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The effect of temporally variable environmental stimuli and group size on emergence behaviour

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Short title: Environmental stimuli and group emergence behaviour

Lay summary: Colonies of humbug damselfish change their behavioural response to a predation threat in accordance with the tide. The majority of work in animal decision making centres on individuals, however, animals are affected by the movements of their near-neighbours. Moreover, whilst environmental factors affecting decision making vary spatially within habitats, the role of temporal variation of environmental factors has been relatively ignored. This study addresses both of these issues in a manipulative field experiment.

Abstract:

How animals trade-off food availability and predation threats is a strong determinant of animal activity and behaviour, however, the majority of work on this topic has been on individual animals, despite the modulating effect the presence of conspecifics can have on both foraging and predation risk. Whilst these environmental factors (food and predation threat) vary spatially within habitats, they also vary temporally, and in marine habitats this can be determined not only by the diel cycle but also the tidal cycle. Humbug damselfish, *Dascyllus aruanus,* live in small groups of unrelated individuals within and around branching coral heads which they collectively withdraw into to escape a predation threat. In this study we measured the proportion of individuals in the colony that were outside the coral head before and after they were scared by a fright stimulus and compared the responses at high tide and low tide. We found that a greater proportion of the shoal emerged after the fright stimulus at high tide and

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in larger groups than at low tide or in smaller groups. We also quantified the pattern of emergence over time and discovered the rate of emergence was faster in larger shoals as time progressed. We show that shoals of fish change their behavioural response to a predation threat in accordance with the tide, exemplifying how temporally variable environmental factors can shape group movement decisions.

Introduction

It is widely recognised that searching for food and evading predators are two major factors influencing animal behaviour. How animals trade off these two factors is a key question in behavioural ecology (Sih 1982; Dill 1983; Lima and Dill 1990; Smith 1997). For example, an animal's selection of certain food types or foraging behaviours may change in response to the level of predation threat, and ultimately areas of higher resource profitability may be partially or completely avoided if the predation threat is perceived to be too great (Abrahams and Dill 1989; Lima and Dill 1990). Predatory threats will also affect the amount of time an animal spends in a safe place before returning to forage (Ydenberg and Dill 1986; Lima and Dill 1990). As the threat of predation exists during times when prey need to perform other activities such as feeding or finding mates, behavioural adaptations of prey should be particularly sensitive to the degree of predation risk and how it balances with current demands and opportunities (Dill 1983; Lima and Dill 1990).

In addition to the need to balance risk against reward, most animals are subject to circadian rhythms (Helfman 1986), while marine animals, particularly those that inhabit shallow waters, are also subject to circatidal rhythms (Gibson 1992). The tide can have significant effects on the appropriateness of habitats and marine animals may have behavioural patterns that are synchronized with the tidal cycle (Northcott et al. 1990; Gibson 1992) in order to improve their fitness. Some juvenile flat fishes time their migrations to different parts of the beach with the tide (Kuipers 1973) and activity levels of monkeyface prickleback, *Cebidichthys violaceus* (Ralston and Horn 1986), and purple marsh crab, *Sesarma reticulatum* (Palmer 1967) are also synchronised with the tide. While much work has been done on how the spatial distribution of animals is affected by the trade-off between foraging and predation, less attention has been given to how this trade-off changes in accordance with consistent temporal rhythms (Metcalfe et al. 1999), such as tidal height, which are vitally important forces that alter the costs and benefits of performing different behaviours.

For animals that live in groups the behavior of conspecifics is an additional factor that interacts with other environmental stimuli to alter the trade-off between foraging and predation. The decisions of animals that live in groups are influenced by the behavior of other individuals in the group (Krause and Ruxton 2002; Ward et al. 2013) and animals need to strike a balance between conformity and individuality (Herbert-Read et al. 2013). Whilst the presence of conspecifics may decrease the risk of predation due to the many-eyes, dilution or confusion effect, food competition generally increases with the number of individuals at a food patch (Ward et al. 2006).

Humbug damselfish, *Dascyllus aruanus*, live in small groups of unrelated individuals (hereafter “colonies”) within and around branching coral heads. Groups of humbug damselsfish are territorial and maintain the same group structure (Jordan et al. 2010). They are planktivores and feed in the water column directly above and around their coral head. One of the suggested explanations for the species' preference for group living is the advantage individuals receive from the increase in predator vigilance and the dilution effect (Sweatman 1985). Like in many group living species, predation threats are reduced through a collective fleeing response (Marras et al. 2011; King et al. 2012; Salazar et al. 2013), and individuals collectively seek refuge within the branches of the coral until the threat has passed. The amount and variety of food available and therefore the feeding rate of humbug damselfish is greatest during high tide, when plankton availability is greatest (Forrester 1991). This therefore creates a good natural study system to explore not only how animal groups trade-off feeding and predation threat, but also how this is affected by consistent temporal rhythms.

