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Development of Predatory Behavior in Juvenile Fish: Evidence of Attraction to Prey Chemical Alarm Cues by Naïve Coral Reef Predator, (Pseudochromis fuscus)

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Development of Predatory Behavior in Juvenile Fish: Evidence of attraction to prey chemical alarm cues by naïve coral reef predator, *(Pseudochromis fuscus)*

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Abstract

Chemical alarm cues and their function on the coal reef has become an area of increasing interest in the study of predator-prey dynamics (Smith 1999, Friesen and Chivers 2006, Holmes and McCormick 2010). One prominent question in understanding the evolutionary basis for the development of chemical alarm cues is determining how these cues benefit the sender directly (Chivers 1996). One way chemical alarm cues found in freshwater systems have been found to benefit the sender of the cue is through attraction of secondary predators to the chemical alarm cue, which then interfere with the primary attack and increase chances of escape for the sender (Mathis et al 1995, Chivers 1996, Wisenden and Theil 1998). Recently it has been found that the predator *Pseudochromis fuscus* is attracted to chemical alarm cues of juvenile prey fish *Pomacentrus amboinensis*, which suggests that these chemical cues may have evolved as a mechanism that attract secondary predators (Lonnstedt 2009). The current study aimed to determine experimentally in an aquarium setting whether this attraction by *P. fuscus* to the chemical alarm cue was a learned behavior, or one which is innate, and thus present in naïve *P. fuscus* as well as the adult. It was found that the naïve juvenile *P .fuscus* were attracted to the chemical cue, highlighting the importance of this interruption as a forging mechanism for *P. fuscus* as well as lending further support for its evolutionary development in the prey fish as a mechanism to increase survivorship.

Keywords: *Pseudochromis fuscus*, predator-prey relationship, chemical alarm cues, juvenile attractants, *Pomacentrus amboinensis*, innate behaviors, coral reefs

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1.0 Introduction

1.1 Background

1.1.1 Predator-Prey Dynamics

Supporting thousands of species of life, the coral reefs of the world represent a dynamic system that is carefully supported through the balanced interactions of marine species. One of the main biological drivers allowing for this balance and determining population dynamics is predator-prey interactions. The interactions between predators and prey help determine the populations and fish assemblages in particular areas. For example, the distribution and population dynamics of newly settled reef fish is largely attributed to predation, with predators causing mortality rates sometimes reaching close to 100% (Holmes and McCormick 2006, Webster 2002, Beuker and Jones 1998). In response to high risk of predation, prey fish have improved their fitness and chance of survival through the development of antipredatory responses that help aid in survival through detection and avoidance of predators on the reef (McCormick and Manassa 2008, Holmes and McCormick 2010). In a complex environment such as the coral reefs, juvenile fish can not rely solely on vision to signal these responses due to their turbidity and 3-D complexity (McCormick and Manassa 2008). Thus marine fish have evolved the ability sense their dynamic environments through the use of the anatomical and physiological structures that allow them to both smell and hear the reef around them. One particular chemical signal that has shown to be especially important predatory detection is chemical alarm cues (McCormick and Manassa 2008).

1.1.2 Chemical Alarm Cues

Chemical alarm cues are an olfactory signal that has become an area of increasing study, especially in marine environments (Smith 1999, Friesen and Chivers 2006, Holmes and McCormick 2010). Chemical alarm cues are a chemical signals that are sent out involuntarily

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due to mechanical skin damage on a prey fish, and are caused by the action or presence of a predator (Lonnstedt 2009). The use of chemical alarm cues have been detected in a variety of aquatic organisms including amphibians (Kiescker et al. 1996; Mirza et. al 2006), crustaceans (Wisenden et. al. 1999), gastropods (Atema and Stenzeler 1977), echinoderms (Snyder and Snyder 1970), as well as freshwater and marine fishes (Pfeiffer 1977; Magurran 1989, Brown and Godin 1997, McCormick and Manassa 2008). These chemical alarm cues are often detected by conspecifics and result in an antipredatory response in these fish. Specifically in marine systems, a common prey fish group, damselfish, have shown to emit a chemical alarm cue that can be detected in conspecifics (Smith 1999, Friesen and Chivers 2006, Holmes and McCormick 2010). This detection has shown to result in an appropriate antipredatory freight response, which includes decreased eating and increased shelter use (Smith 1999, Friesen and Chivers 2006, Holmes and McCormick 2010).

