following the observer, recorded the data. The direction the observer diver was facing when he or she released the larva was randomized. 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 individuals that were not recaptured. Water-column depth was measured by the depth sounder on the support boat at the start of each larval release.

Swimming speed, depth and direction were measured in situ. We attempted to observe each larva for 10 min, taking measurements of swimming depth and direction with a dive computer and compass, respectively, every 30 s. Speed was calculated from distance travelled as measured by a calibrated flowmeter over the full time of observation (Leis and Carson-Ewart [1997](#)). Thus, we measured larva speed and direction (i.e. velocity) relative to a water column that was moving, not velocity relative to the bottom, which would be a vector sum of current velocity and larva velocity. Observations of larvae were made in current speeds up to 80 cm s^{-1}. Larvae were not followed deeper than 15–20 m (depending on the dive) for safety reasons, so observations on some individuals were curtailed. Observations on seven *P. auratus* larvae at Shoal Bay inside Port Stephens were not used for analysis of vertical distribution because of the very shallow water (2.5–5.0 m) in that location. Depth amplitude is the difference between the greatest and least depth observed for an individual.

Data analysis

To determine the best predictor of performance, values of swimming speed were regressed against age (dah) and SL using linear, logarithmic, power and exponential models. In all cases, the linear model provided the best fit (highest R^2), and only these relationships are reported. Relationships using age as the independent variable are not reported as none had a slope significantly different from zero, probably because of the narrow range of ages available. The wide range of sizes of larvae at any age was possibly a result of rearing conditions, although high variability in size-at-age is common in field-collected larvae (Fuiman et al. [2005](#)). Among our study species, growth rates of larvae in the field are unknown except for limited information on one species (Kingsford and Atkinson [1994](#)), so the extent to which the size-at-age distribution of reared larvae varies from a 'natural' distribution is difficult to determine. In some analyses, larvae were partitioned by size, either into > or <10 mm, or into size increments. The increments were 1 mm for the two sparids and 2 mm for the sciaenid for which we had observations over the widest size range.

All bearings are given as degrees magnetic, which is 12–13° to the east of true north in the study areas. From these bearings and the flowmeter data, we estimated swimming direction and speed relative to the water. Standard error is abbreviated as se to avoid confusion with SE (for southeast). Confidence interval is abbreviated as CI.

The 21 observations of swimming depth normally made on an individual may be autocorrelated, thus rendering the data unsuitable for statistical tests which assume that observations are independent. To test for this, autocorrelation charts were generated (by 'Statistix', NH Analytical Software, St. Paul, MN) for individual trajectories (Leis [2004](#)). In about 13% of individuals, no significant autocorrelation was found; so all observations could be used. In about 70% of cases, significant autocorrelation was found only at a lag of 1; so only alternate observations were used. In about 17% of individuals, significant autocorrelation extended to a lag of 2, necessitating use of only every third

observation. In no case was significant autocorrelation detected beyond a lag of 2. Once the autocorrelation was eliminated, the remaining observations were used to construct depth–frequency distributions for all individuals within defined size groupings, and these depicted the proportion of observations within 2.5 m depth intervals. The depth–frequency distributions were then tested for differences among size groups of larvae by the Kolmogorov–Smirnov (K–S) test.

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 (hereafter Ra test) was used for single-sample hypotheses about directional swimming, and the Watson–Williams test was used for multiple-sample hypotheses. Two types of orientation were examined: 1—that of individual larvae, wherein the distribution of the bearings taken every 30 s was tested; and 2—that of mean bearings of sets of larvae, wherein the means of individual larvae were tested. Orientation 1 is referred to as non-random swimming. Orientation 2 is referred to as orientated swimming. For testing distributions consisting of mean bearings of individual larvae (orientation 2), only means from individuals with non-random trajectories were included. Circular statistical procedures were performed with Oriana software (Kovach Computing Services, Wales, UK). For all statistical tests, we report actual P values whenever possible, but consider $P < 0.05$ to constitute a 'significant' result.

Results

A total of 115 larvae provided useful data (Table 1). All larvae were postflexion-stage individuals, with the exception of two *A. japonicus* of 5.0–5.1 mm that were in the late flexion stage. Depending on species, 70–83% of individuals were observed for the full 10 min, and 66–81% were recaptured at the end of the observation period. Of the 26 larvae that were observed for less than 10 min, only two provided less than 4 min of observation. Most were lost by the divers, usually in murky or turbulent conditions, but five *A. australis* were abandoned because they went deeper than our safety depth, one *A. japonicus* (the second largest observed) settled onto sandy bottom after 4.5 min, and two *A. japonicus* were eaten by fish predators, one pelagic and one benthic.

Swimming speed

Swimming speed increased with size, and a linear model was the best representation of this increase, although there was much variation in speed at any size, and the rate of increase with growth differed among species (Table 2, Fig. 1). Speed increased at 0.36, 1.15 and 2.01 cm s^{-1} per mm size increase in *A. japonicus*, *A. australis* and *P. auratus*, respectively. The rate of increase of the latter two species did not differ significantly, but both were greater than that of *A. japonicus* (based on 95% CI, Table 2). Table 3 summarizes speed at size extremes and the sizes at which the three species attained means of 5 and 10 cm s^{-1}. The regression equations in Table 2 provide the best description of the relationship between size and speed across the entire size range, but for the sciaenid (*A. japonicus*) there was an indication of some non-linearity among smaller larvae as the mean speed within 1 mm increments changed little until after 7–8 mm. Differences in speed with location are considered below.

Only a moderate proportion (21–39%) of the variation in speed with size was explained by the best fit lines when all data were considered (Table 2). The difference in speed between the best and worst performer at any size was up to 7 cm s^{-1} in *A. japonicus*, 8 cm s^{-1} in *P. auratus* and 6 cm s^{-1} in *A. australis* (Fig. 1a–c). The speed of the fastest individual in each 1 mm size increment was 1–5 cm s^{-1} more than the mean speed (*A. japonicus* 1–3, *A. australis* 1–2 and *P. auratus* 2–5 cm s^{-1} faster).

Only in *A. japonicus* was there any indication that the speed vs size relationship varied among areas (Fig. 1). For *A. japonicus* observed in the ocean ($n = 25$), the relationship between size and swimming speed was weak although significant, and the rate of increase in speed with size was low (Table 2): the relationship was similar to that for larvae from both areas combined. In contrast, *A. japonicus* larvae observed in the port ($n = 23$) had a much stronger relationship between speed and size, and a much greater rate of increase in speed with size. The 95% CI of the slopes of the two relationships did not overlap (Table 2), corroborating the difference between locations. In situ speed of smaller *A. japonicus* was similar in both the ocean and the port, but in larger larvae, the mean speeds in the port were 2–3 cm s^{-1} greater than speeds in the ocean (Fig. 1), and approached those of the sparids. Further, the 95% CI of

Table 2 Best fit regression lines for relationship between speed (cm s^{-1}) and size (mm, SL)