Many studies have looked at habitat use and decisions of where to feed in response to predation threat (Dill 1983; Lima and Dill 1990; Sih 1982). For the territorial humbug damselfish, there is more flexibility over when to feed than there is where to feed, as the patch is restricted to the immediate area surrounding their coral head. In this system fish exist in a binary state, they are either outside of a coral refuge, in which case they are typically foraging, or they're in the coral refuge, in which case they are not. Certainly there is variance of prey distribution and type around the coral head, but for the purposes of this study the fish are considered to be either within the patch and therefore able to forage, or in hiding. Therefore, we measured the proportion of individuals in the colony that were outside the coral head before and after they were scared by a fright stimulus and compared the responses at high tide and low tide. We showed that groups of damselfish change their behavioural response to a predation threat depending on the tide, exemplifying how temporally variable environmental factors can shape group movement decisions.

Methods

Research was conducted at 3rd Lagoon, One Tree Island (-23° 30’ 26’’, 152° 5’ 25’’), Great Barrier Reef between March 28th and April 10th 2014. Fifty-six colonies of humbug damselfish (*Dascyllus aruanus*) were selected for this experiment, ranging in size from 3 to 24 individuals and each colony was assayed once, half were assayed during high tide (HT) and half during low tide (LT). A trial was considered to occur at one of the two tidal categories if it was performed within 2 hours either side of the maximum or minimum tidal amplitude. As trials were conducted over two weeks, trials at HT (07:50-16:50h) and LT (08:20-15:50h) covered the range of daylight hours. Therefore, circadian rhythm effect was controlled for in the experimental design. The colonies occupied *Pocillopora damicornis* and *Acropora palifera* coral heads and colonies had to be more than 5m from another colony to reduce the chance that fish would travel between colonies, which occurs when the coral heads are closely packed or continuous (Öhman et al. 1998). Care was taken to ensure the colonies used in the two treatments were spatially mixed, evenly dispersed between the two coral species, and not clumped to reduce confounding effects of environmental variables. A precise block design was not possible, however, due to the natural distribution of colonies and because the priority was to have a similar range of group sizes between the two tidal treatments.

Fright stimulus

The fright stimulus apparatus (hereafter “apparatus”) was a custom made device with an aluminum frame with a blue and white 28cm long rubber fishing lure (Williamson® Live Little Tunny Skip Jack 6951221) attached to a zip line made from monofilament line. A pulley system allowed for the user to stand 250cm from the humbug colony and shoot the model predator forwards 200cm. Care was taken to ensure the model predator approached each colony at a consistent speed of approximately 2 ms^{-1}. The apparatus was placed 50cm to the right of the colony and the model predator would reach the colony at a consistent angle and height (50 cm) from the sea floor (Figure 1). The apparatus was weighed down with two pairs of 2kg weights attached with cable ties so that it did not move in the current or when force was applied to propel the model predator towards the colony. All experiments were conducted while snorkeling at depths ranging from 160 and 330cm.

Experimental procedures

A colony was located and in preparation for the assay the apparatus was placed to the right of the coral head facing directly downstream of the current tidal flow (Figure 1). After a period of 10 min the experimenter would then place two Panasonic LUMIX underwater HD cameras 1.5m from the coral and start the film. One camera would film from the left side and one from directly in front of the colony (Figure 1). The experimenter would then stand still at the end of the apparatus for 5 min to allow the colony to resume normal foraging behaviour before pulling the fishing line and propelling the model predator towards the colony. Pilot tests confirmed that 5min was ample time for the fish to resume normal feeding behaviour. The experimenter then stayed still for the next 2 min before moving to stop the film on both cameras.

Data Collection

The videos from both cameras were converted from .wmv to .avs format with DirectShowSource. The .avs files were then opened with VirtualDub (v 1.9.11) and the video was converted from 15 frames per second to 1 frame per second. The footage 60 sec before and 60 sec after the fright stimulus was exported as a stack of 120 individual .jpeg images and opened with imageJ (Image Processing and Analysis in Java, version 1.48, 2014). Here the number of fish that were outside of the coral head were counted for each frame. A fish was considered outside of the coral head if its whole body could be seen without any coral obstructing its body. This was done for both camera angles and the largest value from either camera angle was considered as the maximum number of fish emerged at that frame. This value was then divided by the total number of fish in the colony to give a proportion of fish emerged from the coral head every frame.

