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Maladaptive behavior reinforces a recruitment bottleneck in newly settled fishes

Lee A. Fuiman · Mark G. Meekan · Mark I. McCormick

Abstract Settlement from the plankton ends the major dispersive stage of life for many marine organisms and exposes them to intense predation pressure in juvenile habitats. This predation mortality represents a life-history bottleneck that can determine recruitment success. At the level of individual predator–prey interactions, prey survival depends upon behavior, specifically how behavior affects prey conspicuousness and evasive ability. We conducted an experiment to identify behavioral traits and performance levels that are important determinants of which individuals survive or die soon after settlement. We measured a suite of behavioral traits on late stage, pre-settlement Ward's damsel (*Pomacentrus wardi*) collected using light traps. These behavioral traits included two measures of routine swimming (indicators of conspicuousness) and eight measures of escape performance to a visual startle stimulus. Fish were then released onto individual patch reefs, where divers measured an additional behavioral trait (boldness). We censused each patch reef until approximately 50% of the fish were missing ($\sim$24 h), which we assumed to be a result of predation. We used classification tree analysis to discriminate survivors from fish presumed dead based on poor behavioral performance. The classification tree revealed that individuals displaying the maladaptive combination of low escape response speed, low boldness on the reef, and high routine swimming speed were highly susceptible to predation (92.4% with this combination died within 24 h). This accounted for 55.2% of all fish that died. Several combinations of behavioral traits predicted likely survival over 24 h, but there was greater uncertainty about that prediction than there was for fish that were predicted to die. Thus maladaptive behavioral traits were easier to identify than adaptive traits.

Keywords Swimming performance · Anti-predator behavior · Settlement · Mortality · Survivorship

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Introduction

Phenotypic selection often occurs during periods of intense mortality (Scott et al. 2007; Teacher et al. 2009). This mortality can be selective for traits that affect or correlate with the probability of survival directly (e.g., escape performance and behavior) or indirectly (e.g., growth history, body condition), as documented in a range of taxa (Fuiman 1989, 1993; Kullberg et al. 1996; Vigliola and Meekan 2002; Alzaga et al. 2008; Jones et al. 2009). Traits that act directly, such as escape behavior, operate over short intervals (individual interactions with predators), while traits that act indirectly affect survival over longer time frames. These work together, for example, when growth rate determines the span of time over which individuals are highly vulnerable, the so-called "window of vulnerability" (Cushing 1975; Dahlberg 1979; McGurk 1986; Houde

1987), thereby altering the number of interactions with predators and ultimately stage-specific mortality.

While predation is a ubiquitous process and central to selection over ecological and evolutionary time frames, its effects are difficult to study and often inferred rather than demonstrated (Lima 2002; Lind and Cresswell 2005). Predation pressure is inconsistent through time: prey and predator populations often cycle out of phase with each other, leading to periods of intense predation (e.g., Lotka-Volterra model; Begon et al. 2006); or predation may be more intense on smaller or younger life stages (Houde 2002). These periods of high mortality represent bottlenecks that limit recruitment and where mortality is often selective for phenotypic traits. Predation is not only easier to study during intense predation events, but the patterns of mortality that occur then are crucial for determining the local evolution of behavioral and life-history strategies. Research documents the link between prey attributes and apparent fitness during these bottlenecks, but few studies have examined the importance of more than one prey characteristic at a time (Lind and Cresswell 2005). The trade-offs associated with undertaking anti-predator behaviors, such as sacrificing foraging opportunities for vigilance and energetic costs of high-performance responses to predators, means that assessments of phenotype and behavior must go hand in hand for a robust understanding of the fitness consequences of anti-predator behaviors.

Marine fishes are ideal models to study the link between prey attributes and survival. Settlement from the plankton ends the major dispersive stage of life for reef fishes and exposes them to an intense mortality bottleneck that can shape reef populations and communities. The transition from a pelagic existence to a benthic lifestyle exposes reef fishes to an array of predators and competitors they have not previously experienced. This transition is so complex and widespread that it has been referred to as a distinct phase of life, called the "transition juvenile," which lasts from a few hours for some fish species to weeks for others (Kaufman et al. 1992; McCormick and Makey 1997). Mortality, especially predation mortality, is extreme during this transition period (Doherty et al. 2004). A recent analysis of 24 taxonomically and geographically diverse coral reef fish species estimated that 56% of juveniles are consumed by predators within 2 days of settlement (Almany and Webster 2006). Since post-settlement mortality decreases rapidly over time (Doherty and Sale 1985), the transition period is a critical time during which recruitment levels are often determined for reef fish populations.

