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Odor-mediated Behavioral Responses of Hatchery-reared Blue Swimming Crab *Portunus pelagicus* (Malacostraca, Decapoda) Instars Exposed to Various Chemical Cues

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In this study, the ability of hatchery-reared blue swimming crab *Portunus pelagicus* instars to discriminate various odors was tested in a y-maze aquarium using the following chemical cues: 1) mussel odor, 2) snapper odor, 3) combination of mussel and snapper odors, and 4) seawater as control. Results showed that when given a choice between seawater and mussel odor, a higher percentage of instars preferred to stay along the mussel odor stream. In contrast, avoidance response was elicited when snapper odor was introduced to crab instars. When provided with a choice between mussel odor and snapper odor, the instars exhibited preference to the former. However, when presented with a combination of two conflicting odors (mussel and snapper odors), the crab instars favored to stay in the control chamber. These results suggest that even at its early developmental stage, blue swimming crab instars are highly responsive and can distinguish food from alarm odors, such as those odors coming from perceived potential predators. This study is important in understanding the behavioral capacities of hatchery-reared animals, their responses when released to a new and harsh environment, and possible applications of these behaviors in enabling restocking programs feasible.

Key words: alarm odor, chemoreception, decision-making, stock enhancement

INTRODUCTION

Decision-making in animals and considerations on benefits and trade-offs play a significant role in animal behavioral ecology. In many aquatic communities, chemical cues from a predator can greatly influence the fitness of a prey (Ferrari et al. 2010). Where the transmission of an acoustic or visual stimulus is limited, the presence or even the size of a predator may be chemically perceived through differing cues or the concentrations of cue release (Chivers et al. 2001). Therefore, understanding predator threat assessment is essential to predict consequences for prey survival and other indirect effects.

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Aquatic organisms use a variety of stimuli to obtain information about their environment and locate areas with food resource (Monteclaro et al. 2010; Yan et al. 2010; Delavan & Webster 2012; Kamio & Derby 2017). With the aid of wind and water currents, chemical signals are dispersed from a source to the animal's olfactory organs (Reidenbach & Koehl 2011). The signals are then transmitted to the brain, which decides appropriate behavioral responses (Weissburg et al. 2012).

The innate capacity of the prey to recognize the threat of predation appears to be dependent but not limited to the structure and diversity of its environment (Ferrari et al. 2008). While there are studies indicating the ability of some prey population to develop a response (Kovalenko et al. 2010; Chivers & Ferrari 2013), others may fail to

intuitively show their innate predator recognition which is often attributed either to: 1) the prey's lack of exposure to a specific predator co-occurring over a geographic range, or 2) the absence of evolutionary history between predators and prey (Smith et al. 2008).

Hatchery-raised individuals are reported to respond to predation (Kellison et al. 2000). However, they may fail to recognize and take appropriate evasive action given the fact that being raised in the hatchery, they spend all their time in refuge and under care.

As an important fishery commodity in the Philippines, efforts to initiate and improve culture techniques for blue swimming crabs are being developed, yet little is known about the animal's ecology and behavior during its early stages of development. The blue swimming crab is an excellent study animal to assess an organism's response towards possible danger. As a cannibalistic species, it uses its chemosensory system (Zimmer-Faust et al. 1995) to feed on its prey. There is yet no published report on the risk sensitivity of the blue swimming crab during its primary stages of development such as the instar stage (i.e., the stage after the megalopa phase). Information like these are necessary to promote successful survival of a population.

Thus, this study aimed to examine the behavior and risk sensitivity of hatchery-reared blue swimming crab instars to various chemical odors. Specifically, it aimed to evaluate the behavior of these individuals in response to: 1) mussel odor; 2) odor from a carnivorous fish, red mangrove snapper; and 3) combination of two conflicting odors.