Data Analysis

<u>Do tide and shoal size affect mean emergence?</u>

A linear mixed effects (LME) model was used to assess whether the fright stimulus was effective, by evaluating the effect of stage (before or after the stimulus) on the proportion of fish emerged. To control for the repeated-measures nature of the data (each shoal was assessed multiple times), we included shoal identity as the random factor in the model.

Throughout our analysis, proportion emerged was arcsin transformed to meet the assumptions of normality, which was assessed through visual inspection of quantile-quantile plots and plots of standardised residuals against fitted values.

We used linear mixed effects models to assess the effect of tide (high/low), group size and their interaction on the proportion of fish emerged from the coral head during the 60 seconds before and the 60 seconds after the fright stimulus. Non-significant interactions were removed following Crawley (2005) and only main effects are presented here.

Does the emergence pattern vary as a function of shoal size and tide?

Next, we assessed whether the pattern of emergence from the coral head differed depending on shoal size and tide. For each shoal, we calculated the mean and maximum proportion of the shoal that had emerged from the coral head by 5 time points after the stimulus: 5, 10, 15, 30 and 60 seconds. We also calculated the time at which the maximum emergence for each time category was reached. We used linear mixed effects models to assess the effect of tide, shoal size, time and their interactions on the response variables, which were arcsin transformed to meet the assumptions of normality, assessed through visual inspection of plots as above. Shoal identity was included as the random factor. For analysis, shoal size was included as a continuous variable, but for visualization of interactions, shoal size was also converted into a categorical variable (small: ≤ 8 fish and large: ≥ 9 fish), to give approximately equal numbers of shoals in the small and large category. Both analyses are presented here (Table 1).

All analysis was performed in R v 2.13.0 (R Development Core Team (2011)) with the lme4 package (Bates et al 2011).

Results

Do tide and shoal size affect mean emergence?

The fright stimulus was effective in causing fish to hide: there was a significant effect of stage (before/after) on the proportion emerged ($t = 58.852$, $df = 6719$, $p < 0.001$, effect size = 0.461 ± 0.008), which was lower in the minute after the stimulus than in the minute before the stimulus (Figure 2). There was no effect of either shoal size ($t = -0.625$, $df = 53$, $p = 0.535$, effect size = -0.004 ± 0.006) or tide ($t = -0.945$, $df = 53$, $p = 0.349$, effect size = -0.049 ± 0.052) on the proportion of fish emerged from the coral head before the fright stimulus, and no interaction. After the fright stimulus, however, both shoal size ($t = 4.214$, $df = 53$, $p < 0.001$, effect size = 0.027 ± 0.006) and tide ($t = -2.470$, $df = 53$, $p = 0.017$, effect size $=0.142 \pm 0.057$), but not their interaction, affected the proportion of fish emerged from the coral head. After the stimulus, a greater proportion emerged at high tide (Figure 2, 3) and in larger groups (Figure 3) than at low tide or in smaller groups, respectively.

Does the emergence pattern vary as a function of shoal size and tide?

There was a significant effect of tide, and a significant interaction between time and shoal size on mean emergence (table 1a), suggesting that mean emergence is lower at low tide (figure 4a), and that this increases over time, but does so faster in larger shoals (table 1b, figure 4b). For maximum emergence, there was a significant effect of shoal size (table 1c), with maximum emergence increasing with shoal size, and a significant interaction between time and tide (table 1c, figure 4c). Maximum emergence increased over time, but at a more rapid rate at low tide (figure 4c). There was no effect of tide on the time that maximum emergence is reached, but there was an interaction between shoal size and time, with smaller shoals reaching maximum emerged more rapidly than larger shoals (table 1d, e, figure 4d).

Discussion

The results show that group movement behavior was affected by environmental factors, including those that vary temporally. All shoals showed similar levels of emergence before the fright stimulus, regardless of shoal size and the state of the tide, and the fright stimulus was effective in reducing the proportion of the colony outside of the coral head in the immediate aftermath of the simulated attack. Both tide and shoal size affected how the fish responded to the fright stimulus with a greater proportion of the colony emerging at high tide (when food availability is highest) and in larger groups (where predation risk is likely reduced).

Humbug damselfish, like many animals who live under threat of attack, appear to act as risk balancers (Pitcher et al. 1988), emerging more quickly from their refuge when in larger groups and when there is more food. It is probable that humbug damselfish were less affected by the perceived risk of the fright stimulus at high tide as they traded off the risk of predation for the increased foraging opportunities at high tide, and indeed in this experiment fish were more polarized in the water column and seemed to be feeding more actively and at a greater rate during high tide, when we know plankton density is greatest (Forrester 1991).

