

Influence of prey body characteristics and performance on predator selection

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Abstract At the time of settlement to the reef environment, coral reef fishes differ in a number of characteristics that may influence their survival during a predatory encounter. This study investigated the selective nature of predation by both a multi-species predator pool, and a single common predator (*Pseudochromis fuscus*), on the reef fish, *Pomacentrus amboinensis*. The study focused on the early post-settlement period of *P. amboinensis*, when mortality, and hence selection, is known to be highest. Correlations between nine different measures of body condition/performance were examined at the time of settlement, in order to elucidate the relationships between different traits. Single-predator (*P. fuscus*) choice trials were conducted in 57.4-l aquaria with respect to three different prey characteristics [standard length (SL), body weight and burst swimming speed], whilst multi-species trials were conducted on open patch reefs, manipulating prey body weight only. Relationships between the nine measures of condition/performance were generally poor, with the strongest correlations occurring between the morphological measures and within the performance measures. During aquaria trials, *P. fuscus* was found to be selective with respect to prey SL only, with larger individuals being selected significantly more often. Multi-species predator communities, however, were selective with respect to prey body weight, with heavier individuals being selected significantly more often than their lighter counterparts. Our results suggest that under controlled

conditions, body length may be the most important prey characteristic influencing prey survival during predatory encounters with *P. fuscus*. In such cases, larger prey size may actually be a distinct disadvantage to survival. However, these relationships appear to be more complex under natural conditions, where the expression of prey characteristics, the selectivity fields of a number of different predators, their relative abundance, and the action of external environmental characteristics, may all influence which individuals survive.

Keywords Reef fish · Predation · Body size · Body condition · Burst swimming speed

Introduction

Body characteristics and performance attributes are generally thought to play a large role in determining an individual's probability of survival throughout its lifetime. These traits have been widely linked to the probability of survival during a range of events, including predatory encounters (Litvak and Leggett 1992; Janzen 1993; Twombly and Tisch 2000; Dorner and Wagner 2003; Hoey and McCormick 2004; Alvarez and Nicieza 2006; Husak 2006) and competitive interactions (Smith 1990; Marshall et al. 2006; Persson and De Roos 2006; Van Buskirk 2007; Zedrosser et al. 2007), and threat of starvation and disease (Biro et al. 2004; Lyons et al. 2004; Bystrom et al. 2006; Reim et al. 2006; Hall et al. 2007; Smith et al. 2007). In recent years, the importance of these prey characteristics during predatory interactions has received considerable attention, as predation is widely thought to be one of the major processes influencing the size of populations and the structure of ecological communities (Sih 1987). The

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selective nature of predation means that prey characteristics that decrease an individual's vulnerability to predators will be retained within a population, whilst those that increase vulnerability will be selectively lost. The extent to which predation is selective will be dependent on the preferences and selective profiles of those predators within the community.

Predator selectivity may be of particular importance during periods of high mortality. Such cases are common during transitional periods between life history stages for organisms with complex life cycles (e.g. bipartite life cycle of many amphibians, and marine invertebrates and fishes; Werner 1986; Gosselin and Qian 1997; Hunt and Scheibling 1997; McCormick et al. 2002; Leis and McCormick 2002). If predation is selective during such periods, then it may have a disproportionate influence on those traits that are passed into successive life stages. If, however predation is not selective, then high mortality alone does not necessarily indicate a critical life stage for life history evolution (e.g. Crouse et al. 1987).

Coral reef fishes are an ideal group on which to study the selective nature of predation. At the time of settlement to the reef environment, many species undergo a transitional period between a planktonic larval stage and a more "benthic-associated" adult/juvenile stage, often marked by rapid morphological and physiological changes (McCormick and Makey 1997; McCormick et al. 2002). This period is characterized by high levels of mortality, with upwards of 50% of individuals being lost within the first 1–2 days post-settlement (Doherty et al. 2004; Almany and Webster 2006). Much of this mortality has been attributed to predation by small "reef-associated" fish predators (Carr and Hixon 1995; Holbrook and Schmitt 2002). In addition, at the time of settlement, individuals generally possess moderate to high levels of variability in a number of traits known to influence survival during a predatory encounter (McCormick and Molony 1993; Hoey and McCormick 2004).

Prey body size is one morphological characteristic that is generally thought to play a large role in influencing the outcome of such encounters (Sogard 1997; Schmitt and Holbrook 1999; Brunton and Booth 2003; McCormick and Hoey 2004; Holmes and McCormick 2006). One common theory (the bigger-is-better hypothesis) suggests that from a prey's perspective, being larger at a given life history stage, results in a survival advantage, through reduced predation rates (Rice et al. 1993; Takasuka et al. 2003), enhanced abilities in competitive interactions and the acquisition of shelter space (Holbrook and Schmitt 2002) and decreased susceptibility to starvation (Sogard 1997; Schmitt and Holbrook 1999). Thus, as prey size increases, vulnerability to predation is predicted to decrease. An alternate ecological theory, known as optimal foraging theory (OFT), predicts that predators preferentially prey on prey of an

optimal size in order to maximise the net rate of energy intake (MacArthur and Pianka 1966; Hughes 1980). This theory predicts that, from a prey's perspective, both large and small size conveys a survival advantage during a predatory encounter. The characteristics of the prey that are targeted are contingent on the selectivity profile of the predator, which tend to be dome-shaped (e.g. Rice et al. 1997). From a mechanistic perspective, this may result in disruptive selection whereby both tails of the size distribution are favoured.