Behaviorally, the strategies for prey to maximize their survival are to minimize either encounters with a predator (predator avoidance) or the likelihood of capture by a predator (predator evasion). Numerous traits of developing fishes influence mortality in complex and interacting ways through their effects on encounter rate and evasive ability (Fuiman and Magurran 1994). For example, increasing size makes larvae more conspicuous to predators, but improvements in sensory and locomotor systems that accrue with increasing size improve escape success. Laboratory studies of larval red drum (*Sciaenops ocellatus*) demonstrated that a variety of anti-predator behavioral traits are highly repeatable within individuals, but vary substantially between individuals within (Fuiman and Cowan 2003) and between cohorts (Fuiman et al. 2005). Thus, there is ample variability in behavioral traits for selection to operate. Although several laboratory studies have made logical connections between behavioral traits of young fishes and probable success in encounters with predators (Fuiman 1986; Alvarez and Fuiman 2005), only a few studies have attempted to identify specific behaviors that promote survival by pairing measures of behavior with the outcome of actual predator–prey interactions (Fuiman 1993; Fuiman et al. 2006). However, interactions with predators staged in the laboratory are inherently unnatural, which makes their interpretation difficult. To understand proximate (mechanistic) and ultimate (functional) aspects of behavior (Mayr 1961; Tinbergen 1963), anti-predator behavior must be examined under ecologically relevant conditions.

Our goal was to identify the behavioral traits and performance levels of those traits that are most important in determining which fish survive or succumb to the intense predation pressure to which fish are exposed soon after they settle onto coral reefs. We combined laboratory and field measurements of behavioral traits with exposures of newly settled fish to an array of predators under natural conditions. We found that a suite of detrimental traits and performance levels defined individuals that were highly likely to die within 24 h of settlement, but that defining traits of survivors was more difficult.

Materials and methods

Our research was conducted at Lizard Island Research Station, Queensland, Australia. We measured two behavioral traits (routine swimming and escape performance) of individual late stage, pre-settlement fish in the laboratory, then settled them onto individual patch reefs where we measured a third behavioral trait (boldness) in situ. We then censused the patch reefs periodically until fish from half the reefs were missing (presumably due to predation mortality). Finally, we analyzed the behavioral data to identify traits and performance levels that predict survivorship.

Fish collection

We collected late stage, pre-settlement juveniles using light traps (see Meekan et al. 2001 for design) deployed in nearshore waters in the back-reef habitat of Lizard Island, on the northern Great Barrier Reef, Australia ($14°38'S$, $145°28'E$). The traps were set out daily at 1800 hours and retrieved the following morning at 0600 hours, 8–16 December 2007. Live fish from light trap collections were sorted by species and maintained in outdoor tanks with flow-through sea water at ambient conditions of temperature and photoperiod. Ward's damsel (*Pomacentrus wardi*) was selected for this study because of its high relative abundance in the light trap collections. After sorting, fish were placed individually into a numbered plastic bag and their standard length was measured with calipers through the bag. The fish varied little in size (12.4–14.9 mm, mean 13.4 mm standard length) and were well developed (all fins complete but not fully scaled).

Laboratory assays

Laboratory trials to measure routine swimming and escape performance began immediately after fish were measured. Four fish were transferred to individual glass aquaria ($10 \times 10 \times 10$ cm) and allowed to recover from handling for 1 h. One aquarium was then moved to a testing arena where the fish was left undisturbed for 5 min before measurements of routine swimming and then escape performance were made. After escape performance trials were completed on a fish, it was returned to its numbered plastic bag, fed *Artemia* nauplii, and placed in an outdoor tank with flow-through sea water to maintain ambient temperature. Then, another fish was taken to the laboratory for behavioral testing. This sequence of testing was continued until (usually) 20 fish were assayed each day, and repeated on newly collected fish daily from 8 December until 16 December 2007. On some days, the number of fish tested was <20 because of equipment failure. Water within the bags was changed at least three times prior to them being taken out to a shallow reef the following morning. Laboratory trials generally began at 0830 hours and finished by 1600 hours. Water temperatures in the laboratory ranged from 26.3 to 27.2°C.

Routine swimming and escape performance were measured sequentially without moving the fish or the aquarium between assays. The aquarium was positioned on a laboratory bench adjacent to an easterly facing window which provided indirect illumination. A liquid crystal display (LCD) screen (11.1×8.2 cm) was positioned parallel to each side of the aquarium, such that the four screens completely surrounded the aquarium, each at a distance of 2.75 cm from the glass. These screens were used to present a looming visual stimulus to the fish (see below). A mirror (30.5×30.5 cm) was positioned above the LCD array at an angle of 45° from horizontal so that the movements of the fish in the horizontal plane could be recorded with a high speed video camera (Motionmeter; Redlake Imaging, North Star Imaging, St. Paul, MN, USA) that was positioned on the laboratory bench. Supplemental illumination was provided by an incandescent desk lamp positioned directly above the arena.