	Speed of all larvae	Slope 95% CI
Argyrosomus japonicus, all locations	0.36SL + 0.60, $R^2 = 0.21$, $P = 0.001$, $n = 48$	0.15–0.57
Argyrosomus japonicus, ocean	0.32SL + 0.47, $R^2 = 0.19$, $P = 0.03$, $n = 25$	0.03–0.60
Argyrosomus japonicus, port	0.92SL − 3.03, $R^2 = 0.66$, $P < 0.0001$, $n = 23$	0.62–1.22
Acanthopagrus australis	1.15SL − 3.37, $R^2 = 0.39$, $P < 0.0001$, $n = 44$	0.70–1.60
Pagrus auratus	2.01SL − 10.60, $R^2 = 0.37$, $P = 0.002$, $n = 23$	0.83–3.19

a *Argyrosomus japonicus*

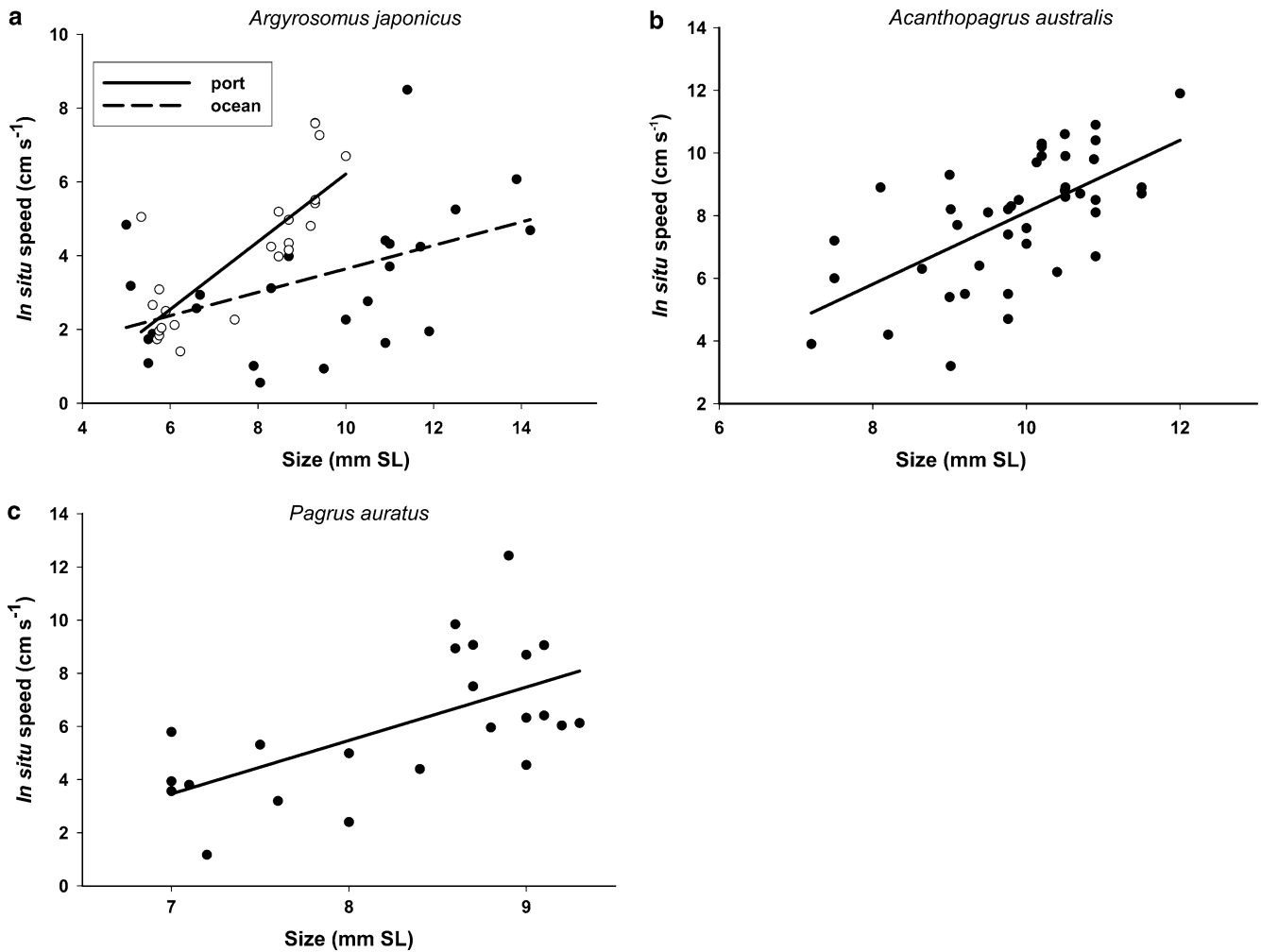**b** *Acanthopagrus australis*

c *Pagrus auratus*

Fig. 1 *Argyrosomus japonicus*, *Acanthopagrus australis* and *Pagrus auratus*. In situ swimming speed (cm s^{-1}) vs size (mm SL) in larvae. Each point represents the speed of an individual, usually over a 10-min period. Table 2 contains details of the plotted regression lines. **a** *Argyrosomus japonicus* (Sciaenidae). The data are partitioned between port (*open circle*, solid line, $n = 23$) and ocean (*filled circle*, *broken line*, $n = 25$) locations. The regression line for larvae from both locations combined (not plotted) is very similar to the ocean (broken) line. **b** *Acanthopagrus australis* (Sparidae), $n = 44$. **c** *Pagrus auratus* (Sparidae), $n = 23$

the rate of increase in speed with size of *A. japonicus* in the port overlapped extensively with those of the two sparids. It should be noted that larvae > 10 mm were observed only in the ocean. In *A. australis* there were too few larvae from too narrow a size range for rigorous testing inshore, but the inshore speeds were well within the distribution of values for larvae observed offshore, providing no indication of on–offshore differences. In *P. auratus* the size range of larvae was too narrow in the ocean for individual testing, but the ocean speeds were not obviously different from those observed in the port.

There was little relationship between body size and scaled speed (Body Lengths per second, BL s^{-1}). Only in *P. auratus* was there a significant, albeit weak, relationship between size and scaled speed (speed $= 1.65$SL-6.48, $R^2 = 0.22$, $P = 0.02$). In the other

Table 3 Speed extremes and milestones

Species	Speed (cm s^{-1}) at smallest size observed	Speed (cm s^{-1}) at largest size observed	Speed (cm s^{-1}) and size of fastest individual	Size (mm) at which speed of 5 cm s^{-1} was attained	Size (mm) at which speed of 10 cm s^{-1} was attained
Argyrosomus japonicus	2.5 at 5.0 mm	6.0 at 14.0 mm	8.4 at 11.4 mm	12.0 mm	Not by 14.2 mm
Acanthopagrus australis	5.0 at 7.2 mm	10.0 at 12.0 mm	11.9 at 12.0 mm	7.3 mm	11.6 mm
Pagrus auratus	3.5 at 7.0 mm	8.0 at 9.2 mm	12.4 at 8.9 mm	7.8 mm	10.0 mm

Mean speeds were used for speed at size and size at speed milestones, and the values were calculated by regression formulae

two species, R^2 was < 0.05, and $P(\gg 0.10)$. The overall mean values of scaled speed (se) were: *A. japonicus* 4.4 (0.30), *A. australis* 8.0 (0.26) and *P. auratus* 7.2 (0.60). If, however, the significant relationship for *P. auratus* was applied, scaled speeds of about 7 BL s^{-1} at 8 mm SL, and 10 BL s^{-1} at 10 mm SL (Table 1) would be expected.