Several theories have been established justifying the evolutionary basis of chemical alarm cues in marine fish, since its role in evoking antipredatory responses in conspecifics does not benefit the sender directly. Such theories include chemical cues benefiting the sender through protecting from pathogens, aiding in healing wounds, and protecting from UV damage (Chivers 2007). Another prominent theory is that the chemical alarm cues are detected by secondary predators, which are then attracted to the cue and interfere with the attack, allowing the sender a better chance at survival (Chivers *et al.* 1996). Thus through sending out this chemical alarm signal, the sender itself benefits directly as this interruption by a secondary predatory allows the potential for escape (Chivers *et al.* 1996). This increase in sender survivorship due to the attraction of secondary predators has been found in freshwater fish (Mathis et al 1995, Chivers 1996, Wisenden and Theil 1998). Yet even if such is the case and is a driver for evolution of the

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chemical alarm cue, the benefits to the sender does not explain the importance to the secondary

predator (Chivers *et al* 1996). Rather, this attraction would have evolved in aid of forging

behavior, in enabling secondary predators their next meal, through either stealing the already

caught prey, or, if big enough, eating the primary predator itself (Chivers *et al* 1996).

1.2 Justification of Study

Evidence of predatory attraction to chemical alarm cues of prey fish has recently been

found in marine systems (Lonnstedt 2009). The chemical alarm cue of a juvenile coral reef prey

fish, *Pomacentrus amboinensis,* has been found to attract a common predator *Pseudochromis*

fuscus (Lonnstedt 2009). This study reinforced the theory that these chemical alarm cues in these

fish may have developed in order to attract a secondary predator, and increase potential

survivorship (Lonnstedt 2009). The current study aims to determine whether this predator

attraction to the chemical cue is a learned behavior, or is genetically based. The establishment of

the innate foundation of such a behavior would further stress the importance of the interruption

of primary predator-prey interactions as a forging mechanism for *P. fuscus.* Through developing

the knowledge base surrounding these chemical alarm cues and their function, we can learn more

about the mechanisms dictating predator-prey interactions. These interactions are important to

maintaining the balanced ecosystem of the reef; thus this knowledge can be especially vital in

developing sustainable management of reef systems.

1.3 Aims of Study

The aim of this study was to see if attraction of the prey chemical alarm cue is unique in

adult *P. fuscus*, or present in naïve *P. fusucs.*. The foundation of the attraction was determined

experimentally in an aquarium setting, by studying the attraction of both adult and naïve *P.fuscus*

to the chemical alarm cues. It was predicted that if the naïve *P. fuscus* were attracted to the

chemical alarm cues, than this behavior is innate rather than a learned behavior.

2.0 Methods

2.1 Study Site

This study was conducted at Lizard Island (14°40'S, 145°27'E), located on the northern

end of the Great Barrier Reef, Australia. Data was collected during November 2010.

2.2 Sample Species

P. fuscus was used as a study species as it is an important predator on the Great Barrier

Reef, and is described as a primary predator of newly settled fish at Lizard Island (Martin 1994).

Adult *P. fuscus* are small carnivores, with a maximum size of ~10 cm and are color polymorphic

(Messmer *et al*. 2005). This color polymorphism is not sex limited (Munday et al. 2003) Both the

yellow and brown morphs are found on the Great Barrier Reef and were used in this study

(Figure 1c,d). The morphs occupy different territories, with the brown morph commonly found

in rubble in association with brown damselfishes, while the yellow morph is found among live

coral cover in association with yellow damselfishes (Munday et al. 2003).