Five minutes after an aquarium containing one fish was moved to the arena, the routine swimming of the fish was recorded for 30 s at the NTSC standard framing rate of 30 Hz. The video recording was immediately transferred from the camera to a laptop computer through a video capture device for subsequent motion analysis.

Escape responses were created by triggering a visual looming stimulus on one of the LCD screens, usually the screen closest to the fish. The stimulus was an animation of a black ellipse (major:minor axis length = 2.0; major axis oriented vertically) on a white background, increasing in size from 0 to 6.35 cm over the course of 1.0 s, simulating the silhouette of a fish attacking at a speed of 68 cm s^{-1}. The fish's response to the stimulus was recorded at a framing rate of 250 Hz. Each fish was tested until it responded three times, and if it did not respond three times after ten presentations of the stimulus, the trial was ended and performance for that individual was based on the data obtained (i.e., one or two responses). The mean number of presentations required to obtain three responses was 4.5. Fewer than three responses were obtained for 12 of 160 (7.5%) fish tested.

Analysis of video recordings took place in laboratory facilities at the University of Texas Marine Science Institute. Video recordings were analyzed frame-by-frame using WinAnalyze motion-analysis software (v. 1.9 2D; Mikromak Service Brinkmann, Berlin, Germany). In a predation context, routine swimming relates to conspicuousness of a fish to predators (Fuiman and Magurran 1994). Routine swimming was characterized by mean speed and turning rate, which we measured over a period of 30 s by tracking the movement of the fish every 10 video frames (0.33 s), producing 31 points for each track. Routine speed (mm s^{-1}) was taken as the average distance between each pair of consecutive points divided by the sampling interval (0.33 s). Turning rate was calculated recreating the swimming path using positions observed at 20 Hz (0.66 s apart) then computing the angle between consecutive path segments. Turning rate (degrees per 1.33 s) was the average of the 14 angles that were computed during the 30 s of routine swimming.

In the escape response assay, eight variables were measured for each response. These variables assessed the timing (apparent distance, response latency) and magnitude

(response distance, duration, mean speed, maximum speed, time to maximum speed, and maximum acceleration) of each response. There was no evidence of habituation to the stimulus and therefore the mean value of each of these variables for each fish was used to characterize the individual (i.e., $n = 3$ for most fish). Escape response variables were defined as follows:

Response latency (in ms): elapsed time from start of movement of visual stimulus until start of escape response.

Apparent distance: calculated distance (in cm) between a responding fish and the visual stimulus, based on the size of the silhouette when the fish responded and the distance between the fish and the wall of the tank at which the stimulus appeared.

Response distance (in mm): distance traveled by fish during response.

Response duration (in ms): elapsed time from start of response to end of response.

Mean response speed (in mm s^{-1}): response distance divided by response duration.

Maximum response speed (in mm s^{-1}): maximum distance traveled during one frame (4 ms) multiplied by framing rate (250 Hz).

Time to maximum speed (in ms): elapsed time between start of response to frame in which speed was maximal for that response.

Maximum acceleration (in m s^{-2}): maximum change in speed between consecutive video frames.

Field behavioral assessment

On the morning following laboratory assays, fish within the labeled bags (usually 20 fish per day) were taken to a shallow sand flat (approximately 3 m deep) and were released onto small patch reefs (assigned haphazardly) between approximately 0900 and 1100 hours. These reefs (18 × 12 × 12 cm), made from dead *Pocillopora damicornis* (a common bushy hard coral), were pulled apart, cleared of any fishes or invertebrates using a hand net and rebuilt prior to releasing the fish. A small wire cage (approximately 30 × 30 × 30 cm, 12 mm mesh) was placed over each patch reef to allow the fish to acclimate to its new surroundings while being protected from predators. Cages were removed 30 min to 1 h after release of the fish. The patch reefs were positioned 4 m apart and 4 m from the edge of a nearby natural reef, and examination of the data suggested there was no trend in fish mortality with position along the reef edge. Studies that used fluorescent elastomer tags to identify individual fish have indicated that newly settled *P. wardi* do not migrate these distances

over sand (Mero 2009), and similarly, high site fidelity has been found in other juvenile damselfishes (McCormick and Meekan 2007; McCormick 2009; Meekan et al. 2010).