We found a strong correlation between in situ measures of swimming speed and a laboratory measure (Fig. 2). The laboratory measure of swimming speed, or critical speed (U crit, sensu Brett 1964), was available for the three species studied here across a range of sizes (Clark et al. 2005). Both U crit and in situ speed estimates were available for 15 size intervals of 1 mm for the three species (eight for *A. japonicus* [5 to > 12 mm], four for *A. australis* [7–11 mm] and three for *P auratus* [7–10 mm]). Although strongly correlated (Fig. 2), U crit and in situ speeds were not equivalent: the laboratory measure was, on average, 2.5 times that of the in situ measure.

Vertical distribution

Larvae of *A. japonicus* moved deeper with increasing size (Fig. 3). Larvae were divided into five size groups of 2 mm (Table 4). In the ocean, the surface interval was avoided by larvae of all sizes (5–14 mm, Fig. 3a). The smallest larvae (5–7 mm) spent 70% of their time in the 2.6–5.0 m depth interval, and the depth–frequency mode moved progressively deeper with size, so that the mode for the largest larvae (13–14 mm) was at 10–12.5 m (Fig. 3a). The depth–frequency distribution was significantly different between adjacent size groups in three cases (5–7 vs 7–9, $P < 0.00001$; 7–9 vs 9–11, $P < 0.01$;
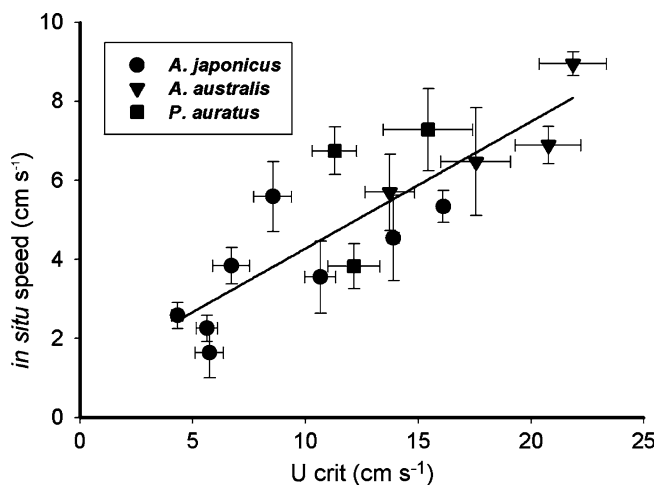

Fig. 2 *Argyrosomus japonicus, Acanthopagrus australis* and *Pagrus auratus*. Relationship between in situ speed and critical speed (U crit) for larvae. *Points* represent mean speed (and standard errors) at 1 mm size increments. U crit data are adapted from Clark et al. (2005), and in situ data from the present study. The plotted *regression line* includes all three species, and is in situ = 0.32 U crit + 1.06, $R^2 = 0.72$, $P < 0.0001$, $n = 15$

9–11 vs 11–13, $P = 0.05$, K–S test), but not between the two largest groups (11–13 vs 13–14, $P > 0.20$, K–S test). However, comparisons involving the 13–14 size group were weak and prone to Type II error because it contained only two larvae. In addition, the depth amplitude increased with size of larvae at a rate of 0.85 m per mm ($R^2 = 0.66$). Much of this was due to larger larvae swimming deeper from the 5 m release depth, but about 40% of the larvae undertook vertical oscillations of 2 m or more. Within Port Stephens in shallower water (< 10 m) and with smaller larvae (5–10 mm, in only three size groups), the depth–frequency distributions of adjacent size groups were also significantly different (K–S test, $P < 0.00001$ for both 5–7 vs 7–9 and 7–9 vs 9–10 comparisons), with a clear ontogenetic descent from the 5–7 mm group to the 7–9 mm group (Fig. 3b), and an apparent ascent by the largest larvae (9–10 mm). However, vertical distribution of larvae in the largest (9–10 mm) size group would possibly have been influenced by the shallow bottom: only two of the six largest larvae were observed in water > 7 m deep. In contrast, five of seven of the larvae in the 7–9 mm size group were observed in water deeper than 7 m. In a clear difference from the ocean where the surface interval of 0–2.5 m was entirely avoided, 11 of the 27 larvae observed in the port entered the surface interval (Fig. 3). The only larva that was seen to settle on the bottom during this study was the second largest *A. japonicus* (13.9 mm SL), which settled on sandy bottom at a depth of 13.8 m at an ocean location.

Larvae of *A. australis* became more surface orientated with increasing size. At the offshore locations, larvae smaller than 10 mm had a bimodal vertical distribution, with a depth–frequency peak in the upper 2.5 m, and a second peak over the 5–10 m intervals (Fig. 4). In larvae larger than 10 mm, the distribution was unimodal, and 47% of observations were in the upper 2.5 m (Fig. 4). Inspection of the data from the 0–2.5 m interval reveals that larvae spent most of their time within a few cm of the surface. Comparing the depth–frequencies of adjacent 1 mm size classes revealed a significant difference only between the 9–10 and 10–11 mm classes ($P < 0.001$, K–S test). The depth–frequency distribution of larvae < 10 mm differed from that of larvae > 10 mm ($P = 0.00001$, K–S test, Fig. 4). In shallow water near the shore, where the *A. australis* larvae observed were 9.1–9.9 mm, 96% of the observations were in the upper 2.5 m. The depth–frequency distributions of 9–10 mm larvae differed between inshore and offshore locations (K–S test, $P < 0.00001$), with the inshore larvae more surface orientated. Depth amplitude in *A. australis* did not change with larval size, unlike in *A. japonicus*.

In contrast, larvae of *P. auratus* moved deeper with increasing size. Inside Port Stephens, only 7–9 mm larvae were observed (Table 4), and larvae > 8 mm preferred greater depths than did larvae < 8 mm (K–S test, $P < 0.01$, Fig. 5a). In the port, there was no difference in depth amplitude between large and small larvae (*T*-test,