Three age ranges of fish were used in the study including adult *P. fuscus* and two groups

of naïve *P. fuscus.* The naïve *P.fuscus* consisted of those newly trapped and indicated as newly

settled fish, and those held a month after trapped and indicated as juvenile fish. The newly

trapped *P. fuscus* normally ranged in size ~1-1.6 cm (Figure 1a) and lacked adult coloration. The

juvenile *P. fuscus* ranged in size from ~ 2.5- 3.0 cm and had brown coloration with a yellow

caudal fin (Figure 1b). Naive *P. fuscus* had yet to develop into piscivores, and since collected

and held in aquarium after newly settled, were naïve to chemical alarm cues and those interaction

that cause their expulsion.

Juvenile damselfish *P. amboinensis* was used as a prey cue in the study as it is an abundant and common coral reef fish in the Indo-Pacific. They are site-attached species once settled, and are most commonly found in small patch reefs (McCormick and Makey 1997).
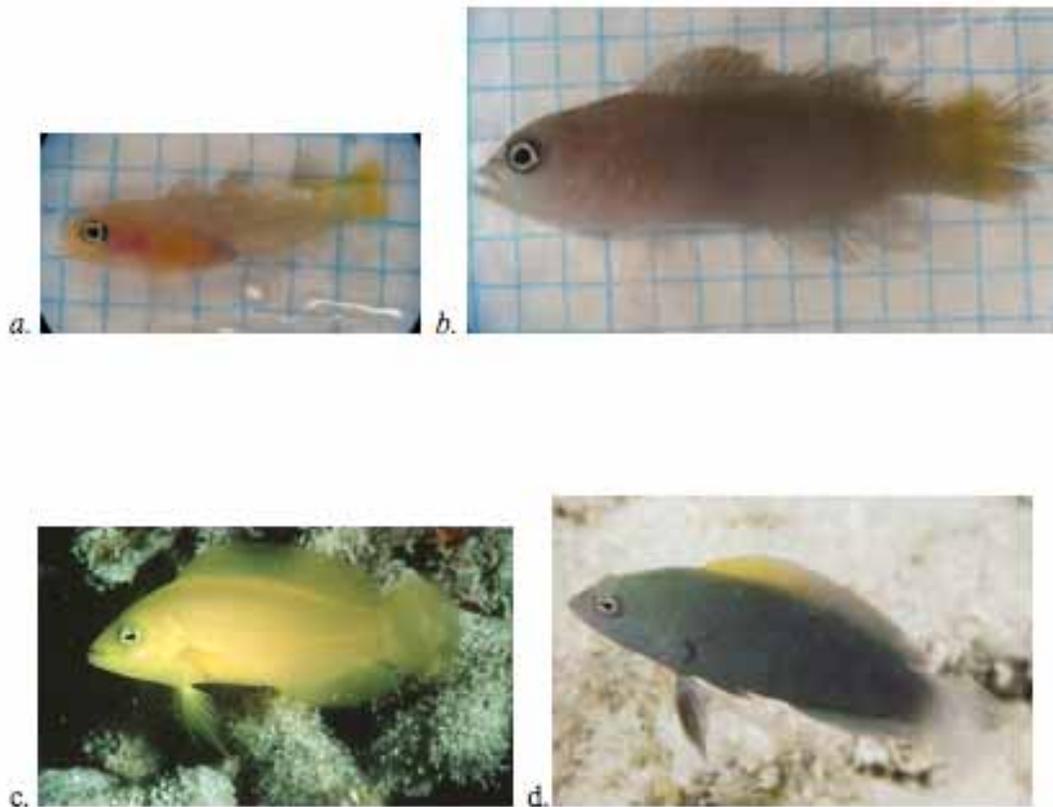
Figure 1. Development stages of *P. fuscus* tested. a) newly settled b) juvenile c) adult yellow morph d) adult brown morph. Each grid box 2 x 2 mm

2.3 Species Collection

The juvenile *P. fuscus* and *P. amboinensis* were collected using light traps (for methods see Meekan *et. al* 2001) put out at dusk , left out overnight, and collected before 6:30 the following morning. The adult *P. fuscus* were collected from the fringing reefs surrounding the island. The collected fish were held in 30L flow through seawater tanks. Fish were fed *Artemia*

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sp. nauplii twice a day. Adult *P. fuscus* were each kept in separate tanks due to their aggressive territorial behavior. Adult tanks were bottom covered with sand and had various tube shelters to reduce stress.