Prey body condition has also been shown to have important implications for survival during the early post-settlement period (Mesa et al. 1994; Booth and Hixon 1999; Booth and Beretta 2004; Hoey and McCormick 2004). However, its direct influence on the outcome of predator–prey relationships remains largely untested. Condition of a fish may be measured in a number of different ways, including growth, lipid content, liver hepatosomatic indices, body robustness and developmental state (McCormick and Molony 1993; McCormick 1998; Ferron and Leggett 1994; Hoey et al. 2007). Although a number of studies have shown evidence of predator selectivity with respect to prey body characteristics (Sogard 1997; Booth and Hixon 1999; Vigliola and Meekan 2002; Holmes and McCormick 2006; McCormick and Meekan 2007), to date no study has directly examined how such traits influence the outcome of individual predatory interactions during this early period.

The present study focuses on individual- and community-level predator selectivity on a common Indo-Pacific coral reef damselfish (*Pomacentrus amboinensis*) during the early post-settlement period. Experiments were conducted with respect to three "non-destructive" body and performance attributes known to show moderate levels of variability at the time of settlement: body length, body weight and burst/escape swimming speed. Specifically, the aims of the study were: (1) to examine the interrelationships between body characteristics and performance attributes, including pre-settlement growth and burst/escape swimming speed; (2) to determine whether predation by the common predator *Pseudochromis fuscus*, was selective with respect to prey body size, body weight and burst swimming speed; and (3) to determine whether predation by a natural multi-species predator community was selective, and how it differed from the selectivity regime demonstrated by *P. fuscus*.

Materials and methods

Study site

This study was conducted at Lizard Island (14°40'S, 145°28'E), northern Great Barrier Reef (GBR), Australia

during November and December 2005 and 2006. The flow-through salt water aquarium system at Lizard Island Research Station was used to conduct the aquarium trials, whilst the surrounding shallow lagoonal reefs and sand flats were used for the patch reef trials.

Study species

The damselfish *P. amboinensis* was used as the prey species for all experimental trials. This species is common within coral reef fish communities in the Indo-Pacific, particularly in the central GBR. Individuals of the species settle to a wide variety of habitats on the northern GBR, but are found in highest densities associated with small reef patches at the base of shallow reefs. *P. amboinensis* has a pelagic larval phase of between 15 and 23 days and settles at 10.3–15.1 mm standard length (SL) (Kerrigan 1996) with its juvenile body plan largely complete (McCormick et al. 2002). Once settled, *P. amboinensis* is site attached, making it an ideal species for experimental manipulation. The species recruits in substantial numbers at Lizard Island around the new moon during the austral months (October–January), and is easily collected at the time of settlement with light traps (Milicich and Doherty 1994).

The brown dottyback, *P. fuscus*, was used as the model predator species for the aquarium trials. *P. fuscus* is a small (maximum size 72.4 mm SL), site-attached predator common on shallow reefs throughout the Indo-Pacific. This species is an active pursuit predator that generally lives in close proximity to prey populations. *P. fuscus* is known to consume newly settled and juvenile fishes in both the laboratory and field (Holmes and McCormick 2006; Almany et al. 2007) and is diurnally active.

In the natural system, newly settled reef fishes are subject to a range of resident and transient predators. At Lizard Island the most common predators have been identified as the brown-barred rock cod (*Cephalopholis boenak*), moonwrasse (*Thalassoma lunare*), two species of lizardfish (*Synodus variegatus* and *Synodus dermatogenys*), and the brown dottyback (*P. fuscus*; Martin 1994, Beukers and Jones 1997, Holmes and McCormick 2006).

Fish collection

Settlement-stage *P. amboinensis* were collected using light traps moored overnight close to the reef crest, and transported back to the Lizard Island Research Station at dawn. Prior to the predation experiments, fish were maintained in 25-l flow-through aquaria systems for ~24 h, and fed newly hatched *Artemia* sp. twice per day ad libitum to allow for recovery from the stress of capture. Growth during this period was minimal. Fish used in

the prey condition/performance analysis were taken straight from light trap catches and processed on the same day.

Adult *P. fuscus* (38–71.4 mm SL) were collected from surrounding reefs using clove oil and hand nets. All fishes were maintained in individual 57-l flow-through aquaria systems for 48 h before use in aquarium trials. Fish were not fed during this period to standardize for satiation, and to avoid handler-associated learning.

Correlation of prey condition/performance measures

Ninety-four *P. amboinensis* were randomly selected from a single day's light trap catch and measured for nine potential indicators of body condition and performance: SL, maximum burst speed, mean burst speed, wet weight, recent pre-settlement growth, dry weight, lipid content, overall body condition and Fulton's condition factor (Fulton's *K*). To obtain SL, individual fish were placed into small clip-seal polyethylene bags with a small amount of sea water and measured using calipers (± 0.1 mm).

To measure maximum and mean burst speed fish were placed individually into a narrow aquarium (10 × 150 × 200 mm) filled to 30-mm depth with fresh seawater. The narrow shape of the aquarium effectively forced the fish to move in two dimensions, minimising errors associated with movement away from the viewing plane. Escape bursts in this species were generally observed to occur within this "side on" viewing plane (McCormick and Molony 1993), as opposed to the "top down" viewing plane used in previous burst speed studies of Red Drum larvae, *Sciaenops ocellatus* (Fuiman and Cowan 2003; Fuiman et al. 2006). A 5 × 5-mm reference grid was positioned on the back of the aquarium. Fish were maneuvered to one end of the aquarium and a rubber ball pendulum was dropped from a 45° angle against the glass end of the aquarium immediately behind the fish, to induce the burst response. The fish was allowed to recover from stress before being maneuvered back to the end of the aquarium. This process was repeated until either five reliable bursts were recorded or the fish became too stressed to produce reliable bursts. Only those fish that recorded two or more successful bursts were included in the analysis. A digital camera (frame speed 0.04 s), positioned facing the front of the aquarium, was used to record each burst. These recordings were analysed, and the 5 × 5-mm grid was used to determine the distance travelled over the first two frames (0.08 s) of each burst. From these measurements, maximum and mean burst speeds were calculated for each fish. Absolute distance travelled was used, as opposed to relative distance travelled (i.e. scaled for body size) as this is thought to be a more appropriate estimate of an individual's ability to escape a predation event.