Divers (M.I.M. and M.G.M.) assessed "boldness" of each fish on its patch reef after the cage was removed. This was done over a 3-min observation period conducted from a distance of 1.5 m with the aid of a ×4 magnifying glass. Boldness was recorded on a scale from 0 to 3 at increments of 0.5, where: 0 was hiding in hole and seldom emerging; 1 was retreating to hole when scared and taking more than 5 s to re-emerge, weakly or tentatively striking at food; 2 was shying to the shelter of the patch reef when scared but quickly emerging, purposeful strikes at food; and 3 was not hiding when scared, exploring around the coral patch, and striking aggressively at food. At the end of the 3-min observation period, the fish was approached with a finger and the fish's reaction and time to emerge from shelter was taken into account in the assessment of boldness. Previous studies had shown that 3 min was long enough to obtain a representative behavioral assessment due to high consistency in behavior in newly settled fish of this species over short time scales (up to 1 h; Mero 2009). Divers conducted a census and behavioral assessment of all fish on patch reefs 30 min to 1 h after removing the cages at approximately 1000 hours, and additional censuses at 1600 hours the same day and at 0800 hours the following day. When approximately 50% of the larvae were missing from the reefs (presumed eaten by predators), all remaining larvae were collected and the patch reefs were prepared for the next field trial.

Statistical analyses

Classification tree analysis was used to determine which measures of routine swimming, escape performance, and boldness could be used to identify individual fish that were likely to survive or die when settled onto patch reefs. Classification tree analysis functions for categorical dependent variables in a similar way that regression tree analysis operates on continuous dependent variables. The procedure uses a set of predictor variables (here, measures of routine swimming, escape performance, and boldness) to assign cases (individual fish) to known categories. Here, the categories were whether or not a fish was present on its patch reef at the time when the experiment was concluded (fish present on 50% of reefs). The analysis builds a decision tree consisting of binary branching points (nodes) at which the observations are divided into two subsamples on the basis of a threshold value for one of the predictor variables. Branching of nodes continues until a goodness of fit criterion, proportion of reduction in error (PRE), cannot be improved significantly. The result is that all cases are distributed among a set of terminal nodes that separate the

categories as well as possible based on the predictor variables. In this way, classification tree analysis is much like discriminant function analysis, except that it does not require normally distributed variables and it allows individual predictor variables to enter the tree multiple times, thereby improving the contribution of predictor variables that are not monotonically related to the known categories.

The classification tree analysis included 11 variables (2 for routine swimming, 8 for escape performance, and boldness). Because of the very narrow size range of fish collected in the light traps, correction for size was not necessary for any of the variables. Regression analysis confirmed the absence of a significant size effect within our dataset. There was, however, significant variation in several escape response variables (response distance, response duration, mean response speed, maximum response speed, time to maximum speed) with respect to the angle between the fish's longitudinal body axis and the LCD screen containing the stimulus at the time of the response. These response variables were independent of stimulus angle for angles <90°, but these response characteristics increased as angles increased beyond 90°. To adjust for the effect of differences in stimulus angle, a piecewise regression was computed for each escape response variable using the model:

$$Y = a + b \times (A_s - 90) \times (A_s > 90)$$

where, Y is an escape response variable, a and b are empirical coefficients, A_s is the stimulus angle in degrees, and $(A_s > 90)$ is a logical statement (0 if false, 1 if true for each case). For relationships in which the 95% confidence interval for b excluded zero (i.e., presence of a significant change in slope when $A_s > 90$), residuals were calculated for each response and the mean residual for each fish was used to characterize that fish's performance in the classification tree analysis. Classification trees were computed using the least squares fitting method and default values for the algorithm (minimum split index value = 0.05, minimum improvement in PRE = 0.05, minimum count allowed in each node = 5). All statistical analyses were computed using SYSTAT (version 11).

Results

Routine swimming was measured for 163 fish and escape performance was measured for 159 fish (four fish failed to respond to the stimulus). Measurements were made every day over 9 days, with an average of 18 fish per day. Equipment failure on 10 December 2007 reduced the number of fish assayed on that day to 8. Field assessment of boldness began during the third field trial, so data included in the analyses were from field trials 3–9 only.

Most traits varied appreciably among individuals and were roughly symmetrical around a central mean value (Table 1), which provided ample phenotypic variability for one or more of these traits to influence post-settlement survival. Coefficients of variation for time to maximum speed, boldness and routine speed were highest, being 50% or more of the mean. Variability of all traits exceeded 20% of the mean, except response latency, which exhibited remarkably little variability (3% of mean).

Of the 163 fish assayed for routine swimming and escape performance, 152 were successfully released on a patch reef. All but one of the nine field trials was terminated after about 24 h (third census). For one trial, mortality happened more quickly; 35% of larvae died within 7.3 h. Overall survival rate in the nine field trials was 43.4% for the 152 larvae for which behavioral traits were measured (Table 2).

The ability to discriminate survivors from non-survivors on the basis of a single behavioral/performance variable was poor. The distribution of survivors was nearly identical to that of non-survivors for 10 of the 11 survival skills and their means were not significantly different (two-sample Student's t test, $P > 0.89$ after Dunn-Sidak correction for multiple comparisons). One trait, boldness, exhibited a nearly significant difference in means ($P = 0.06$) between survivors (mean = 1.85) and non-survivors (mean = 1.42; Fig. 1). Broad overlap in the distributions, however, severely limited the use of this variable to determine survivorship of individuals.