2.4 Tank Set- up

Y-mazes with two distinct water flow channel choices, one containing the chemical cue and one held as a control with untreated ocean water, were used in order to assess the attractiveness of *P. fuscus* at different life stages to the prey chemical alarm cue. The Y-mazes (600mm x 250mm x 110mm) were set up and trials were performed according to methods used by Lonnstedt (2009). Mazes were divided along half its length, with an acclimation area partitioned off by a transparent screen in front of the water flow. Mazes were floored with sand and included a piece of coral for the young fuscus and shelter for adult fuscus to aid with acclimation. Newly settled fish, juvenile fish, and adult fish were acclimated for at least six, four, and two hours, respectively. All fish were acclimated overnight when possible. Dye tests were performed prior to trials to determine equal and uniform water flow rate between both channels without mixing of water into the other channels.

2.5 Alarm Cue Preparation

The chemical alarm cue was prepared for each trial using four *P. amboinensis.* Donors were sacrificed using cold shock, and then placed into a clean Petri dish. The fish were severed six times on each side lightly with a clean scalpel, cutting through the first few layers of skin and avoiding flesh damage.. The fish were then placed in 60mL of ocean water and then filtered to remove any solid particle. Cue was then drawn into a 60 mL syringe for extract during trials.

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2.5 Experimental protocol

Cues fed to each side through 1.4 m of thin plastic tubing fixed behind the water flow. Fifteen milliliters of cue was released into one channel and the other channel was held as a control with 15mL of ocean water being released simultaneously using 60 mL syringes. Both sides were then flushed with 60 mL of ocean water, with timing beginning immediately after. Cues were released every three minutes, a rate determined by dye tests. A total of four cues were released per fish observation. Fish were observed through a small viewing window in a black screen surrounding the tanks as to not disturb behavior. Two stopwatches were used to record the amount of time spent outside of the acclimation area. Position of fish was taken every thirty seconds, and number of times the fish entered either side from the other side or the acclimation area was also recorded. Equal amounts of trials were performed with the chemical cue on either side. No fish was used more than once, and fish that did not acclimate after the given period were not used.

2.5 Data Analysis

Mean values were taken for each age time in reference to time spent in either channel as well as number of times either channel was entered in order to compare magnitude of preference to the chemical alarm cue. In order to determine attraction toward the cue, differences between channel entrances and times spent within either channel were analyzed for significance for each age group and color morphology using t-tests in JMP. One-way ANOVAS were taken to determine if age had a significant effect on the amount of time spent within and the entrance of the cue channel versus the control channel.

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3.0 Results

A total of 54 *P. fuscus* were tested, including 17 newly trapped, 19 month old and 18 adult individuals.