Fish were lightly blotted dry and weighed to the nearest 1 mg using a mass balance (wet weight). Euthanised fish were then placed into a freeze drier for 24 h before being weighed to the nearest 1 μg using a mass balance to obtain a dry weight. Recent pre-settlement growth was determined by examining the microstructural increments deposited within the sagittal otolith. Otoliths were ground to produce a thin transverse section (as per Wilson and McCormick 1999) and increment widths were measured along the longest axis, the most sensitive axis to growth changes recorded in the otolith profile. Once all samples were completed, increment widths were re-measured to avoid bias. The mean width of the outer seven increments was used as a relative measure of recent pre-settlement growth. The assumptions that the frequency of increment formation is daily and the distance between consecutive increments is proportional to fish growth have been validated for *P. amboinensis* juveniles by Pitcher (1988) and Hoey (1999).

To determine total lipid content each fish was homogenized in 1 ml distilled water immediately after freeze drying. A 300- μm aliquot of each homogenate sample was analysed for lipid content by first extracting the lipid material using chloroform–methanol extraction (Mann and Gallager 1985). This material was subsequently analysed using the phosphosulphovanillin method, as described by Barnes and Blackstock (1973). The method uses a cholesterol standard calibrated against gravimetric values to convert chlorometric values to total lipids. Chlorometric values were obtained using a spectrophotometer (Labsystems iEMS Reader MF) and associated computer software (Genesis 3.04), at a wavelength of 520 nm. The cholesterol standard was mixed at concentrations of 0, 2.5, 5, 7.5 and 10 mg ml^{-1} and run through the same extraction process as the homogenate samples, to produce a calibration line between chlorometric values and cholesterol concentration. Once completed, a known ratio of 4:5 (cholesterol:lipid) was used to convert the resulting values from cholesterol to lipid concentration (mg ml^{-1}). The initial dry weight obtained for each sample was then used to express the total lipid content as mg g^{-1} dry weight.

A measure of overall body condition was obtained using residual regression analysis (Koops et al. 2004). This method uses the residuals of a SL/wet weight regression as an index of relative condition. Although its validity is currently questionable, Fulton's *K* was previously used widely as a measure of body condition (e.g. Booth and Hixon 1999; Hoey and McCormick 2004). To permit comparison with such previous studies, Fulton's *K* was also calculated using the equation:

$$K = 10^5 \times \left[\text{wet weight (g)} / \text{standard length (mm)}^3 \right]$$

Experiment 1: laboratory trials

Pomacentrus amboinensis were taken from light trap catches and sorted into groups of two (weight or burst speed trials) or three (size trials), for each of three measures of body and performance attributes: prey body size, body weight, and burst swimming speed.

For trials testing prey body size, individual *P. amboinensis* were first placed in a clip-seal plastic bag containing a small amount of aerated seawater and measured for SL using calipers (± 0.1 mm). Fish were placed into “groups” of three, such that one individual of each of three size classes was present. These size classes were set at 10.8–11.5, 11.9–12.1, and 12.5–13 mm SL. The classes were chosen to span the entire size range of individuals at the time of settlement. The size difference of individuals between classes for all trials was always at least 0.5 mm. Overall, the size of individuals caught in light traps during the course of the experiment ranged between 10.8 and 13 mm SL, with a mean of 11.94 mm. Thus, a difference of 0.5 mm between size classes represents $\sim 4.2\%$ of the mean prey size.

To test the influence of prey body weight, *P. amboinensis* were randomly selected and placed into one of two identical 25-l aquaria with flowing seawater. Fish in one aquaria were fed ad libitum (high feed treatment) with *Artemia* sp. nauplii, whilst those in the other aquaria were fed 1/5 ad libitum (low feed treatment). The different feed trials were used in order to accentuate the level of variability in standardized body weight amongst individuals. After 2 days, the fish were removed from both aquaria, measured for SL (± 0.1 mm using calipers) and weighed (± 1 mg). In order to decrease fish stress during the weighing process, fish were first anaesthetized using MS-222 (0.1 mg ml^{-1} sea water). *P. amboinensis* from the high feed treatment and of heavier weight (“heavy” individual) were paired with those from the low feed treatment and of lower weight (“light” individual), but equal SL. A standardized weight difference of 5–10 mg was maintained between individuals within a pair throughout the experiment. Individuals within the pair were tagged with either a red or black subcutaneous fluorescent elastomer tattoo using a 27-gauge hypodermic needle for the purpose of individual identification, as per Hoey and McCormick (2006). Tag colours were alternated between replicate trials to avoid the possibility of predators selecting prey based on tag colour. Hoey and McCormick (2006) found that the tagging technique had no influence on survival or growth of *P. amboinensis* in aquaria over a 2-week period. The wet weight of individuals used for trials during the experiment ranged between 22 and 74 mg, with a mean of 52.04 mg. Thus, a difference of 5–10 mg between weight

classes represents ~ 9.6 – 19.2% of the mean prey weight. The mean SL of prey was 12.2 mm.

In order to test the influence of prey burst speed, individual *P. amboinensis* were firstly transferred to a 25-l flow-through aquarium for 24 h. After this period, fish were removed and measured for SL using calipers (± 0.1 mm). Individuals were then measured for burst swimming speed as described above. In order to reduce stress on the fish, two to three reliable bursts were obtained per individual only. *P. amboinensis* with a high burst speed (“fast”) were paired with those with a low burst speed (“slow”), but equal SL. Individuals were tagged for identification purposes in the same manner as above. The difference in burst speed between fast and slow individuals in a pair ranged from 110–280 mm s⁻¹. The burst speed of all individuals measured during the course of the experiment ranged between 201 and 825 mm s⁻¹, with a mean of 423.98 mm s⁻¹. Therefore, the difference of 110–280 mm s⁻¹ between individuals in a pair represents ~ 25.9 – 66% of the mean prey burst speed. The mean SL of prey was 11.98 mm.