A classification tree was computed for 105 fish for which complete data were available. Among this group, 47 (44.8%) individuals survived on their patch reef. The

Table 1 Summary statistics for routine swimming, escape performance, and boldness of Ward's damsel (*Pomacentrus wardi*)

Trait	n	Mean	SD	CV (%)
Routine speed (mm s^{-1})	163	12.3	6.1	50
Turning rate (deg per 1.33 s)	163	55.6	13.6	24
Response latency (ms)	159	891.1	25.9	3
Apparent distance (mm)[a]	159	5.9	2.3	39
Response distance (cm)[a]	159	31.6	12.0	38
Response duration (ms)[a]	159	93.9	23.8	25
Mean response speed (mm s^{-1})[a]	159	352.1	81.6	23
Maximum response speed (mm s^{-1})[a]	159	915.7	192.5	21
Time to maximum speed (ms)[a]	159	26.4	16.0	61
Maximum acceleration (m s^{-2})	159	168.2	43.7	26
Boldness	109	1.62	0.83	52

Data from all trials are included (n)

SD Standard deviation, *CV* coefficient of variation

[a] Raw data; corrected for effect of stimulus angle for use in classification tree analysis

Table 2 Survival of newly settled Ward's damsel (*Pomacentrus wardi*) on patch reefs

Field trial	Trial duration (h)	Number of reefs	Number of fish surviving	Percentage of fish surviving
1	23.0	17	4	23.5
2	23.0	15	6	40.0
3	7.3	8	7	64.6[a]
4	23.0	18	6	33.3
5	23.4	19	10	52.6
6	22.2	21	8	38.1
7	24.4	20	10	50.0
8	24.0	17	7	41.2
9	25.0	17	8	47.1
Mean or total	21.7	152	66	43.4

[a] A total of 17 larvae were placed on patch reefs and 11 survived after 7.3 h, but laboratory behavioral traits were measured on only 8 of those larvae, 7 of which survived
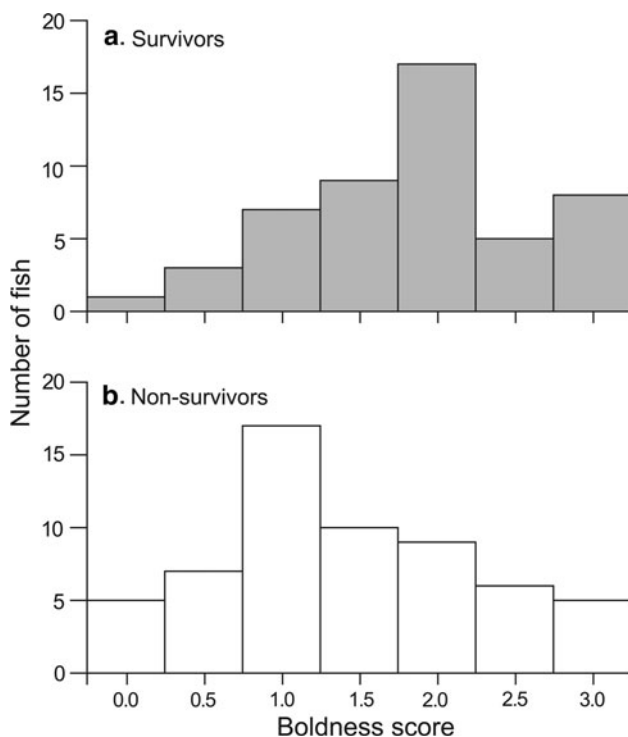
Fig. 1 Distribution of boldness scores for Ward's damsel (*Pomacentrus wardi*) that **a** survived (*solid bars*, $n = 50$) and **b** did not survive (*open bars*, $n = 59$) within 24 h after settlement on patch reefs

classification tree used three variables (mean response speed residual, boldness, and routine speed) to divide the sample of fish into four terminal nodes (Fig. 2). Three of the terminal nodes described combinations of behavioral traits and performance levels for groups of fish in which most individuals survived. The other node represented traits and performance of fish that mostly died.

The first split in the classification tree divided the full set of 105 fish according to their mean response speed residual (Fig. 2). Individuals whose mean response speed residual was more than 57.0 mm s^{-1} were assigned to terminal node 1. Seventeen of those 24 fish (70.8%) survived. The 81 slower individuals were subdivided into a group that sheltered briefly or not at all while on the reef (boldness ≥ 2) and a more timid group (boldness < 2). Terminal node 2 contained the 37 bolder individuals, 21 of which (56.8%) survived on the patch reefs. The 44 slower and more timid fish were further subdivided according to their routine speed. Nine of these fish with routine speeds less than 6.6 mm s^{-1} were assigned to terminal node 3. Six of these nine fish (66.7%) survived on their patch reef. The remaining 35 fish occupied terminal node 4, the only node that predicted mortality (i.e., proportion surviving <50%). Thirty-two of the 35 fish (92.4%) in this node did not survive for 24 h on their reef.