Fig. 3 *Argyrosomus japonicus.*
Depth–frequency distribution
of larvae of different sizes (mm,
SL) in two locations. **a** In the
ocean (bottom depth 14–20 m)
and (**b**) in the port (bottom
depth 4–9.5 m, see text). An
ontogenetic descent (detected
by K–S tests, see text) is evident
in the ocean. For numbers of
individuals and observations
(made at 30 s intervals) for each
size group, see Table 4
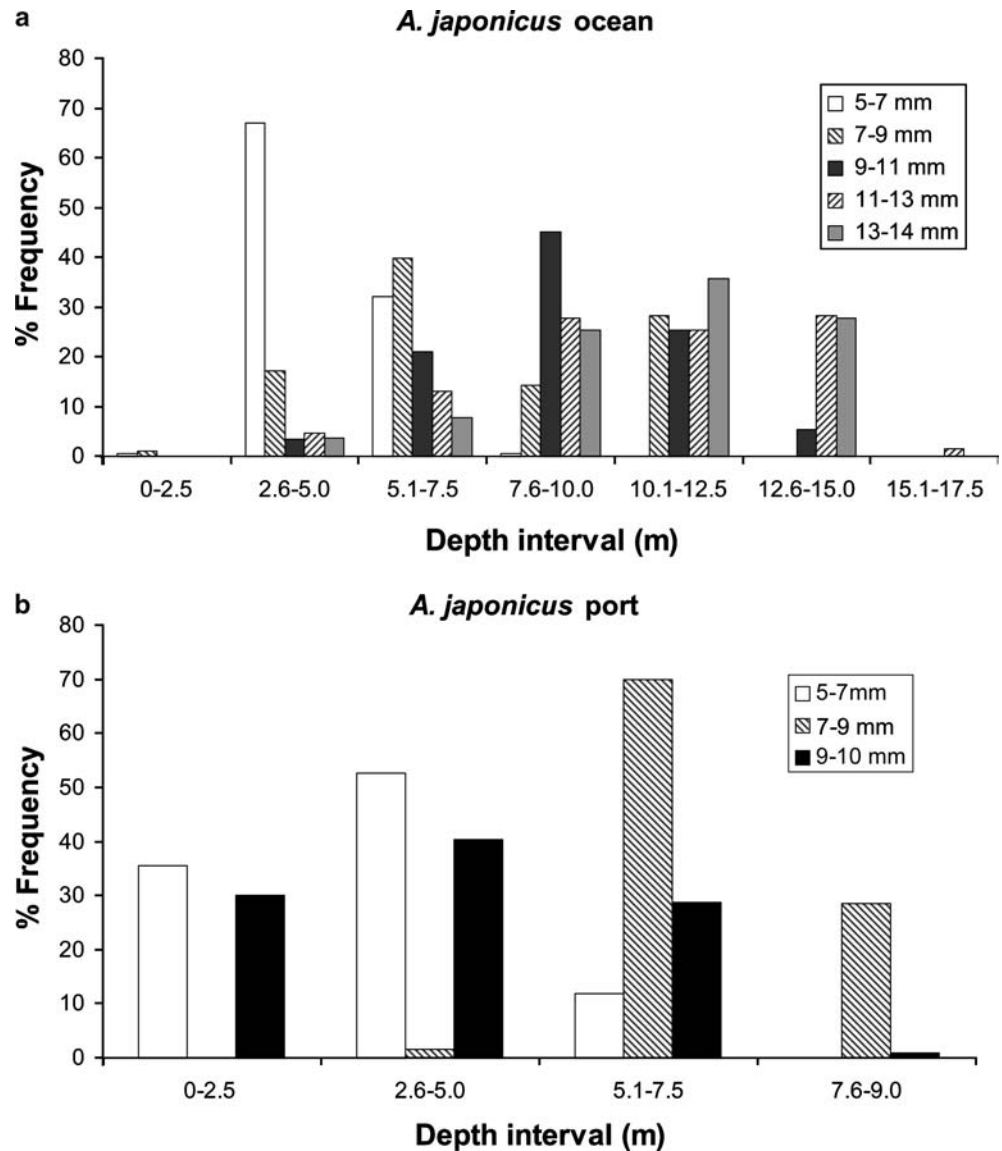
$P(\gg 0.10)$. In the ocean where *P. auratus* larvae of only
the 9–10 mm size group were observed, there was a
more-or-less uniform distribution of frequencies with
depth between 5 and 15 m (Fig. 5b). Although the 9–
10 mm larvae had a deeper vertical distribution than the
7–9 mm larvae (K–S test, $P = 0.001$), it is not possible to
determine if they swam deeper because they were in
deeper water in the ocean or because they were larger. In
the ocean, it was not possible to determine if depth
amplitude changed ontogenetically due to the small
numbers and limited size range of larvae observed.

Orientation

The large majority of individual larvae of all three spe-
cies had swimming trajectories that were significantly
different from random (Ra test, $P < 0.05$, hereafter, non-
random), and we found little ontogenetic change in

either the percentage of non-random individuals or the
precision of their directionality (Table 4). In no case was
length of the mean vector (r), a measure of directional
precision, either correlated with size, or significantly
different among size groups. In total, 72% of individual
A. japonicus larvae had non-random trajectories
(Table 4). In the ocean, 62% of small larvae (< 10 mm)
swam non-randomly, whereas 83% of large individuals
(≥ 10 mm) were non-random, but these proportions were
not significantly different ($P > 0.10$, G test). Similarly, in
the port, 74% of larvae were non-random (all were
< 10 mm). Thus, there was no clear indication of
ontogenetic change in individual directionality in
A. japonicus. In *A. australis*, 84% of all larvae swam
non-randomly. Of these, 90% of small (< 10 mm) and
80% of large (≥ 10 mm) larvae were non-random, but
these proportions were not significantly different (G test,
$P(\gg 0.10)$), indicating no change in individual direction-
ality with size. Most *P. auratus* larvae swam

Table 4 Size groups of larvae observed at different locations

Argyrosomus japonicus Size group Ocean	N	Obs	% n–r	*Acanthopagrus australis* Size group Ocean offshore	N	Obs	% n–r	*Pagrus auratus* Size group Ocean	N	Obs	% n–r
5–7	7	147 (74)	57	7–8	3	63 (33)	66	7–8			
7–9	4	84 (41)	75	8–9	3	63 (30)	100	8–9			
9–11	6	120 (67)	83	9–10	8	149 (76)	88	9–10	5	97 (44)	60
11–13	6	116 (60)	83	10–11	21	427 (247)	76	10–11			
13–15	2	30 (20)	50	11–12	3	48 (23)	66	11–12			
Subtotal	25	497 (262)	72	Subtotal	38	750 (409)	82		5	97 (44)	60
Port				Ocean inshore				Port			
5–7	10	186 (104)	70	7–8				7–8	7	138 (77)	100
7–9	7	147 (77)	100	8–9				8–9	9 [4]	83 (43)	78
9–11	6	117 (97)	50	9–10	6	82 (47)	100	9–10	2 [0]		0
Subtotal	23	450 (278)	74	Subtotal	6	82 (47)	100		18	221 (120)	78
Total	48	947 (540)	73	Total	44	832 (456)	84	Total	23	318 (164)	74

Size groups are mm SL (the size intervals are given in whole numbers for simplicity, but do not overlap: e.g. 5–7 is actually 5.0–6.9), N is number of larvae observed, *Obs* is total number of observations made at 30 s intervals (parenthetical values are those remaining for analysis of vertical distribution once autocorrelation was eliminated, see 'Methods'), % *n–r* is the percentage of individuals that swam non-randomly (i.e. directionally, Ra test, $P < 0.05$). Some observations of *Pagrus auratus* in very shallow water in the port were omitted from analysis of vertical distribution, resulting in reduced N (shown in square brackets)

non-randomly (74%), and the data for both ocean and port were pooled for analysis because only 23 larvae from a narrow size range (7.0–9.3 mm) were observed. The proportion of *P. auratus* larvae that swam non-randomly decreased monotonically from 100% at 7–8 mm to 43% in the 9–10 mm increment (Table 4). The distribution among the size increments of individuals with significant non-random swimming was not significantly different from that expected by chance ($P(\gg 0.10$, G test), so no ontogenetic change in individual directionality was indicated.

In contrast to individual directionality, indications of ontogenetic change in overall swimming directionality (orientated swimming) were found in all three species. Analyses of overall directionality included only data from individuals with significantly non-random swimming trajectories (Ra test, $P < 0.05$), with the distribution of the mean bearings of these individuals constituting the data under analysis.

In *A. japonicus* we found equivocal indications of ontogenetic change in overall orientation. In neither ocean nor port did either small (< 10 mm) or large (≥ 10 mm) *A. japonicus* larvae have significantly orientated swimming (Ra test, $P(\gg 0.10$). When larvae from the port and ocean were combined, the overall mean swimming direction of NE (29°) was not significantly orientated ($r = 0.24$, Ra test, $P = 0.13$). The mean direction was northerly in all the 2 mm size increments (NE, 24–79°, except, NW, 342° for the smallest increment), and the overall swimming orientation of none of the groups was significant (Ra test, $P = 0.11$–0.80). However, r increased monotonically from 0.15 to 0.60 with increasing size of larvae, indicating increasing directional precision with increased size.