Eighteen identical flow-through aquaria were constructed, as per Almany et al. (2007). Each aquarium had an internal volume of 57.4-l (600 × 255 × 375 mm). Aquaria were divided into two equal-sized sections by a removable opaque perspex partition. A 15-cm-length of 105-mm-diameter PVC pipe cut in half was placed into one section of the aquarium as a predator shelter. A single, artificial (white moulded resin) branching coral (item no. 21505; Wardleys/TFH, Sydney; dimensions: 140 × 115 × 50 mm) was placed in the other section as prey shelter. Aquaria were surrounded by black plastic to visually isolate them from each other and other external disturbances. A small hole was cut in one side of the plastic to allow observation of the trials.

At the commencement of each trial, aquaria were divided in two with the opaque partition. A single *P. amboinensis* group/pair was placed into one half, along with the artificial branching coral. A single predator (*P. fuscus*) was allowed to acclimate in the opposite section of the aquaria for 48 h prior to the trials. Prey were acclimated for 1 h before the partition was removed and the trial started. Prey abundance was continuously monitored for the first 20 min and every 10 min thereafter. When one or more of the prey individuals were found to be missing, the trial was ended. Any survivors were either re-measured for SL (body size trials), or their tag colour was recorded (body weight and burst speed trials) to determine the identity of the missing individual(s). If more than one prey were found to be missing, the trial was discarded. If a result had not occurred within 24 h, the trial was discarded. The mean SL of predators over all trials was 55.89 mm. Thirty-four successful trials were run testing prey body size, whilst 25 successful trials were run to test both prey body weight and burst swimming speed.

Experiment 2: field trial

Pomacentrus amboinensis were taken from light trap catches and sorted into pairs as per the protocol set out in the prey body weight trials in experiment 1. Each pair consisted of one light and one heavy individual for a standardised body length. The wet weight of individuals weighed for trials during the course of the experiment ranged between 46 and 74 mg, with a mean of 59.04 mg. The weight difference of 5–10 mg between weight classes represents ~ 8.5 – 16.9% of the mean prey weight. The mean SL of prey was 12.61 mm.

A series of small patch reefs (20 × 20 × 20 cm) were constructed on the sand flat immediately adjacent to the edge of a shallow lagoonal reef. Patches were arranged approximately 2 m from the reef base and approximately 3–4 m apart within a 50-m-wide section of reef edge. Each patch consisted of a combination of live and dead *Pocillopora damicornis* (a bushy scleractinian). Such patch reefs are common settlement sites for this species (McCormick and Hoey 2004). All patches were open to the full array of reef-based and transient predators at each site.

Prior to releasing a tagged pair, the patch reef was cleared of all resident fishes and large invertebrates using small hand nets. A single *P. amboinensis* pair was then placed onto patch reefs and shielded by a diver from predators for 5–10 min until acclimated to the new environment. Within 30 s of release, fish were observed feeding on food items from the water column, which suggested a rapid acclimatization to their new environment.

Survival of each of the experimental pairs was monitored 3 times per day (morning, mid-day, evening) by visual census. Each replicate trial ended when one or both of the tagged fish were found to be missing from a patch, at which point the identity of the remaining fish was recorded and the surrounding reef area was searched to determine whether the missing individual had emigrated. If a result was not obtained within 24 h, the *P. amboinensis* pair was removed and the trial was abandoned. Trials where both individuals were found to be missing were discarded from the replicate group. A total of 48 trials were run in order to obtain 23 successful results.

Analysis

Pearson’s correlations were used to examine relationships among the eight condition measures. The coefficient of variation (CV) was calculated for the burst speed of each individual, using replicate recordings obtained from the correlation experiment. This was used to obtain an estimate of performance consistency among replicate bursts for individuals. CVs were calculated using the number of successful bursts, which varied between 2 and 5.

Tests of significance for Pearson's correlations were not corrected for multiple tests, due to the exploratory nature of the analysis. The frequency of first mortality between treatments, within each set of predation trials, was compared using a χ^2 goodness of fit test. With the exception of the size-based aquarium trials, Yates' correction was incorporated in all analyses to correct for $df = 1$.

Projected survival over the 24-h period of predation trials, incorporating censored data previously excluded in χ^2 tests, was analysed using survival analysis. Projected survival curves of each treatment within a trial set were calculated and plotted using the Kaplan–Meier product–limit method (Kaplan and Meier 1958). The Kaplan–Meier method is a nonparametric estimator of survival that may incorporate incomplete observations, such as those cases in this study where two prey individuals were found to be missing before the trial could be closed. Projected survival between treatments within trial sets was compared using a Cox–Mantel test (weight- and burst speed-based laboratory trials, weight-based field trial) or a χ^2 test for multiple groups (size-based laboratory trials).

Results

Correlation of prey condition/performance measures

The nine measures of condition/performance of *P. amboinensis* at settlement displayed markedly different levels of variability among fish (Table 1). Maximum and mean burst speed were the most variable (CV = 25.9 and 23.2%, respectively), followed by lipid content (CV = 17.4%). Wet weight (CV = 14.3%), dry weight (CV = 13.2%) and Fulton's *K* (CV = 10.5%) displayed moderate levels of variation, whilst SL (CV = 3.1%) and recent pre-settlement growth rate (CV = 8.1%) displayed the lowest levels. An accurate estimate of variability for overall body condition (obtained during residual regression analysis) was

not possible, due to the positive and negative expression of the variable measures (range = 0.01348 to –0.01349, SD = 0.00525)

Correlations between the nine measures were generally poor (Table 2). The morphological measures were the general exception, with SL, wet weight and dry weight all displaying strong positive correlations. Body condition, wet weight and Fulton's *K*, as well as maximum and mean burst speed, also displayed strong positive relationships, whilst lipid content and dry weight showed a slightly weaker negative relationship. Weaker correlations also existed between SL and lipid content (negative), dry weight and body condition (positive), SL and recent pre-settlement growth (positive), and dry weight and recent pre-settlement growth (positive). Correlations between the performance (maximum or mean burst speed) and morphological/condition measures were poor overall, with SL being the only measure correlated with maximum burst speed, albeit only weakly ($r = 0.252$, Table 2).