Considering all three response variables (mean emergence, maximum emergence and time to maximum emergence) both shoal size and tide were important in determining the pattern of emergence behaviour after the fright stimulus. Smaller shoals reached their maximum proportion emerged faster than larger shoals did, although this is likely to be a result of fewer of them emerging in total, hence the number being reached faster. As expected the maximum proportion of shoal emerged was greater for larger shoals and, crucially, shoal size was also important in determining the pattern of emergence, with the mean proportion of shoal emerged increasing over time faster in larger shoals. There is initially little effect of shoal size on mean emergence at early time points, straight after the fright stimulus, however, the difference increased as time progressed. A possible explanation for this is that as the mean proportion of fish outside the coral head was a greater absolute number in larger groups, this promoted the increased rate of emergence for the remaining fish as they perceived the environment to be safer than if the absolute number of fish emerged was lower. This is comparable to a social amplification effect and positive feedback found in fleeing response of cockroaches, allowing larger groups to respond faster than smaller groups (Salazar et al. 2013).

Distinguishing between potential causes of this pattern of emergence, however, is problematic. Although it may be that each individual’s assessment of its own per capita risk was lower in larger groups, it may be that larger groups assessed the potential predation risk more accurately than smaller groups by a combination of division of vigilance and information transfer (Morgan 1988; Ward et al. 2011). Larger groups are generally more effective at collecting and integrating information and then using the information to make effective decisions than smaller groups (Couzin 2009). These processes are not mutually exclusive, however, and it is likely that a combination of increased group decision accuracy and the dilution effect contributed to the observed pattern.

Tide was also an important factor determining the pattern of emergence following the fright stimulus, with a higher mean proportion of the shoal emerging at high tide. The maximum proportion of fish emerged increased over time at both tidal heights, and although it was always greater at high tide, the rate of increase over time was faster at low tide. Once again, this may be because the absolute number of maximum proportion emerged is lower at low tide.

Whilst there is more food in the water column for fish at high tide, there is often also an increase in predation threat, especially if high tide coincides with dawn or dusk (Munz and McFarland 1973; Helfman 1986). In this experiment, there were certainly more predators active during high tide, predominately large schools of piscivores such as spangled emperors (*Lethrinus nebulosus*), and occasionally the damselfish made directed movements towards their coral heads as large predatory fish swam past (Pers. obs.). Despite this increased predatory threat at high tide, humbug damselfish still feed more at this time (Forrester 1991), which suggests that feeding efficiency is large enough to overcome their tendency to display risk sensitive behavior in the face of a threat. The tide affects the costs and benefits of many behaviours as it significantly alters the environment, particularly for those that are inter-tidal or living at shallow depths. Many of these species are group living, and the results of this experiment highlight the importance of tidal effect on group movement properties.

Sixty seconds after the fright stimulus the proportion of fish outside of the coral head still had not returned to the levels before the fright stimulus, regardless of tide or shoal size. We should expect a gradual return to foraging activity levels, or perhaps even an increase to overcome the opportunities lost whilst in hiding, however, this will increase in relation to the time passed since the predation threat and depend on the severity of the threat and the likelihood of the threat returning. Juvenile Atlantic salmon, 20 min after the predation threat, only returned to 33% of their pre-predator intake rates (Metcalfe et al. 1987). Although actual intake rates were not calculated, humbug damselfish responded surprisingly quickly to the predation threat, returning to a vulnerable position where foraging was once again possible. Perhaps it was because they face constantly high levels of predation risk threat on the coral reef and have adapted to recover from a threat quickly (particularly a false one) in order to achieve a sufficient intake of energy. Guppies from environments with high levels of predation, for example, are known to feed at greater rates and display greater tenacity after a predation threat than guppies from low predation environments (Fraser and Gilliam 1987). Another possible explanation for the fast nature of the damselfish's response to a predation threat is that it is driven by competition for resources. If competition is high for resources, which is probable in areas with a high predation threat, larger groups are expected to emerge faster than smaller groups.

Inter-individual variation between damselfish (for example size) was not recorded in this study, however, it is known that larger individuals feed further from the coral head than smaller individuals (Forrester 1991; Pers. obs.) where they have first selection of preferred prey (Coates 1980) and this is strongly related to their linear dominance hierarchy. African cichlid fish, *Melanochromis chipokae,* further from a shelter begin their retreat to safety before fish closer to the shelter (Dill 1990) and in many bird species, the sequence of the resumption of feeding after a predation threat follows the dominance hierarchy with subordinates emerging first (Hegner 1985; Laet 1985; Hogstad 1988) (it is suggested that subordinance in these systems may be strongly correlated with energetic need (Lima and Dill 1990)). Future research would do well to focus on individual phenotypic variability within groups, how it interacts with differences in internal state, and whether it can predict the first responder to a threat or how information is transferred throughout the group. Humbug damselfish colonies are an appropriate study system to answer these questions although a more advanced video monitoring system, with higher frame rates and ideally automated multi-agent tracking, would need to be employed to accurately measure phenotypically determined behavioural differences between individuals within each shoal.