3.1 Channel Entrance

Both the juvenile and the adult *P. fuscus* showed preference to entering the cue channel over the control channel (Figure 2). The newly settled fish showed no difference in their preference for entering the cue over the control water (p=0.1280), showing a trend of entering the control channel more, and on average entering the cue channel 0.76 times and control channel 0.97 times (Figure 2). The juvenile *P. fuscus* entered the cue channel significantly more (p=0.0248) , 1.38 times on average, than the control that was entered 0.98 times on average (Figure 2). The adult *P. fuscus* showed a trend of entering the cue channel more, though not significantly (p=0.0627), as they entered the cue channel 2.18 times and the control channel 1.83 times on average (Figure 2). In addition, ANOVA test showed *P.fuscus* entered the cue channel significantly more times with increasing age (p<0.0003) , entering the cue channel almost twice the amount of times from newly settled to juvenile, and 0.80 times more from juvenile to adult (Figure 2).
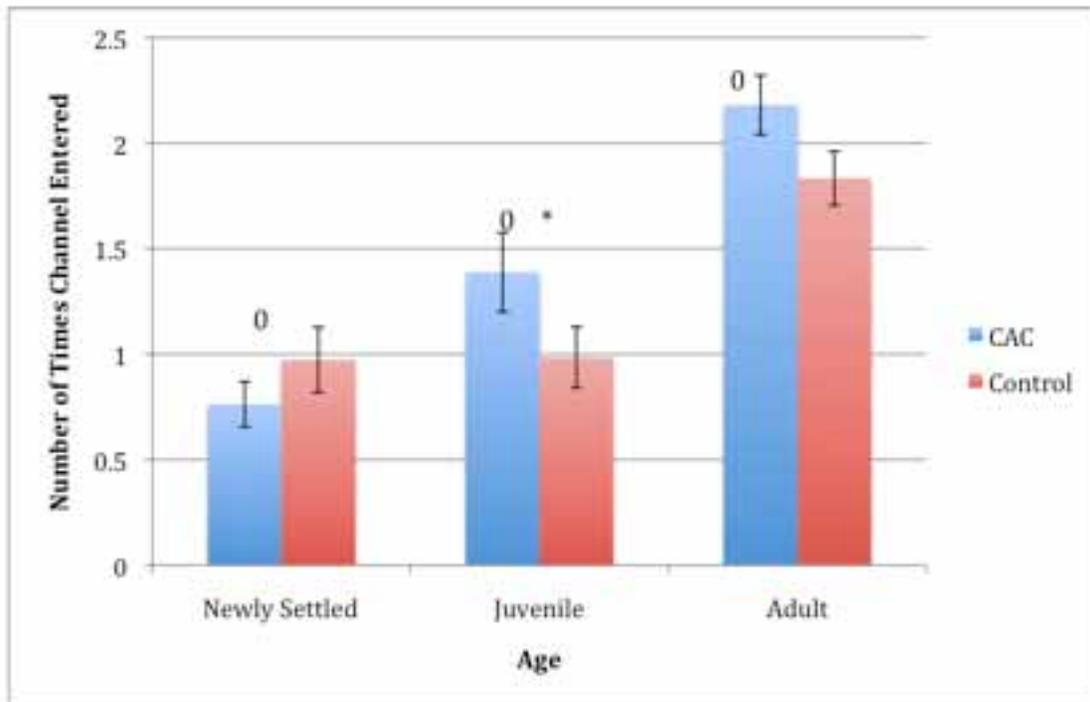
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Figure 2. Channel Entrance. The mean amount of times fish entered either channel per three minute observation period for each age group. CAC= chemical alarm cue. *=significant difference between entering either channel within age group. 0=significant difference between number of times entering channel between age groups Significance determined at p<.0.05

3.2 Time Spent in Channels

Overall, *P. fuscus* spent more time in the channel with the chemical cue as a function of increasing age (p <.0001 (Figure 3). In addition, juvenile *P. fuscus* spent significantly more time on average within the cue channel than the control channel, while the newly settled and adult showed no significant difference in time (Figure 3). The newly settled *P. fuscus* showed no difference in time spent in the cue channel and control channel (p=0.3489) as they spent 19.9 and 26.6 seconds, on average, in each channel respectively (Figure 3). The juvenile *P. fuscus* spent significantly more time in the channel with the cue (p=0.0350), on average double the amount of