Fig. 4 *Acanthopagrus australis.* Depth–frequency distribution of larvae of different sizes (mm, SL) in areas > 20 m deep. An ontogenetic ascent (detected by K–S test, see text) is evident. For numbers of individuals and observations (made at 30 s intervals) for each size group, see Table 4
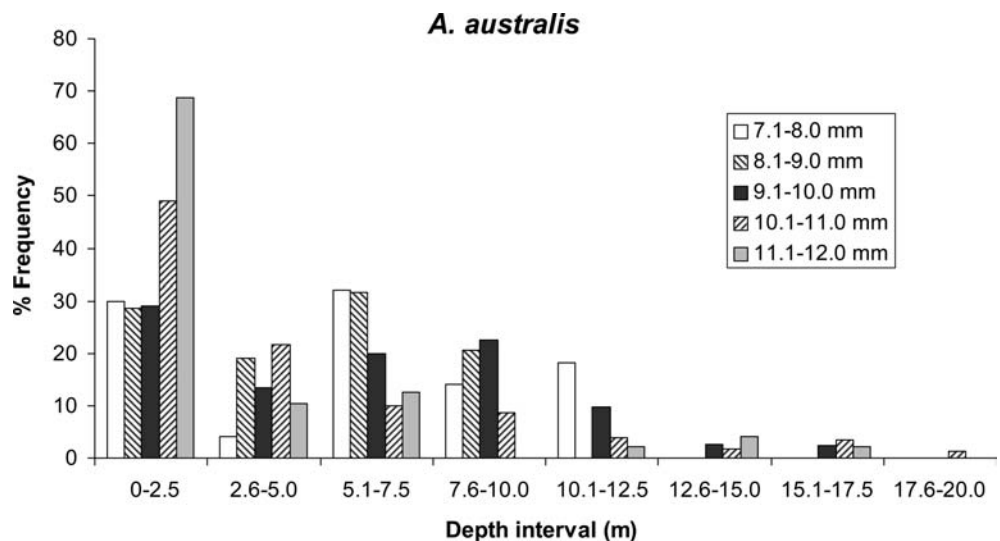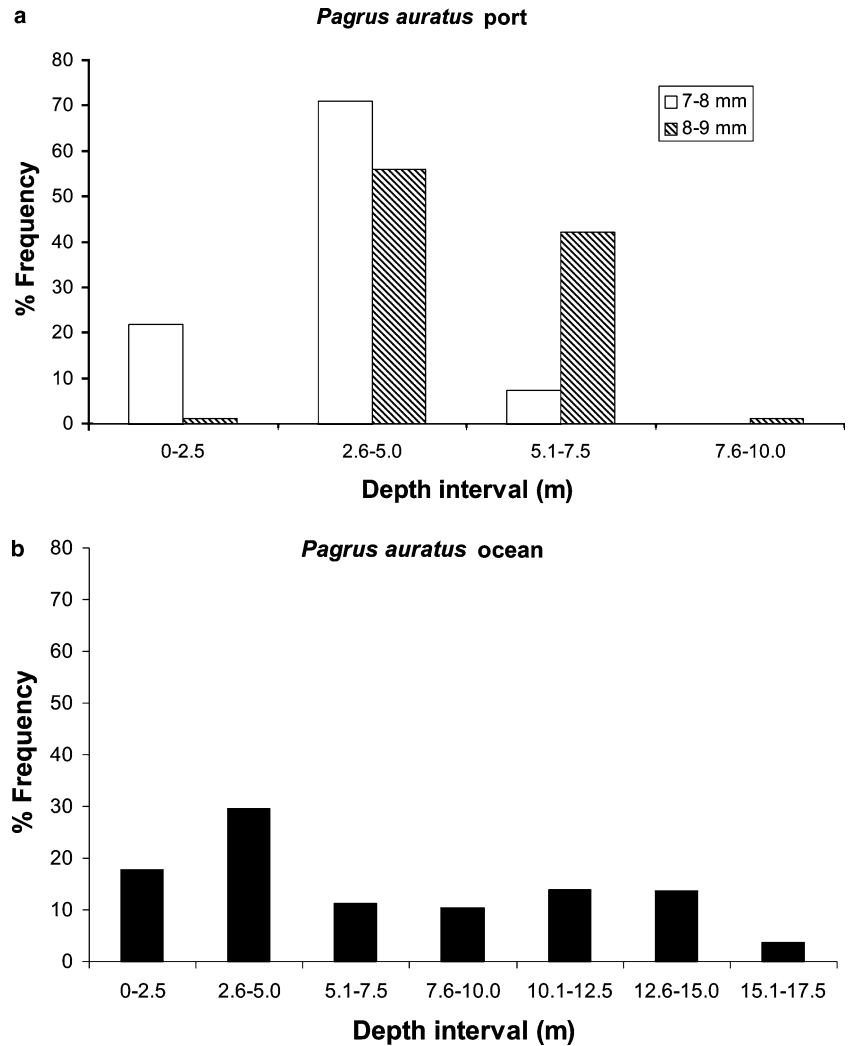
Fig. 5 *Pagrus auratus*. Depth–frequency distribution of larvae. **a** Of two size groups in the port (bottom depth, 6–8 m), and (**b**) of one size group (9–10 mm SL) in the ocean (bottom depth > 20 m). An ontogenetic descent (detected by K–S test, see text) is evident in the port. For numbers of individuals and observations (made at 30 s intervals) for each size group, see Table 4

In *A. australis*, overall swimming directions of large and small larvae differed significantly. The mean overall swimming direction for all larvae was northerly (346°), but this was not significantly orientated ($r = 0.16$, Ra test, $P = 0.16$). Small (< 10 mm) larvae had a significant swimming orientation to the WNW (291°, $r = 0.40$, Ra test, $P = 0.05$), whereas in large (≥10 mm) larvae, the overall swimming orientation of NE (42°) approached significance ($r = 0.38$, Ra test, $P = 0.06$) (Fig. 6). The distribution of mean swimming directions of large and small *A. australis* larvae were significantly different ($P = 0.0007$, Watson–Williams F test), thus showing an ontogenetic change in orientated swimming. Of the 1 mm size increments (Table 4), only the 9–10 mm and the 10–11 mm increments contained enough larvae to be tested individually, and the result was similar to that of the < 10 and ≥10 mm groupings, with $P = 0.003$ and 0.055 (Ra test), respectively.

In *P. auratus*, larger larvae had a significant overall swimming orientation in contrast to smaller larvae. There was no significant swimming orientation for all *P. auratus* larvae or for the smallest (7–8 mm) larvae

($P(\gg 0.10$, Ra test). In contrast, the 8–9 mm larvae had a significant swimming orientation to the ESE (107°, $r = 0.73$, $P = 0.017$, Ra test, Fig. 7). The 9–10 mm size group had too few non-random larvae (Table 4) for the Ra test to return meaningful results, although there was no indication of overall orientation among these three larvae.