The consistency of burst speed within individuals was moderate, with a mean CV of 14.38% ($\pm 0.95\%$ SE) and a median CV of 15.44% for the 89 individuals measured.

Experiment 1: laboratory

During aquarium trials, where prey from three size classes were exposed to the predator *P. fuscus*, prey fish from the largest size class (12.5–13 mm SL) were found to be selected first significantly more often than those of the small and medium size classes ($\chi^2_{df 2} = 24.772$, $P < 0.001$; Fig. 1). This result occurred in 25 (73.5%) of the 34 trials run, whilst small and medium prey sizes were selected first in only five (14.7%) and four (11.8%) trials, respectively. A similar pattern was found in the projected survival schedules of the three different size classes, with survival analysis showing a significant difference over the 24-h duration of the trials ($\chi^2_{df 2} = 17.258$, $P = 0.0002$; Fig. 2). Projected mortality of large individuals was initially high, with 50% mortality occurring within 0.3 h and 80%

Table 1 Statistical summary of the nine measures of condition/performance obtained from newly settled *Pomacentrus amboinensis* collected from light traps ($n = 94$)

Condition measure	<i>n</i>	Mean	Range	CV
Standard length (SL) (mm)	94	12.3	11.4–13.3	3.1
Wet weight (g)	94	0.05	0.035–0.069	14.3
Dry weight (g)	93	0.01	0.009–0.016	13.2
Body condition index	94	–0.00028	–0.01398–0.01348	N/A
Fulton's <i>K</i>	94	25.9	18.9–32.1	10.5
Lipid content (mg/g)	87	102.9	60.9–150.3	17.4
Maximum burst speed (mm/s)	89	491.3	125–800	25.9
Mean burst speed (mm/s)	89	423.8	125–608.8	23.2
Recent pre-settlement otolith growth rate (mm/day)	74	16.9	13.3–19.9	8.1

CV Coefficient of variation

Table 2 Correlations among nine measures of condition/performance of newly settled *P. amboinensis* collected from light traps ($n = 94$)

	SL	Wet weight	Dry weight	Body condition	Fulton's <i>K</i>	Lipid content	Maximum burst speed	Mean burst speed	Recent pre- settlement growth
SL	1.00	0.647***	0.809***	0.001 ns	-0.001 ns	-0.338**	0.252*	0.207 ns	0.3**
Wet weight		1.00	0.735***	0.761***	0.758***	-0.167 ns	0.089 ns	0.112 ns	0.265*
Dry weight			1.00	0.271**	0.263*	-0.351***	0.074 ns	0.065 ns	0.361**
Body condition				1.00	0.995***	0.059 ns	-0.086 ns	-0.021 ns	0.106 ns
Fulton's <i>K</i>					1.00	0.062 ns	-0.092 ns	-0.03 ns	0.101 ns
Lipid content						1.00	0.051 ns	0.113 ns	-0.127 ns
Max. burst speed							1.00	0.924***	-0.051 ns
Mean burst speed								1.00	-0.01 ns

Pearson correlation coefficients are given

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

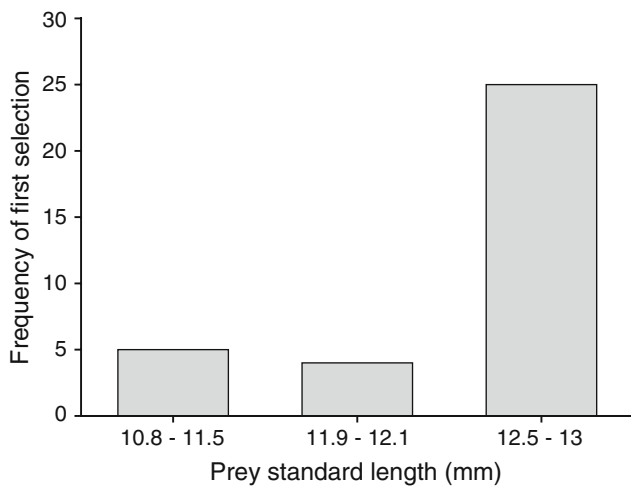


Fig. 1 Frequency of selection of newly settled reef fish *Pomacentrus amboinensis* by the common predator *Pseudochromis fuscus* during size-based aquarium trials

mortality occurring within 1.3 h. Survival then became relatively stable for the remainder of the trial period. Projected mortality of both small and medium individuals was comparatively more constant over the duration of the trials, with ~50% mortality occurring at 3.5 and 5.7 h, respectively. One hundred percent mortality was predicted for all groups 19.6 h after the commencement of trials

No difference in predator choice was detected in either the weight-based or burst speed-based trials during the aquarium experiments (both $\chi^2_{df 1} = 0.00$, $P = 1.00$). The mortality of both treatments within a pair was almost identical in both cases, with lighter and slower individuals being selected marginally more frequently (both chosen first in 52% of trials) than their heavier and faster counterparts during respective trial sets. Similarly, no difference was found between the projected survival