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time, as they spent 34.4 seconds within the cue channel and 16.5 seconds in the control (Figure 3). The adult *P. fuscus* showed no difference in the average amount of time spent in either channel (p =0.6810) as they spent on average 47.8 seconds in the cue channel and 45.1 seconds in the control channel (Figure 3).
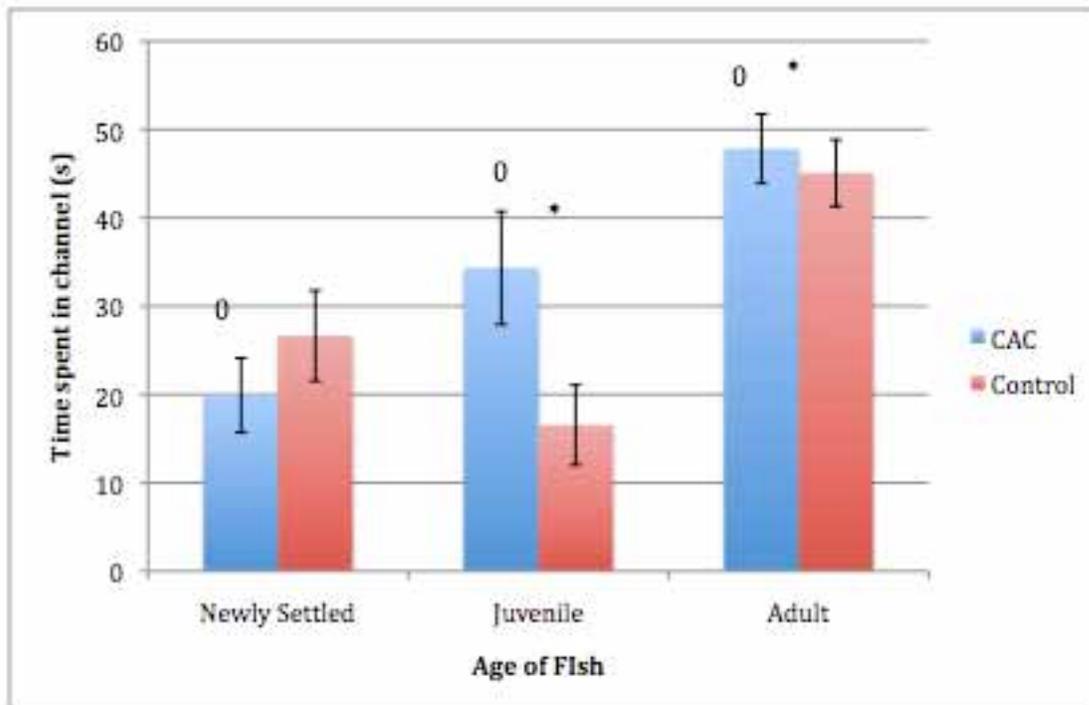

Figure 3. Time in Channel. The mean time spent in each channel per three minute trial for each age group. *=significant difference between time spent in each channel within age group.

3.3 Differences Among Adult Color Morphs
   Within the adult *P. fuscus* tested, the yellow morphs showed a trend of spending more time in the cue channel than the control channel (Figure 4). A total of 18 adult *P. fuscus* were tested, of which 7 were yellow morphs and 11 were brown morphs. The yellow morphs showed a trend of spending more time on average in the cue channel, as they spent 47.9 seconds in the cue and 33.2 seconds in control water on average, though the difference was not significant

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(p=0.2094) (Figure 4). The brown morphs showed no significant difference in the amounts of time spent in either channel choice (p=0.5490), and showed a trend of spending more time in the control water (Figure 4). On average brown morphs spent 47.7 seconds in the channel with the cue and 52.6 seconds in the control per three minute trial (Figure 4).
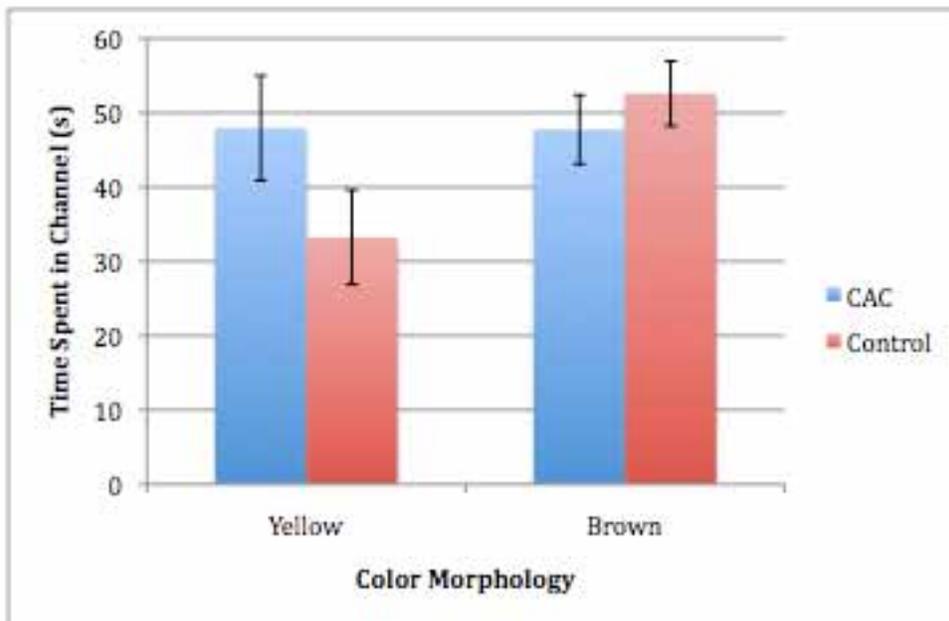