Discussion

This study confirms that useful observations of behaviour of fish larvae as small as 5 mm can be made in situ, even in temperate waters. Previous in situ work on larval-fish behaviour has been limited to settlement-stage larvae of ca 1 cm SL or greater (Ninos 1984; Leis and McCormick 2002; Trnski 2002; Hindell et al. 2003), and most studies have taken place in relatively clear, tropical waters. No in situ studies have addressed the ontogeny of behaviour in larval fishes, so the present study provides some of the first data based on direct field observations. This will be helpful in understanding the
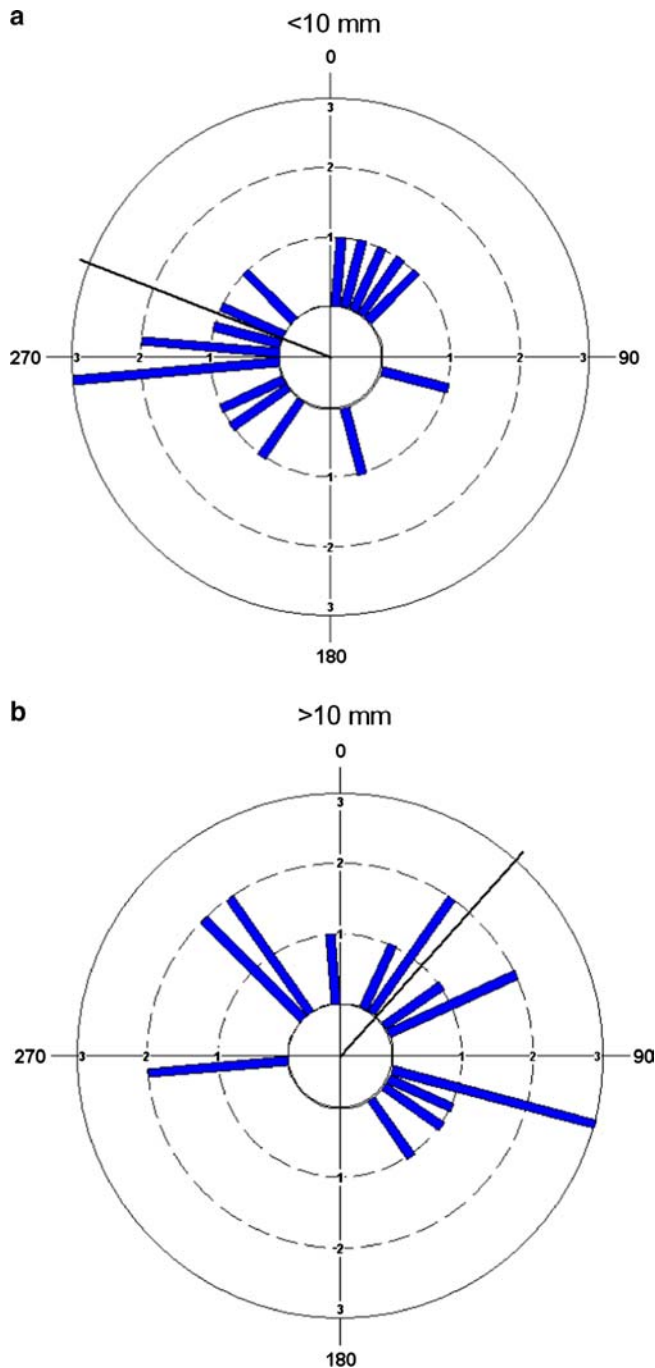
a

b

Fig. 6 *Acanthopagrus australis*. Frequency distribution of the mean
swimming direction of directional larvae ($n = 37$). The overall mean
is the radius that pierces the outer circle. **a** Small (<10 mm SL)
larvae. The overall mean swimming direction was 291° and the
distribution was significantly different from random ($r = 0.40$, Ra
test, $P = 0.05$, $n = 18$). **b** Large (>10 mm SL) larvae. The overall
mean swimming direction was 42°, and the distribution approached
significance ($r = 0.38$, Ra test, $P = 0.06$, $n = 19$). The distributions of
small and large larvae were significantly different (Watson–
Williams test, $P = 0.0007$)

contribution that behaviour of larvae throughout the
pelagic phase makes to dispersal trajectories. Although
we were unable to work with the smallest larvae in the

field, we did work with larvae ≥5–7 mm, and this may
encompass most of the behavioural ontogeny of these
species (Fisher et al. 2000; Clark et al. 2005). It is more
difficult to work with small larvae in the sea than in the
laboratory, but it is important to corroborate laboratory
observations of behaviour with field studies. Further,
combining laboratory and field approaches provides a
more complete understanding of behavioural ontogeny
than either alone (Clark et al. 2005; Leis et al., in press).

We found both similarities and differences in the
behavioural ontogeny of the three study species. In all
three, there was a linear increase in swimming speed, and
early development of and little change in the ability to
swim non-randomly. The development of behaviour in
A. australis included an increase in speed with size of
1.2 cm s^{-1} per mm, reaching a maximum speed of
12 cm s^{-1}, an ontogenetic ascent to the surface, and a
change in orientation from inshore swimming towards
swimming parallel to shore at about the size (10 mm) at
which the ontogenetic ascent was complete. *P. auratus*
increased in speed at 2.0 cm s^{-1} per mm, reaching a
maximum speed of 12 cm s^{-1}, with an ontogenetic
descent, and development of orientated swimming at
8–9 mm. In *A. japonicus*, swimming developed more
slowly at 0.3–0.9 cm s^{-1} per mm (depending on loca-
tion), reaching a maximum of only 8 cm s^{-1}, and there
was a strong ontogenetic descent, but only a trend to-
wards orientated swimming. The sciaenid was the only
species with a location-specific difference in speed: it
swam faster in the port, at least after about 7–8 mm.
This may be because the bottom was generally visible in
the shallow waters of the port, at least to the divers, thus
potentially providing a point of reference by which
swimming speed might be regulated. Vertical distribu-
tion was also influenced by location (Leis 2004).