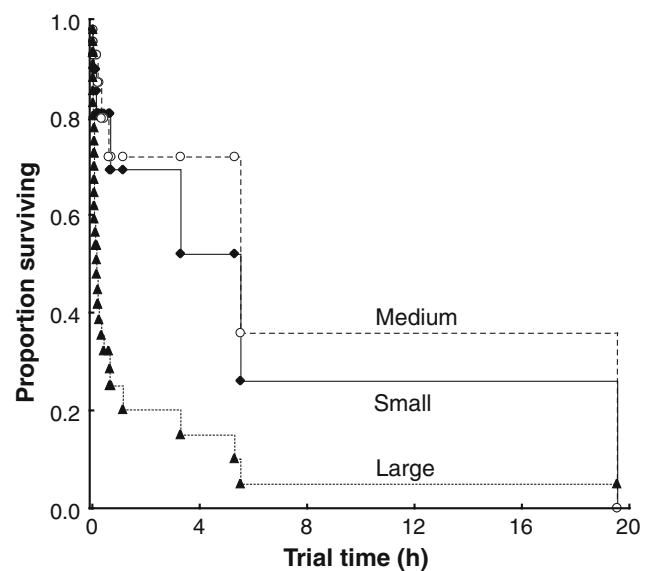


Fig. 2 Kaplan–Meier product–limit plot for predicted survival of small [10.9–11.5 mm standard length (SL); filled diamond], medium (11.9–12.1 mm SL; open circle) and large (12.5–13 mm SL; filled triangle) size classes of prey during size-based predation trials with *P. fuscus*

schedules of either treatment in both the weight-based and burst speed-based trials over the 24 h trial period (Cox–Mantel_{38,38} = 0.000, $P = 1.000$; and Cox–Mantel_{26,26} = 0.000, $P = 1.000$, respectively). Projected mortality was initially high during the weight-based trials, with ~70% mortality occurring within 0.7 and 0.9 h for light and heavy individuals, respectively. Mortality then eased, until 100% mortality occurred for both groups at ~4.4 h. For the burst speed-based trials, projected mortality remained extremely high for the duration of the trials, with 50% mortality occurring at 0.09 and 0.14 h for slow and fast individuals, respectively, and 100% mortality occurring at 0.58 h for both groups.

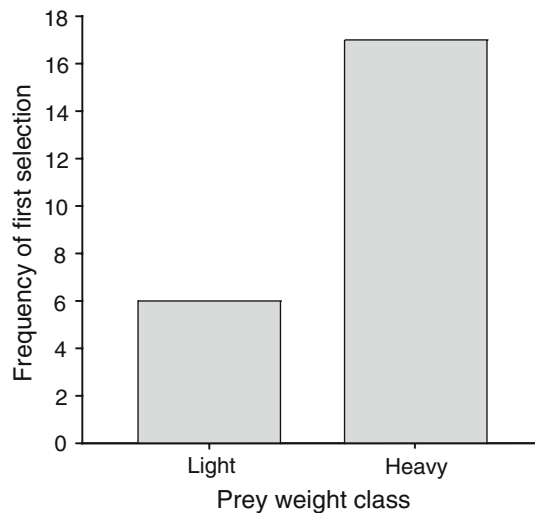


Fig. 3 Frequency of selection of light or heavy newly settled *P. amboinensis* during weight-based trials on open patch reefs. Heavy individuals were defined as having a higher wet weight for a standardized SL (~ 9.6 – 19.2% greater) than light individuals

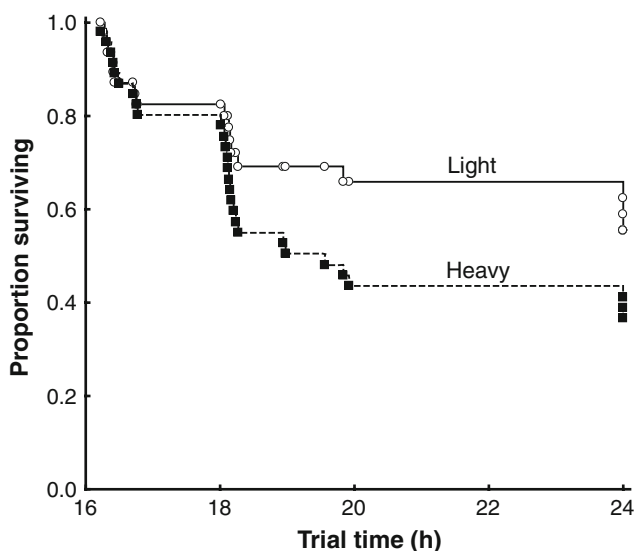


Fig. 4 Kaplan–Meier product–limit plot for predicted survival of light (open circle) and heavy (filled diamond) standardized weight classes of prey during weight-based predation trials on open patch reefs

Experiment 2: field trials

There was a significant difference in survival between heavy and light individuals during the weight-based predation trials on open patch reefs, with the “heavier” individuals found to be missing more frequently than their “lighter” counterparts ($\chi^2_{df 1} = 4.348$, $P = 0.037$; Fig. 3). This result occurred in 17 (73.9%) of the 23 trials. However, the difference between the projected mortality curves of the two treatments was non-significant over the 24 h

trial period when analysed using survival analysis (Cox–Mantel_{34,56} = 1.662, $P = 0.096$; Fig. 4). Due to the fact that trials were started in the late afternoon, and censuses could not be completed overnight, the first recordings of mortality did not occur until 16–18 h into the trial. Any mortality that occurred overnight was therefore recorded in the 16- to 18-h period. As such, projected survival of light individuals decreased from 100% at 16 h to $\sim 70\%$ at 18 h, before stabilizing to reach $\sim 55\%$ survival at the end of the trial period (24 h). Projected survival was lower during the 16- to 18-h period for heavy individuals, with a drop from 100% to $\sim 55\%$. The mortality rate eased over the following 6 h, leaving $\sim 35\%$ survival at the end of the 24-h trial period.