This experiment has tested how animal groups may adjust their behavior to meet the costs and benefits produced by varying environmental stimuli. Specifically we show that humbug damselfish colonies under natural environmental conditions responded to a predation threat by adjusting their decision-making process in relation to the tide and shoal size. A greater proportion of the colony emerge after the fright stimulus at high tide and they show evidence of a social response in larger shoals with a greater proportion of the colony emerging in larger shoals and the mean proportion of the shoal emerging at a faster rate in larger shoals. This is the first study, to the authors' knowledge, to show that shoals of fish change their collective behavioural response to a predation threat in accordance with the tide. The humbug damselfish system has previously been used to explore the mechanisms of group movement decisions (Mann et al. 2013; Ward et al. 2013), however, this finding, that the state of the tide affects emergence behaviour, allows us to conduct new experiments to further our understanding of the effect of risk sensitivity on decision-making and information transfer - whilst simultaneously controlling for inter-group differences by performing repeated measures on the same group at different times when costs and benefits vary. This study has furthered our understanding of how social interactions and environmental heterogeneities can affect group behavior and, crucially, has shown the capability and importance of testing emergent group properties in the field.

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Table legends

Table 1: Linear mixed effects models assessing the effect of time, tide and shoal size on mean emergence (a, b), maximum emergence (c) and time to maximum emergence (d, e). Shoal size is included as a continuous variable (a, c, d) and as a categorical variable (b, e) where it is involved in a significant interaction effect.

	Fixed effect	Value	Std Error	DF	t	p
a) Mean emergence (figure 4a)						
	Time	<-0.001	0.001	222	-0.078	0.938
	Tide	-1.556	0.053	53	-2.942	**0.005**
	Shoal Size	0.008	0.006	53	1.300	0.199
	Time*Shoal Size	<0.001	<0.001	222	7.008	**<0.001**
b) Mean emergence (categorical shoal size; figure 4b)						
	Time	0.004	<0.001	222	12.037	**<0.001**
	Tide	-0.160	0.056	53	-2.839	**0.006**
	Shoal Size	-0.034	0.058	53	-0.598	0.555
	Time*Shoal Size	-0.002	0.001	222	-3.412	**<0.001**
c) Maximum emergence (figure 4c)						
	Time	0.008	0.001	222	11.053	**<0.001**
	Tide	-2.279	0.082	53	-3.383	**0.001**
	Shoal Size	0.025	0.009	53	2.774	**0.008**
	Time*Tide	0.002	0.001	222	2.358	**0.019**
d) Time to maximum emergence						
	Time	0.050	0.005	222	10.936	**<0.001**
	Tide	0.090	0.098	53	0.922	0.361
	Shoal Size	0.085	0.015	53	5.559	**<0.001**
	Time*Shoal Size	-0.001	0.000	222	-2.725	**0.007**
e) Time to maximum emergence (categorical shoal size, figure 4d)						
	Time	0.034	0.004	222	12.146	**<0.001**
	Tide	0.073	0.114	53	0.637	0.527
	Shoal Size	-0.524	0.148	53	-3.543	**<0.001**
	Time*Shoal Size	0.0103	0.004	222	2.649	**0.009**