In situ observations have practical advantages over
laboratory observations (von Westernhagen and Ro-
senthal 1979; Theilacker and Dorsey 1980), especially as
larvae swimming at average speeds measured in the field
can in seconds traverse the small containers typically
used in the laboratory. Also, it would be challenging to
provide laboratory conditions that would allow mean-
ingful study of vertical distribution behaviour or orien-
tation. One clear limitation of the in situ approach,
however, is that observations can be made only during
daylight, thus shedding no light on behaviour at night.
We have implicitly assumed that the in situ behaviour of
larvae under observation is similar to that without
SCUBA divers present, but there is no practical way of
directly testing this assumption at present. Indirect
considerations indicate that in situ behaviours constitute
the best available measure of what larvae actually do in
the field and are not unduly biased by the observing
divers. Most of these considerations have been presented
elsewhere (e.g. Leis et al. 1996; Leis and Carson-Ewart
1997, 1998; Leis and McCormick 2002; Trnski 2002;
Hindell et al 2003). In addition, in spite of the constant
presence of observer divers, in situ behaviours are
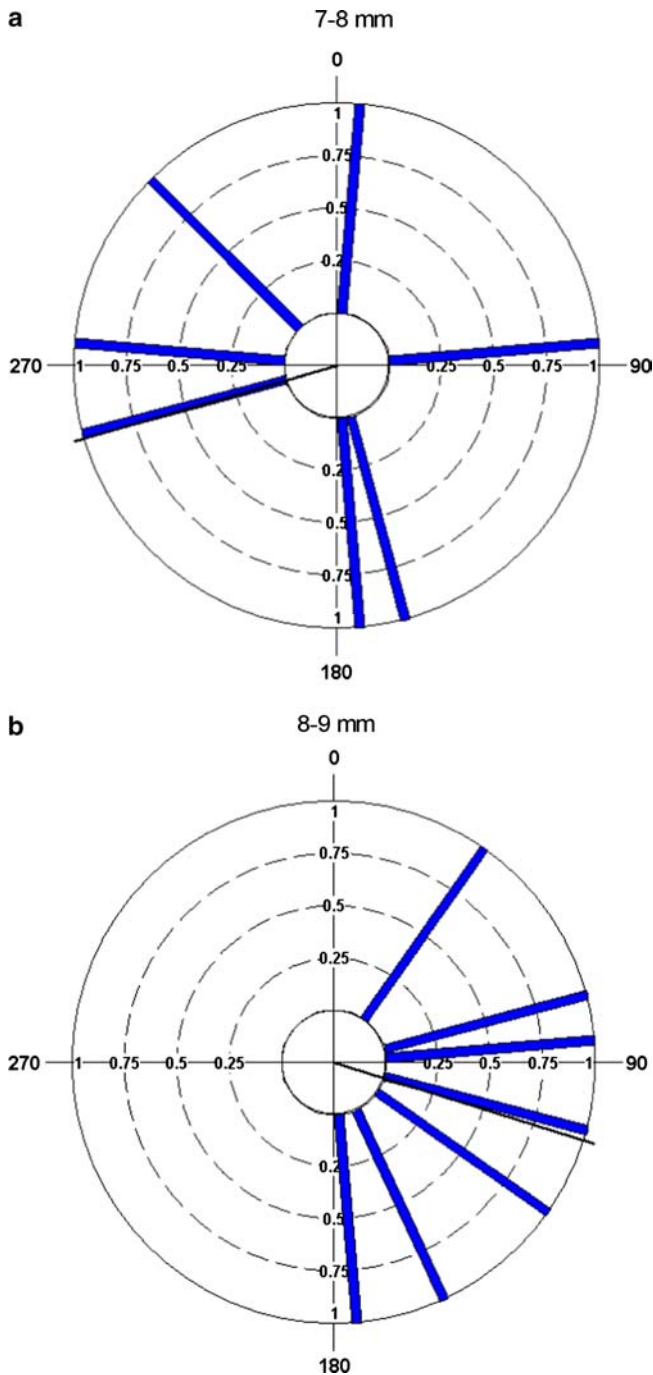repeatable, and can vary among habitats, times and

Fig. 7 *Pagrus auratus*. Frequency distribution of the mean swimming direction of directional larvae (*n* = 14). The overall mean is the radius that pierces the outer circle. **a** 7–8 mm larvae. The overall mean swimming direction was 254°, but the distribution was not significantly different from random (*r* = 0.19, Ra test, *P* = 0.24, *n* = 7). **b** 8–9 mm larvae. The overall mean swimming direction was 107°, and the distribution was significantly different from random (*r* = 0.73, Ra test, *P* = 0.017, *n* = 7)

swimming directions (Shanks 1995; Leis and Carson-Ewart 2001, 2002, 2003; Leis et al., in press), and larvae cruise in the sea at speeds far below their potential (Fisher and Wilson 2004; Leis and Fisher, in press; Leis et al., in press).

For the purposes of comparison, few in situ speed measurements are available other than those of settlement-stage larvae of coral reef fishes. The mean in situ speed of settlement-stage reef-fish larvae of 60 taxa from 16 families (Leis and Fisher, in press) was considerably faster than that of settlement-stage larvae of the three species studied here, but the latter swam at speeds within the range of those reported for reef fishes. Among the reef-fish taxa, apogonids and nemipterids were probably the most similar in speed, morphology and size at settlement to the species we studied (Neira et al. 1998; Leis and Carson-Ewart 2004). Morphological development and size are important factors for determining swimming abilities (Fisher et al. 2005), and likely to be more so than is whether adults are temperate or tropical in distribution (Clark et al. 2005). In situ speeds of larvae less developed than settlement stage are not available for comparison with our results.

The strong correlation between U crit and in situ speed means, at least for the three species studied here, makes it possible to predict swimming performance in the field from a relatively easily obtained laboratory measure (Leis and Fisher, in press), and this will be particularly useful for the smallest larvae, which are very difficult to work with in the sea. The strong correlation between laboratory (U crit) and in situ measures of swimming speed is perhaps surprising. The former is an investigator-controlled measure of potential performance whereby larvae in a raceway are forced to swim incrementally faster over periods of several minutes until they can no longer maintain position, whereas the latter speed is chosen by the larva, and, in contrast to U crit, is subject to a wide variety of behavioural inputs. Previous comparisons of the two measures are consistent with our results in showing U crit to be greater than in situ speed by a factor of 2–4 (Leis and Carson-Ewart 1997; Leis and Stobutzki 1999; Leis and Fisher, in press). Thus, the larvae observed in the sea were actually swimming much slower than their capabilities, as one would expect (Fisher and Bellwood 2002). Possibly, this large difference between actual and potential performance constitutes a reserve for dealing with currents or turbulence when approaching settlement sites or for rapidly leaving the vicinity of adverse physical conditions or predators.

The in situ swimming speeds presented here were measured over periods of only 10 min, but two of the study species can swim from a few to many kilometres at similar speeds in the laboratory, even when they were unfed (Clark et al. 2005). Fed larvae can swim much greater distances (Fisher and Bellwood 2001; Leis and Clark 2005), and we saw larvae of all three species feed in situ with little or no alteration in speed or direction. Thus, although it seems clear the in situ swimming speeds presented here would be sustainable over long periods and distances, realistic predictions of endurance are problematical. We have no in situ swimming-speed data from night time, but laboratory studies suggest the possibility that the in situ speeds we measured during the

day might be conservative over 24 h periods (Fisher and Bellwood 2003).

The ontogenetic changes in vertical distribution behaviour found in these three species mean that different sizes of larvae will experience different conditions of light, temperature, food and current velocity, all of which can greatly influence growth, survival and dispersal. The ontogeny of vertical distribution behaviour varies among the three species, and this means that dispersal trajectories probably differ not only among species but also among developmental stages even if horizontal swimming and orientation are ignored, because current velocity often differs with depth (Sponaugle et al. 2002). The ontogenetic descent of *A. japonicus* is similar to that of some sciaenid larvae that become epibenthic (Barnett et al. 1984), and could explain why postflexion larvae of *A. japonicus* are generally absent from plankton tows even when smaller larvae are common (Smith 2003; AG Miskiewicz, personal communication). Our results are in accord with what is known of the vertical distribution of larvae of the two sparids. Over the continental shelf off Sydney, preflexion larvae of *A. australis* were found at greater depths than postflexion larvae (Smith 2003), which agrees with the ontogenetic ascent we observed in postflexion larvae. Wild *A. australis* larvae of 9.6–11.0 mm in an estuary were largely surface orientated (Trnski 2002), as were our larvae of similar sizes. In fact, our observations of *A. australis* show the species can accurately be described as neustonic after 10 mm. Both preflexion and flexion stages of *P. auratus* were found in midwater (Smith 2003), which is not inconsistent with our observation of ontogenetic descent in postflexion larvae. Wild *P. auratus* larvae of 10–15 mm swam near the bottom in an estuary (Trnski 2002), which is consistent with the ontogenetic descent we observed with larvae of 7.0–9.3 mm.