As there was no evidence of emigration away from patches during the experiment and all prey individuals were released in good condition, any mortality during the trials on open patches was directly attributed to localised predation by fish predators.

Discussion

The generally selective nature of mortality has been well documented during the last decade (Gosselin and Qian 1997; Sogard 1997; Blanckenhorn 1998; Meekan et al. 2006; Anderson et al. 2008). The causes of such selective loss have varied, with examples of starvation, disease, competition and predation all being shown in a range of different systems. There is now also increasing evidence to suggest that predation is selective on coral reef fishes at the time of settlement (e.g. Booth and Hixon 1999; Booth and Beretta 2004; Hoey and McCormick 2004; McCormick and Hoey 2004; Holmes and McCormick 2006; Gagliano et al. 2007). The relative importance of this to the structure of future populations may well be amplified by the high, type III mortality characteristic of this period (Almany and Webster 2006). Our study contributes significantly to this body of literature, and provides direct evidence of size-selective predation by a single predator species during this period. The dottyback *P. fuscus*, a common predator of small reef fishes (Beukers and Jones 1997), was found to be highly selective towards individuals of larger SL when tested in an aquarium system. This finding confirms the suggestion of positive size selection by the dottyback from a previous field experiment (McCormick and Meekan 2007). Interestingly, the same predatory species was found to be non-selective towards both prey body weight and burst/escape swimming speed when the confounding influence of variable fish length was experimentally removed.

With the exception of morphological characteristics (i.e. SL, wet weight, dry weight), correlations between

measures of body condition were generally found to be poor. This result is similar to the findings of other studies by McCormick and Molony (1993), Kerrigan (1996) and Hoey and McCormick (2004) who consequently suggested that selection with respect to one trait has little influence on the patterns of variability in other traits. Both SL and dry weight were found to be correlated with lipid content, displaying a fairly strong negative correlation in both cases. Interestingly, similar relationships were obtained between SL and lipid content in studies by Kerrigan (1996) and Hoey and McCormick (2004), indicating that lipid content may decrease with increasing size during this life history stage. This relationship may be the result of trade-offs carried over from the larval life stage. For example, fast growth during the larval period may result in smaller size at settlement and higher lipid levels. However, if larval growth is slower (due to cooler water temperatures, poorer environmental conditions, or just as a phenotypic trait), fish may settle when older, larger and with less lipids (Meekan et al. 2003; Hoey and McCormick 2004). Growth rate at the end of the larval phase was also found to be positively correlated with SL and dry weight, indicating that events occurring late in the larval stage may be important to subsequent survival during the early post-settlement period (Searcy and Sponaugle 2001).

Although the two measures of burst speed (i.e. mean and maximum) were correlated with one another, neither was found to be strongly correlated with morphological measures. The exception was a weak positive relationship between maximum burst speed and SL. Previous studies have presented a much stronger link between these two traits, with both Bailey (1984) and Fuiman (1986) showing a positive relationship between burst speed and fish length. Indeed the positive relationship between the two has been widely integrated into fish ecology through the bigger-is-better hypothesis, which often associates increased speed as a characteristic of larger size (Fuiman 1989; Paradis et al. 1999). However, the results presented in this study suggest that the two might not be as closely related as previously thought, at least during this life stage. McCormick and Molony (1993) made a similar conclusion in a study of newly settled goatfish (*Upeneus tragula*), finding a comparable correlation coefficient between SL and burst speed (0.158) to those obtained in this study (0.207 and 0.252). The difference between these and other studies that find a relationship between size and performance may be because other studies have integrated findings over the whole of the larval phase, thereby encompassing a wide range of different developmental stages and performance capabilities. Meanwhile, the present study and that of McCormick and Molony (1993) examined the relationship at a specific developmental stage (metamorphosis and settlement).

According to the bigger-is-better hypothesis, larger size should convey a survival advantage for prey during such predatory encounters (Rice et al. 1993). Indeed, there is a significant body of literature to suggest that such is the case during the early juvenile period in coral reef fishes (e.g. Schmitt and Holbrook 1999; Searcy and Sponaugle 2001; Brunton and Booth 2003). In contrast to these previous findings, however, this study shows that larger body size may actually be disadvantageous to settlement stage individuals during encounters with *P. fuscus*. This result is consistent with a recent field study by McCormick and Meekan (2007), who found that the removal of *P. fuscus* from territories resulted in a shift in the direction of local juvenile size selection from negative (i.e. selection of larger individuals) to random. The source of the inconsistency between studies lies in the duration over which selective processes are measured, with previous studies largely assessing selection over a period of days to weeks. This has the potential to mask those processes occurring immediately around the time of settlement, when individuals are naïve to reef-based predators and hence most vulnerable to predation. In contrast, the current study assesses predator selectivity during the initial 24 h only, and is therefore thought to be a more accurate representation of the processes occurring during this potentially critical period.

There are a number of mechanisms that may underlie the negative size selection observed in this study. Predators may be making an active choice to select the prey size that provides the highest energy return, in keeping with OFT, which predicts that predators should prey upon those individuals that will maximize the energy return per unit of handling time (MacArthur and Pianka 1966; Hughes 1980). In the current predator–prey interaction, *P. fuscus* may be actively selecting larger prey due to the associated higher energy return for three reasons: burst speed did not influence whether an individual *P. amboinensis* was captured (i.e. faster individuals are selected equally as often as slower individuals); correlations between escape/burst speed and body size were generally poor, and energy return increases with prey body size (Holmes and McCormick, unpublished data).