Figure legends

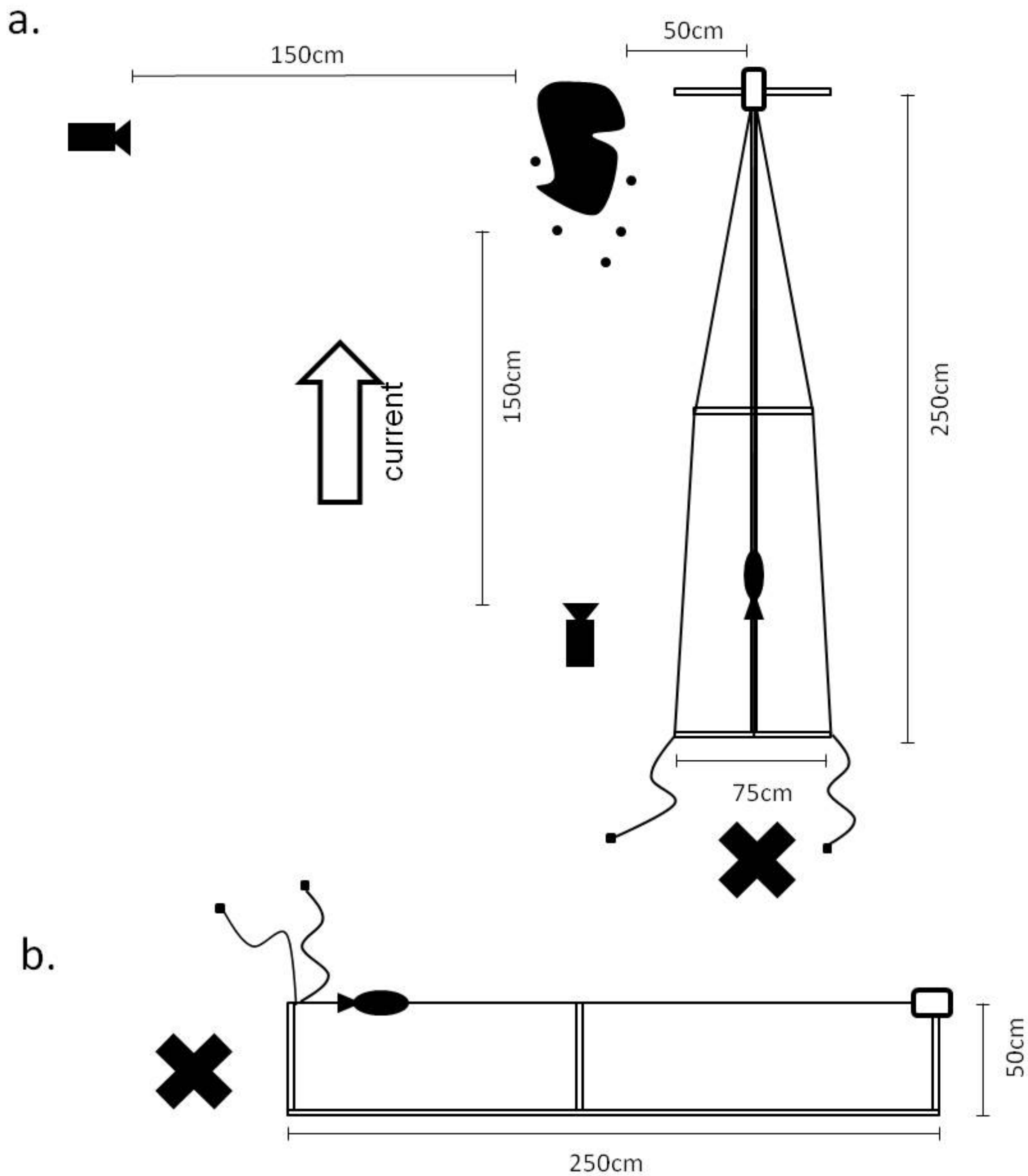

Figure 1. Diagram of experimental set-up showing placement of the fright stimulus apparatus in a.) aerial and b.) profile perspectives in relation to the direction of the current and position of the coral head (irregular black shape, dots represent fish), cameras and position of experimenter (X).