The classification tree performed reasonably well. Proportional reduction of error (PRE) in the analysis improved by 0.094 with each variable added to the tree, resulting in a final PRE value of 0.281. Overall classification success was excellent for fish that died on the patch reefs (91.4%) but poor for individuals that survived (62.9%).

Discussion

While predation is believed to be responsible for the high mortality rates of fishes and invertebrates during their settlement transition (Gosselin and Qian 1997; Almany and Webster 2006), there is poor understanding of the mechanisms that determine which individuals survive. Our analysis of survivors exposed to near natural conditions on patch reefs demonstrated that it is possible to identify the behavioral traits that increase an individual's susceptibility to predators. These become apparent quickly through the loss of individuals that possess those traits, which in our study were a combination of low escape speed, shyness (low boldness), and high routine swimming speeds. More than 91% of 35 individuals exhibiting that combination of traits died within 24 h of settlement.

To interpret survival skills, good or bad, it is useful to decompose the predator–prey interaction into a three-step sequence typical of all such interactions: encounter–attack–capture (O'Brien 1979; Endler 1986; Lima and Dill 1990; Fuiman and Magurran 1994). Optimally, prey should first minimize the risk of encounter, usually by remaining inconspicuous to the senses of the predator. Failing that, the prey should minimize the likelihood of an attack once an encounter occurs. Options in this regard are few for young fishes attacked by much larger fishes, but being vigilant of predators and moving toward shelter prior to the

Fig. 2 Classification tree for discriminating early post-settlement survival on patch reefs for individual Ward's damsel based on three behavioral traits: **a** residual of mean response speed, **b** boldness, and **c** routine speed. Survival on reef 24 h after settlement is categorized as yes (*Y*) or no (*N*). Starting in panel (**a**), each group of fish is divided according to a threshold value (*broken vertical line*) for one trait until a terminal *node* is reached. Sample sizes (*n*) are shown for each group of fish and percent survivors is noted in each terminal node box. Boldness assumes discrete values, so data points in panel (**b**) were offset randomly for visibility. See text for further explanation
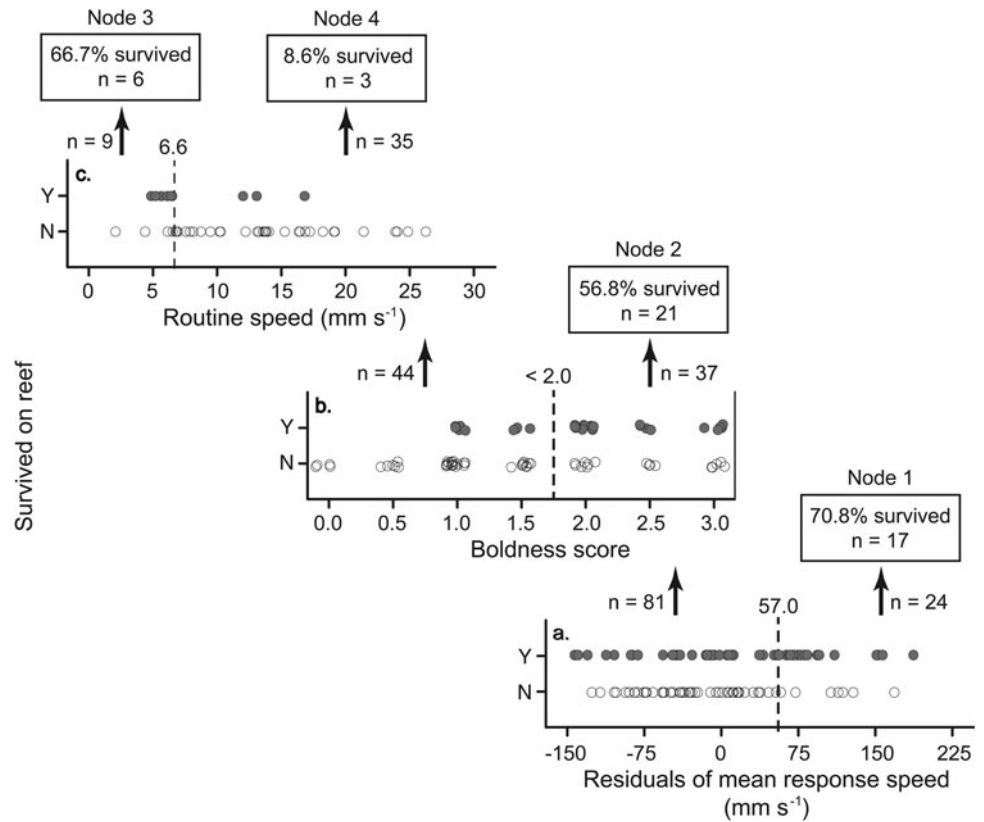
attack (predator avoidance) are common responses (Fuiman and Magurran 1994; McCormick and Manassa 2008). After an attack has begun, the final action that prey must take to survive is an effective escape response (predator evasion). Timing, magnitude, and/or direction of a response determine its effectiveness (Fuiman 1993; Fuiman et al. 2006; Stankowich and Blumstein 2005).