Figure 4. Time in Channel by Color Morphology. Mean time spent in each channel per three minute trial among the adult *P. fuscus* are compared by color morphology. *=significant difference between time spent in each channel within color morphology

In addition to showing a trend of spending more time in the channel, yellow color morphs also entered the channel with the cue significantly more times than the control channel (p=0.0232) (Figure 5). The brown morphs showed no difference in number of times they entered either the cue channel or the control channel (p=0.5697), as they entered each on average 2.18 and 2.05 times respectively (Figure 5). They yellow morphs entered the channel with the cue

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0.68 times more than the control channel, as it entered the cue channel 2.18 times and the control channel 1.5 times on average (Figure 5).
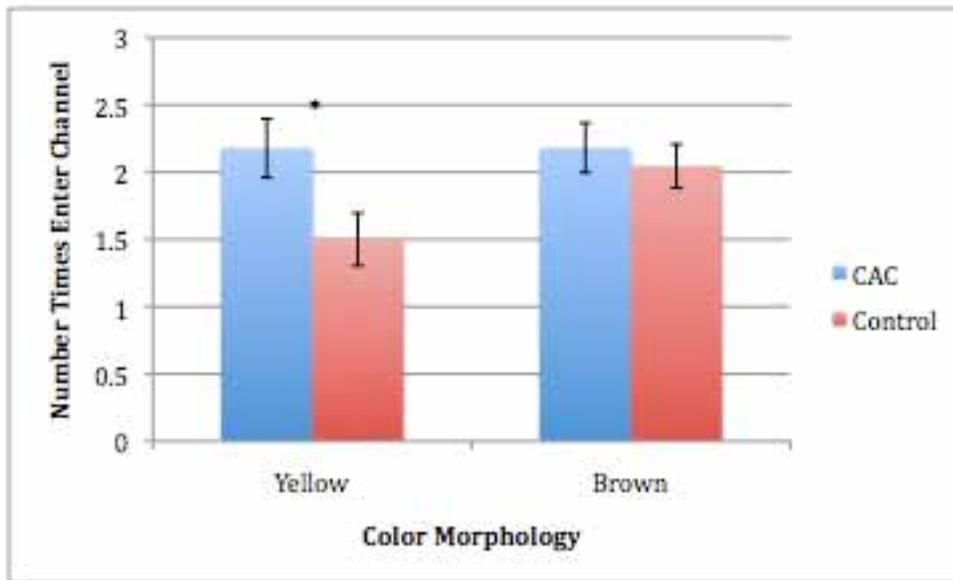

Figure 5. Channel Entrance by Color Morphology. Mean amount of times channel was entered per three minute trial by adults of each color morphology. *=significant difference between times of entrance within color morph

4.0 Discussion

4.1 Attraction to Chemical Cue

The juvenile *P. fuscus* were attracted to the prey chemical alarm cue, spending significantly more time in the channel with the cue and entering it significantly more than the control. Since these juveniles were caught as newly settled fish, kept in aquarium, and had not yet developed into piscivores, these fish were naïve to predation, interactions on the reef that induce the release of chemical alarm cues, as well as chemical alarm cues themselves. Thus their attraction to the chemical alarm cue shows that this is not a learned behavior. Therefore the attraction to the prey chemical alarm cue may be innate, and grow in strength as the fish

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develops. Furthermore, if this attraction is innate, its genetic foundation underscores how predation through the interruption of primary predator attacks is an important forging mechanism for *P. fuscus*. Since *P.fuscus* has such an important role on the reef as a common predator on juvenile fish on the Great Barrier Reef, this information furthers the base of knowledge on predator-prey interaction and is thus is vital in developing appropriate management for these reef system (Martin 1994).