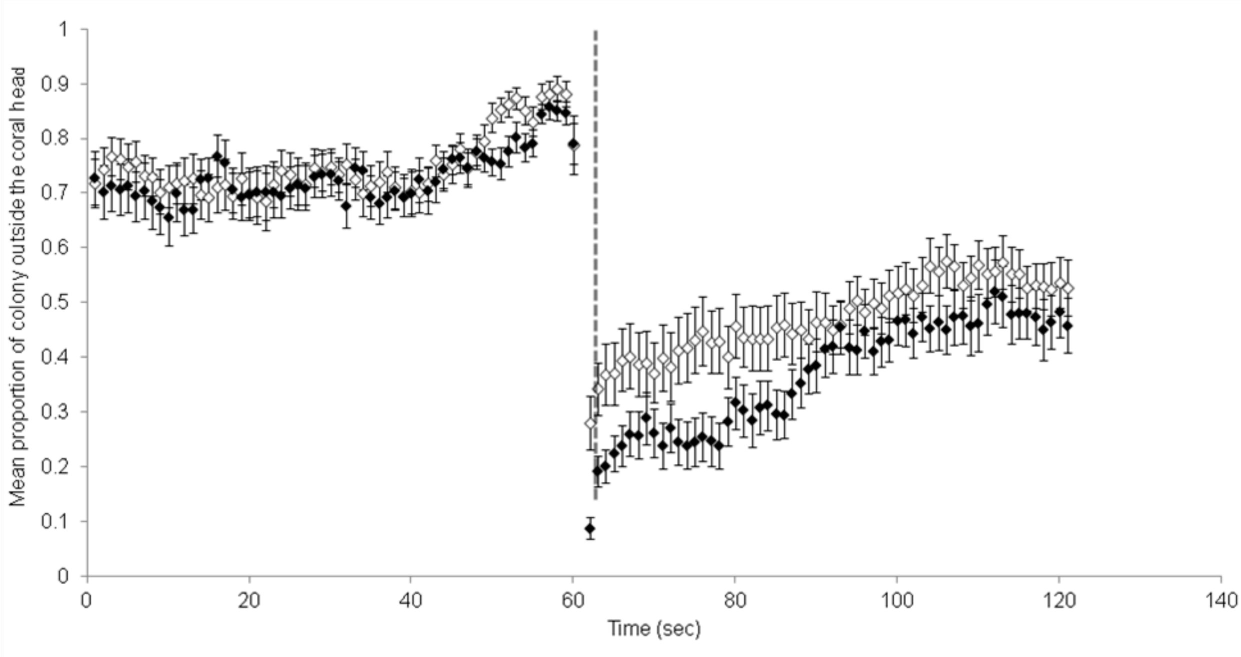

Figure 2. The mean proportion of the colony that is outside of the coral head at each frame (1 frame per sec) 60 sec before and 60 sec after the fright stimulus. The dotted black line represents the time at which the fright stimulus reached the colony. Empty markers markers represent the mean of colonies assayed at high tide, filled markers represent the mean of the colonies assayed at low tide. Error bars are standard error of the mean.

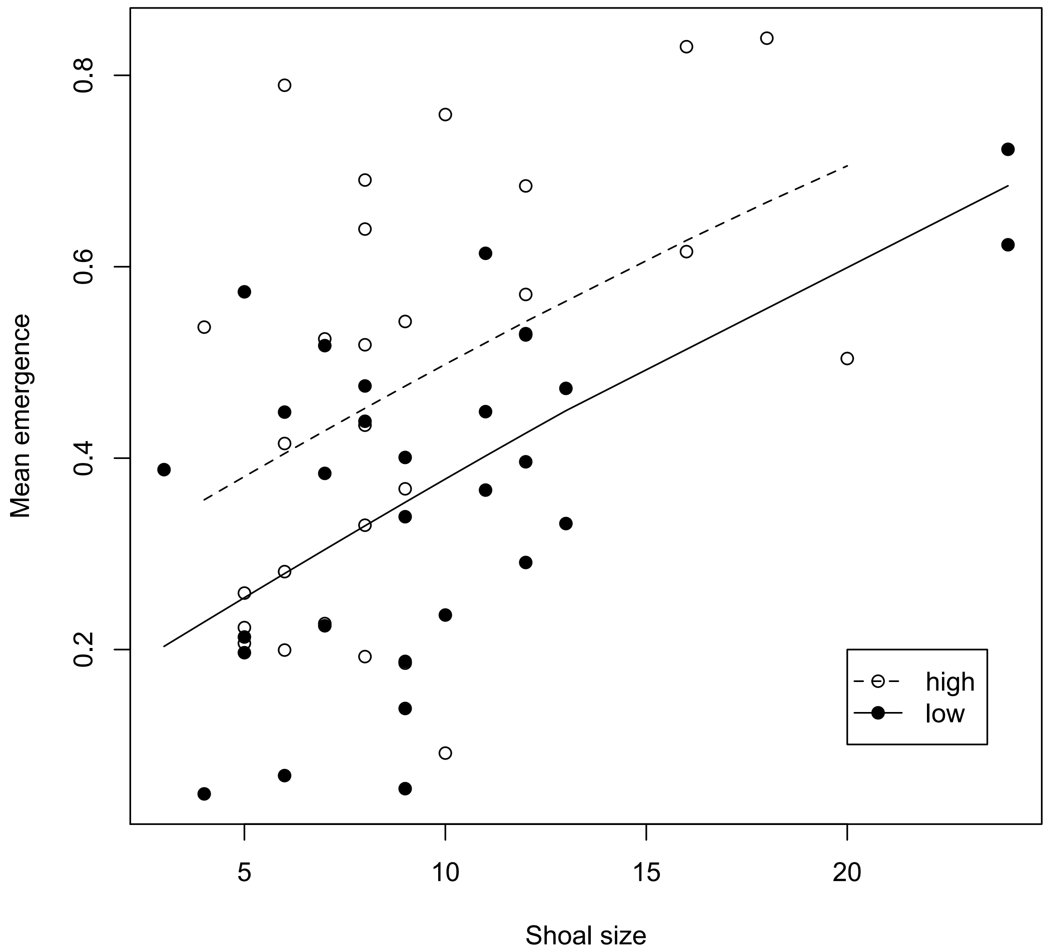

Figure 3. The mean proportion of fish emerged as a function of shoal size, at high (open circles, dashed line) and low (filled circles, solid line) tide. Fit lines are extracted from a linear model assessing the effect of shoal size and tide on the mean proportion emergence (arcsin transformed) for each shoal (tide: $t = -2.502$, $p = 0.015$, shoal size: $t = 4.354$, $p < 0.001$).