Alternately, patterns of prey body size selection by *P. fuscus* could be explained by behavioural differences between large and small prey. Huntingford (2007) discussed the idea that an individual's behaviour can be classified as either “proactive” (bold) or “reactive” (timid), in relation to how they react in a given situation. She further suggests that how aggressive an individual is to a conspecific is often correlated with its readiness to take risks in other contexts. Arguments in favour of such “behavioural syndromes” have recently gained significant momentum, and have now been documented in a range of animal groups, including insects (Johnson and Sih 2007),

freshwater fishes (Bell and Sih 2007; Wilson and McLaughlin 2007), birds (Dingemanse et al. 2004), lizards (Stapley and Keogh 2005) and mammals (Dochtermann and Jenkins 2007). Given that size-based dominance hierarchies are commonly observed within reef fish communities during the early post-settlement period (personal observations), larger more aggressive individuals may be proactive in their behavioural decisions, making them more susceptible to certain forms of predation.

Another possible explanation is that predation by *P. fuscus* may have been selective towards lipid content rather than SL. SL was found to be negatively correlated with lipid content in this study, meaning that the larger individuals selected in trials were also likely to have lower lipid reserves than their smaller counterparts. If this in some way co-varied with an unmeasured characteristic, such as relative “boldness” (Stamps 2007; Biro and Stamps 2008), then this could be the underlying mechanism of selection, as opposed to body length. Hoey and McCormick (2004) recorded a similar result to that alluded to in this study, with predation being selective towards low lipid content during field experiments on newly settled reef fish. However, the problems associated with reliably assessing lipids without causing harm to the subject mean that this is a difficult characteristic to manipulate and test during size-standardised predation trials. It is likely that lipid levels and size are closely related at the time of settlement as a result of growth tradeoffs imposed during the larval stage (Meekan et al. 2003). Therefore, during this life stage, a difference in one may also be associated with a difference in the other variable and the target of selective processes will be difficult to identify.

It is interesting to note that the recorded positive correlation between SL and recent pre-settlement growth, means that selection by *P. fuscus* favours slower growth at the time of settlement. Although this contradicts findings by Searcy and Sponaugle (2001) and Meekan et al. (2006) it is supported by more recent studies by Gagliano et al. (2007) and Meekan et al. (in review), who both found mortality to be selective against faster pre-settlement growth at the time of settlement. Although such differences could be a result of different prey and predatory species (e.g. Takasuka et al. 2007), the major factor is thought to be the difference in the time frame over which selection was measured, as described above.

Burst speed was expected to influence survival because prey with a faster escape response should have a survival advantage over slower counterparts. Burst speed was also highly variable among individuals making it an ideal candidate for selection. However, the present study found that burst speed did not influence whether a fish was captured during a predatory encounter. In one of the only other studies to directly examine the influence of prey

performance on survival during predatory interactions for any aquatic system, Fuiman et al. (2006) came to a similar conclusion, finding that burst/escape speed did not influence the survival of red drum larvae (*Sciaenops ocellatus*) during predatory encounters with the longnose killifish (*Fundulus similis*). This outcome, combined with the moderate level of variability in burst speed across repeated bursts for an individual, suggests that escape ability may have a random factor that is intrinsic to the prey and their state at the time of escaping a predator. Survival may be more related to the proactive or reactive coping styles of individuals, rather than a set measure of individual performance (see Sih et al. 2004a, b; Bell 2007; Huntingford 2007; Stamps 2007). Detailed behavioural assessments of how *P. amboinensis* responds to predators are yet to be undertaken.

Alternately, burst/escape speed may not relate to the probability of capture by a predator at settlement because they do not know when to use the burst capability because they have not yet learned to identify predators within the new environment. Holmes and McCormick (2006) suggested that the new recruits have to learn the identity of predators before an escape response can be initiated. Research suggests that juveniles of many aquatic organisms with complex life cycles need to learn the identity of predators to efficiently escape encounters with them (Mathis et al. 1996; Brown and Laland 2003). If this hypothesis is correct, fish that have experimentally learned the identity of a predator could be expected to display the predicted negative relationship between burst speed and capture success by a predator.

The results of this study show that the patterns of selectivity displayed by a single predator species under controlled aquarium conditions were different from the selective signature of the multi-species predator community on open patch reefs, with respect to prey body weight. In the field the pattern of body weight selection was highly significant, with individuals of lower standardised weight having a higher probability of survival. It is interesting to note that Holmes and McCormick (2006) found selection at the same field site to act against larger SL, indicating that selective preferences of the predator community at this location may simply be removing larger individuals. Alternately, this result may relate to the higher predation pressures placed on the prey within the confines of the aquarium trials, as displayed by the Kaplan–Meier product–limit plots. Although the confines of aquaria, a lower habitat complexity, and a lack of alternate prey all potentially played a role, this increase in predation pressure was also observed to be a result of changing predator behaviour, with species periodically changing in activity level over time. This resulted in increased activity during the aquarium-based standardized weight and burst speed trials in particular. Despite the fact that this was uncontrollable, it is

possible that this elevated mortality masked any selective processes operating during these trials. However, results may also be explained through an understanding of the feeding ecology of different predator species and the interaction of prey characteristics with the prey-selectivity profiles of those predators (e.g. Takasuka et al. 2007, Allen 2008).

Compared to terrestrial and other aquatic systems, we currently know very little about predation on tropical reef fishes. In addressing this issue, the present study has provided us with direct and unconfounded evidence of the selective processes underlying predation by a key predator during a period potentially critical to adult population dynamics. Our results suggest that under controlled conditions, larger size at the time of settlement may actually be a distinct disadvantage to prey during interactions with some predator species. However, these relationships appear to be more complex under natural conditions, where the expression of prey characteristics, the selectivity fields of a number of different predators, their relative abundance, and the action of external environmental characteristics, may all influence which individuals survive. A greater knowledge of these interactions and their underlying mechanisms is crucial for the management of fisheries and conservation of tropical marine ecosystems. It is only by understanding predator–prey dynamics that we can predict how prey may respond to changing predator populations or vice versa.

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