In addition, overall it was found that both the amount of time spent within the cue channel as well as the number of times the cue channel was entered increased with increasing age, which is a result that would be expected, as *P. fuscus* can not feed on the fish until later ages. Since the newly settled fish were not attracted to the chemical alarm cue, evidence of chemical cues is not a driver in regulating where the young larval *P. fuscus* settle on the reef. Thus this attraction to the chemical alarm cue does not immediately dictate populations of predator-prey fish assemblages on the reef in terms of settlement choice.

4.2 Differences Among Color Morphs

The current study found there only to be a trend of the adults entering the channel with the cue more than the control channel, and spending no difference in time between the two channels. This may highlight the importance of visual stimulus for *the P. fuscus* to continue in pursuit toward the chemical alarm cue, once the chemical is detected. Furthermore, this result differs from the results found in the study by Lonnstedt (2009), as the study found that the adult *P. fuscus* spent significantly more time in the channel with the chemical cue than that with control using the same Y-maze set up. One explanation for this difference, may be that it is the result of different ratios of color morphologies tested. This study found that the yellow morphs of the adult *P. fuscus* entered the channel with the cue significantly more than the control channel,

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while the brown morph did not and showed a trend of spending more time in the channel with

the cue over the control (Figure 4, Figure 5). On the Great Barrier Reef each color morph has

been found to populate different areas of the reef and are each associated with different colored

damselfish (Munday 2003). Munday found that the yellow morphs associated in areas of the reef

where yellow damselfish were found, and brown morphs associated where brown damselfish

were found, which indicated the likelihood of *P. fuscus* using aggressive mimicry in predation

(2003). The current study focused on chemical alarm cues from *P. amboinensis,* which is a

yellow damselfish. Thus, these results indicate that *P. fuscus* may be able to differentiate

between alarm cues of different damselfish, and are attracted to those of which they are

associated. Thus the yellow morphs may have shown a stronger attraction to the chemical alarm

cue than the brown morphs, because the yellow damselfish cue is a preferred prey. *P. fuscus*

have shown to be able to differentiate chemical cues of different ontogeny of damselfish, as well

as between poorly fed and well fed based damselfish, thus showing that this attraction is

specialized (Lonnstedt 2009). Therefore the idea that different color morphologies of *P. fuscus*

are attracted to specific colors of damselfish is a possible explanation for the current study's

findings.

5.0 Conclusions

The current study found juvenile *P. fuscus* to be attracted to chemical alarm cues of the

juvenile prey *P. amboinensis.* Since the juvenile *P. fuscu*s used in the study are naïve to the

chemical alarm cues, as well as not yet developed enough to include eat the juvenile fish, it is

suggested that this attraction to the chemical alarm cue has a genetic basis. These findings are

based on aquarium observations, thus it must be stressed that field studies must be performed to

ensure this behavioral occurrence in a natural setting. Furthermore, this study differed with

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Lonnstedt's study, in that adult *P. fuscus* were not significantly attracted to the chemical cue (2009). Further studies which run many more trials should be performed, as the current study was limited its performance time and test source pool The differences in attraction level among different color morphologies of adults in this study should be further investigated as an explanation for differences from Lonnstedt's study through additional trials with the two color morphs (2009). These differences can be further investigated through studies using the chemical alarm cues of brown damselfish *Pomacentrus adelus* or *Pomacentrus chrysurus*, which brown *P. fuscus* morphs are associated with, to see if level of attraction to the chemical cue is prey color dependent. Studies that conduct studies on a larger spectrum of *P. fuscus* ages could further narrow when this attraction to the chemical cue is formed in development.

The genetic foundation of the attraction of *P. fuscus* to the chemical alarm cue stresses the importance of olfactory cues in forging for *P. fuscus*. Recent studies have shown how ocean acidification can have a serious impact on detection and interpretation of olfactory cues for reef fish (Dixson 2010). Thus further studies should investigate if increased CO_2 affects P. fuscus ability to detect these chemical alarm cues, as this could have detrimental effects on predator-prey dynamics and thus the coral reef system. Thus much further study should be conducted in order to determine how the results found in the current study truly affect predator-prey dynamics of the coral reef.

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