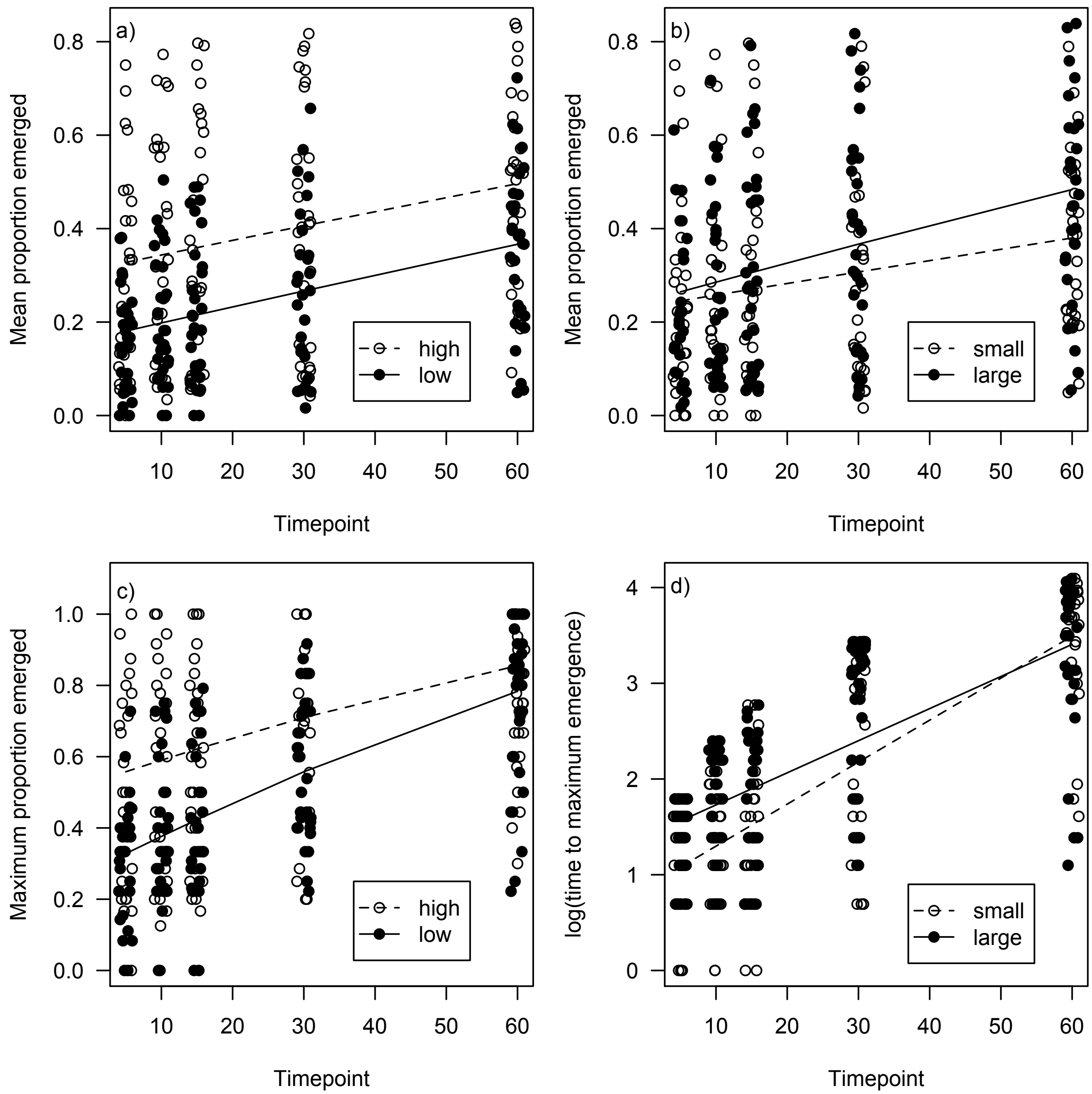

Figure 4. The mean (a, b), maximum (c) and time to maximum (d) proportion of fish emerged from the coral head. Data are presented as a function of time, at high (open circles, dashed line) and low (filled circles, solid line) tide (a, c), and in small (open circles, dashed line) and large (filled circles, solid line) shoals (b, d).