The three traits that defined the individuals that were most susceptible to predators in our study—low mean response speed, low boldness, and high routine speed—influence different parts of the predation sequence. Mean response speed is one of several measures we made of escape response magnitude (others being distance, duration, maximum speed, time to maximum speed, and maximum acceleration). Our finding that relatively slow responses to the artificial visual stimulus were detrimental to survival makes sense, intuitively. Lower magnitude escape responses do not move the prey out of the predator's reach quickly enough. The fact that a measure of response effectiveness was the first variable used to discriminate survivors confirms the high predation pressure experienced by these fishes. If predation rates had been much lower because of, for example, excellent predator avoidance skills of the damselfish, attacks and responses would have been reduced and a trait that minimizes conspicuousness might have been the first variable in the classification tree. Instead, the structure of the tree suggests that young

Pomacentrus wardi generally are not effective at minimizing encounters or attacks, and the high mortality rates indicate that these small fish are not capable of highly effective responses against at least some of the predators they naturally encounter.

Two traits whose benefits apply to earlier stages in the predation sequence entered the tree later. Boldness, the only survival skill measured in situ, might be interpreted as an indicator of vigilance, which promotes survival by minimizing the risk of attack. Fish that scored 2 or greater for boldness were not strongly intimidated by a diver. They retreated to the shelter of their patch reef briefly or not at all, but remained attentive to nearby activity and/or judged the diver as no threat. Vigilant individuals are attentive to risks to their survival and are able to gauge threats prior to an actual attack. The more timid individuals that scored below 2 for boldness likely were not as vigilant and at greater risk from predators. Our results are similar to those of Réale and Fest-Blanchett (2003) who found that, for bighorn sheep (*Ovis canadensis*), bold individuals had greater survival than shy sheep under threat from cougars (*Puma concolor*). Godin and Davis (1995) found that bold guppies (*Poecilia reticulata*) tended to inspect predators, and predator inspection discouraged attacks and enhanced survival (Bell et al. 2009).

Routine speed is a measure of spontaneous activity that is probably related mostly to foraging and exploratory

behavior in young fishes. It does, however, have the potential to alter the risk of encounter with predators because moving objects are more conspicuous to predators, regardless of taxon (Ware 1973; Zaret 1980; Utne-Palm 2000; Sperry and Weatherhead 2009). Highly active fishes are more visible targets against the static background of the patch reef and surrounding sandy bottom. Thus, the combination of detrimental traits leading to terminal node 4 of the classification tree could compromise survival at every stage of the predation sequence, resulting in extraordinary risk of predation mortality for those individuals.

A fish that was most likely to die in our study could be characterized as one that was conspicuous to predators (high routine swimming speed), was less vigilant, and/or had difficulty in assessing a predatory threat (low boldness), and was less likely to escape an attack (low response speed). However, identifying the traits that defined survivors is a more complex problem. While the first days after settlement constitute a mortality bottleneck for most reef fish species, with individuals removed at rates of 41% in 24 h (our results), 56% in 2 days (Almany and Webster 2006), or even 61% overnight during settlement and 9–20% per day thereafter (Doherty et al. 2004), mortality does not cease after this point. The majority of remaining individuals will soon die in the following weeks on the reef (e.g., Doherty and Sale 1985; McCormick and Hoey 2004). For this reason, enormous sample sizes would be necessary to yield a reasonable number of individuals whose behavioral traits could be interpreted as indicative of general success in predation encounters. In our classification tree, at least 30% of the individuals in any of the terminal nodes that described likely survival (nodes 1, 2, and 3) did not survive 24 h after settlement. Most of the rest of the predicted survivors would certainly have died too, if we had continued the field trials even for a few days.

For this reason, interpreting our regression-tree results in terms of traits that may promote survival (as opposed to likelihood of death) may not be entirely appropriate. However, a reasonable explanation is possible. If attacked, fast escape speeds promote survival (node 1). Then, those individuals that lack adequate escape performance can survive if they use bold, vigilant behavior (node 2) to reduce the likelihood that a predator attacks. Boldness, however, may not be very effective because 43% of damselfish that scored 2 or greater for boldness did not survive 24 h on their patch reef. Individuals that lack both effective escape performance and sufficient boldness can survive if they can reduce encounters with predators by being less conspicuous (node 4). The nearly equal proportions of survivors in terminal nodes 1 and 4 suggests that eventual survival may depend both on encounter rates and on escape success, rather than one or the other.