In all three species, a high proportion of individual larvae swam non-randomly, and there was no detectable ontogenetic trend in this, indicating that the ability to swim in a non-random manner develops early in ontogeny. The direction that non-random swimmers chose to swim did, however, have an apparent ontogenetic component in all three species, and the size at which orientated swimming develops appears to vary among species. There may be ecological implications to these behaviours. In the sparid, *A. australis*, smaller (7–10 mm) larvae swam WNW (towards the Australian coast), whereas larger larvae (10–12 mm) had an overall swimming direction that approached statistical significance to the NE, approximately parallel to the coast. Swimming towards shore by 7–10 mm *A. australis* larvae might assist them in remaining near the shore. The change in swimming orientation at 10 mm coincides with the size at which *A. australis* larvae are competent to settle (Neira et al. 1998), and the size at which they are found in surf zones (JM Leis and T Trnski, unpublished data), and entering estuaries (Trnski 2002). Swimming NE, parallel to the coast, particularly once close to shore, should maximize encounters with estuarine plumes (Kingsford 1990) as would the surface orientation of *A. australis* at this size, and this might facilitate detection of estuarine nursery areas. In the other sparid, *P. auratus*, 7–8 mm larvae had no swimming orientation whereas 8–9 mm larvae swam E (although larvae of these sizes were observed only in the semi-enclosed port). The eastward swimming of *P. auratus* in the port is not easily interpreted without more information on behaviour in the ocean to place this orientation behaviour in context. In the sciaenid, *A. japonicus*, although an ontogenetic trend towards orientated swimming to the NE was evident, statistically significant swimming orientation had not developed by 13–14 mm. The trend towards NE swimming (parallel to shore) in *A. japonicus* might be interpreted in a manner similar to NE swimming in *A. australis*, but *A. japonicus* is found well away from the surface at this size. The northerly swimming orientation of some stages of these species might also be a means of countering the generally southerly currents that prevail over the continental shelf off SE Australia. Orientated swimming by fish larvae is not unprecedented (Leis et al. 1996; Stobutzki and Bellwood 1998; Leis and Carson-Ewart 2003), but this is the first indication of how this behaviour develops.

The influence that the behaviours measured might have on dispersal is location specific, because current velocities vary with location and time. So whereas an 8 mm larva of *A. australis* might be an effective swimmer (sensu Leis and Stobutzki 1999, meaning its mean speed is ≥ mean current speed) in one location, at another location, a 12 mm larva might not be. Where average current speed was 10 cm s^{-1}, average larvae of the two sparids would achieve 'effective swimming' as they approached settlement at 10–11 mm SL, but average 7 mm SL sparid larvae would not be effective swimmers because they swam at ca 5 cm s^{-1}. In contrast, in the same area (where average currents were 10 cm s^{-1}), average larvae of the sciaenid (*A. japonicus*) would not become effective swimmers prior to settlement. Of course, the fastest swimmers can potentially have more influence than average larvae over their dispersal. Even if a larva cannot swim faster than the mean current speed, swimming normal to the flow can result in major alterations to passive trajectories, particularly over continental shelves where the non-tidal flow is typically parallel to depth contours, and the direction towards inshore nursery habitats is normal to the current. Numerical models of larval dispersal indicate that swimming speeds of just 0.3–2.0 cm s^{-1} can have a major influence on dispersal trajectories (e.g. Werner et al. 1993; Pepin and Helbig 1997; Porch 1998) if the swimming is orientated. All three species studied here are capable of such speeds over the full range of sizes we studied, with species-specific rates of increase of speed with size that potentially make them rapidly more influential with development. Further, all three species can swim non-randomly from a very small size, and the two sparids in an orientated manner from 7 to 9 mm.

We used reared larvae from aquaculture facilities in our work, and reared larvae might behave differently than wild larvae (e.g. Smith and Fuiman 2004). Fortunately, in situ observations of wild, settlement-stage larvae of the two sparids we studied (Trnski 2002) indicate that the behaviours of reared and wild larvae were similar. Wild larvae of *A. australis* of 9–11 mm SL and *P. auratus* of 10–15 mm SL had mean in situ speeds of 5.5–7.5 and 5–11 cm s^{-1}, respectively (Trnski 2002), which is similar to the in situ speeds we observed in similar-sized reared larvae (Fig. 1). Similarly, as already noted, the vertical distributions of reared and wild larvae of the two sparid species were similar. The majority of both wild (Trnski 2002) and reared larvae of the sparids swam non-randomly. Unfortunately, there is no information on the behaviour of wild larvae of *A. japonicus*. The high variation in swimming speed at the sizes found in the reared larvae we studied was similar to that found in wild, settlement-stage larvae of other species (Fisher et al. 2005; Leis and Fisher, in press), and therefore was unlikely to have been an artefact of rearing conditions. One reviewer expressed concern that fast- and slow-growing larvae might differ in behavioural performance, thus confounding attempts to study ontogeny of behaviour in reared larvae that had variable growth rates. This idea has been tested in the larvae of a sciaenid, and no relationship between growth rate and behavioural performance was found (Fuiman et al. 2005). The average growth rates (mm day^{-1}) of our reared larvae were: *P. auratus*, 0.26; *A. japonicus*, 0.28 and *A. australis*, 0.50 (Clark et al. 2005). Although these are within the range of reported growth rates of wild larvae of other species, such values are available only for *P. auratus* among our three study species (0.25–0.28 mm day^{-1}, Kingsford and Atkinson 1994). The equivalence of growth rates of wild and reared *P. auratus* provides a further indication that the reared larvae did not provide spurious results.

We anticipate that the observations of development of behaviour in the sea provided here will be useful to dispersal modellers, but incorporation of behaviour into dispersal models may not be straightforward. Such models will have to accommodate the relatively high variation in speed at any size, and also the possibility that it may be primarily the best performers that actually survive and are of relevance to considerations of dispersal. The mortality rates of fish larvae in the ocean are very high, and work on other aspects of larval biology has frequently shown that the best performers—for example, the fastest growers (e.g. Vigliola and Meekan 2002)—are the individuals most likely to survive. Some of the variation in speed at size is undoubtedly caused by variation in capacity (e.g. muscle development or physiological condition), but purely behavioural factors are also involved as shown by the differences between locations we detected in swimming speed and its development. Like this study, others have detected location-dependent differences in swimming speed, depth selection and orientation in fish larvae (Leis and Carson-Ewart 1999, 2001, 2002; Trnski 2002; Hindell et al. 2003; Leis and Carson-Ewart 2003), and it is likely that other factors will influence behaviour. These include sensory cues emanating from both biological and physical sources, diel or tidal variables, and individual variation in motivation (such as competency to settle, or hunger—a hungry fish might be either less or more inclined to swim than a sated one), and morphological development at any size. All this constitutes additional layers of complexity in attempting to model dispersal and in applying laboratory results to the sea.

From the field-based observations presented here, it is clear that larvae of perciform fishes as small as 5–7 mm (postflexion stage) have the ability to influence their dispersal. These larvae can swim at speeds greater than those heuristic modelling indicates have the potential to exert major influence on dispersal trajectories (e.g. Werner et al. 1993; Pepin and Helbig 1997; Porch 1998). They can control their vertical distribution, thus achieving substantial indirect influence over dispersal. They can swim directionally, which is a prerequisite for horizontal swimming to be effective in influencing dispersal. All these behaviours changed in a species-specific manner over the developmental intervals we studied: speed increased with size at a linear rate; vertical distributions changed with increasing size; and population-level orientation changed with size. Some behaviour also differed among locations. Including these types of behaviours in dispersal models will be challenging but necessary if the goal is a realistic depiction of larval-fish dispersal.

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