Few other studies have attempted to assess survival skills for young fish, and those studies were conducted in the laboratory where attacks were staged, making it impossible to determine which skills contribute to the risks of encounter or attack. Based on a comparison of successful and unsuccessful escape attempts by larval Atlantic herring (*Clupea harengus*) attacked by larger conspecifics, Fuiman (1993) surmised that responsiveness (likelihood of responding to an attack) was the primary determinant of survival since predators rarely failed to capture prey that did not respond, and that responses were most effective when initiated when the predator was very near the prey (i.e., implicating response timing as an important survival skill). In a subsequent investigation of larval red drum (*Sciaenops ocellatus*) using laboratory assays similar to those we used, Fuiman et al. (2006) used regression tree analysis to determine that routine speed, reactive distance (closely related to the response latency and apparent distance measurements made in the current study), and response distance were related to the outcome of predation trials staged in the laboratory. As in the earlier study of herring, Fuiman et al. (2006) observed that responsiveness to the actual predator was the primary factor in surviving an attack. Although responsiveness was not included among our measured behavioral traits, responsiveness is a prerequisite for response speed to have an effect on the outcome of a predator–prey interaction and, therefore, must be a critical anti-predator trait once an attack occurs. Fuiman et al. (2006) also reasoned that the laboratory measures identified by their analysis as being important to survival might be merely indirect indicators of responsiveness, and not mechanistically related to corresponding attributes in actual predation interactions. The same holds for our current study; response speed, boldness, and routine speed may be consequences of other traits that are correlated with survival, such as physiological condition.

Despite strong selective pressures for particular traits and performance levels, substantial variation in those traits remains within a population. Stamps (2007) reviewed the possible mechanisms that maintain variance in behavioral phenotypes among individuals under selective pressure. These include trade-offs with mortality (Stamps 2007; Biro and Stamps 2008), frequency-dependent selection (Roff 1998), temporal and spatial variation in the intensity and direction of selection (Mangel 1991), and a balance between mutation and selection (Santiago 1998). In addition, some of the behavioral traits we measured in newly settled larvae may be the objects of selection during different life-history stages or in different habitats, predator regimes, etc. Although field studies are rare, in coral reef environments there is growing evidence that the spatial and temporal landscape of selective pressure is extremely variable. For example, Meekan et al. (2010) found that

selective mortality removed fast-growing and larger fish at settlement, while a month later, slow-growing, smaller fish were preferentially removed from cohorts. Similarly, McCormick and Meekan (2007) found that, for young damselfish settling on the reef, smaller fish survived within adult territories while larger, faster-growing fish survived outside. Thus, the importance of any particular trait for survival can vary in both time and space, and is unlikely to be determined by a single selective event.

Variation in behavioral performance can arise from a variety of sources, including genetic, non-genetic parental, and environmental effects. In fishes, for example, routine swimming behavior is especially sensitive to environmental conditions (e.g., thermal history, Fuiman and Ottey 1993; food quality, Davis and Olla 1992; and contaminant exposure, Alvarez and Fuiman 2005), and other measures of performance and survival potential are related to growth rate (McCormick and Hoey 2004; Fuiman et al. 2005; Meekan et al. 2010), larval diet (Nakayama et al. 2003), and maternally transferred stress hormones or fatty acids (Gagliano and McCormick 2009; L.A. Fuiman and A. Ojanguren, unpublished data). Similar relationships have been documented in other animals (Kullberg et al. 1996; Scott et al. 2007; Alzaga et al. 2008; Jones et al. 2009). Our wild-caught fish represent a natural range of genetic, maternal, and environmental experiences which could have generated wide variability in behavioral performance. However, our studies of red drum larvae reared under uniform environmental and dietary conditions have documented significant variation in routine swimming and escape performance: (1) among individuals relative to variability expressed within those individuals (Fuiman and Cowan 2003), (2) among larvae with inherently different growth rates (Fuiman et al. 2005), (3) among offspring from different parents (Fuiman et al. 2005), and (4) among larvae from different batches obtained from the same parents (L.A. Fuiman and A. Ojanguren, unpublished data). So, even in the absence of genetic and environmental variability, there can be substantial variation in behavioral traits that are critical to survival.

Life history bottlenecks are a feature of all organisms that undergo ecological shifts associated with stage-specific migrations (Wilbur 1980; Werner 1988). Our study is the first to assay multiple traits and link them to survivorship of young fishes as they pass through a critical life history transition on the reef. We show that the hallmarks of failure for individuals during this time are relatively obvious, but identification of the traits that engender ultimate success will require much larger studies and investigation over a greater portion of the juvenile life span.

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