MATERIALS AND METHODS

Animal Collection and Maintenance

A total of 200 instar stage blue swimming crabs *Portunus pelagicus* (Linnaeus, 1758) (day 4, ~0.5-0.8 cm carapace width) were used in the study. These test animals were obtained from the hatchery of the Philippine Association of Crab Processors, Inc. (PACPI) in Tigbauan, Iloilo and were transported about 15 km to the Fish Biology Laboratory, University of the Philippines Visayas in Miagao, Iloilo. Crabs were kept in four separate 30-L holding tanks filled with filtered seawater (32-35 ppt) for at least 2 days with a density of 50 crab instars/tank. The animals were kept on a 12:12 D:L cycle with a water temperature of 27-28°C. Constant and gentle aeration was provided and plastic straws that served as shelters were placed in each holding tank to minimize cannibalism. Chopped fish was provided *ad libitum* every other day between 0800H and 1700H. Holding tanks were cleaned (80% water change, as needed) daily. Test animals were not provided with food 24 h before the start of the trials. Crabs with incomplete appendages and appeared to be weak were not used in the tests.

Y-maze Aquarium

A y-maze aquarium was used to determine preference or avoidance of blue swimming crab instars to test odors. The y-maze was a flow-through glass tank that measured 46 cm long x 30 cm wide x 23 cm high. The aquarium was divided by a glass panel (22 cm long), which separated the two sides of the maze as shown in Fig. 1. A removable perforated fiberglass barrier was placed to isolate the acclimation chamber (15 cm long, extending beyond the end of the maze) of the crab instars from the test area.

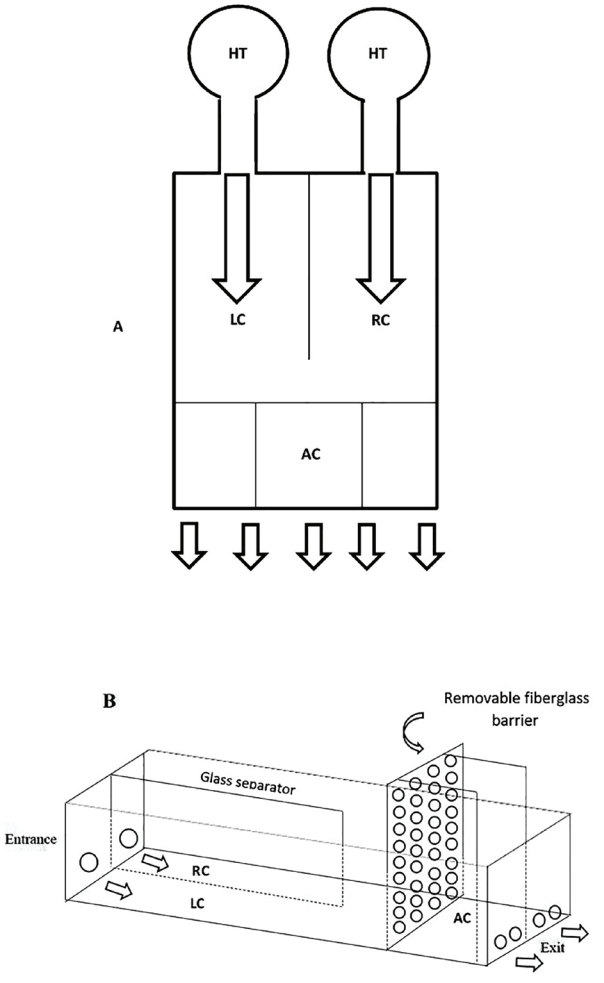

Figure 1. A) Illustration and layout of the y-maze tank used in the experiment. HT, header tanks; LC, left chamber; RC, right chamber; AC, acclimation chamber for blue swimming crab instars prior to the selection of left or right chamber. B) Detailed structure of the y-maze tank (not in scale) used in the study. Arrows indicate the flow of test odors in and out of the test tank.

Test odor solutions were freshly prepared at the start of each test and were randomly assigned to the left or right chamber of the y-maze tank. Test odors were separately placed in 20-L capacity header tanks. A dye test was initially conducted to determine the flow rate and to establish a uniform flow of test solutions between the two chambers. Based on this dye test, each test odor was introduced using a tubing connected to perforated PVC pipes inside the fluvarium at a rate of 4 L/min. At this flow rate, the test odors were expected to reach the crab instars in about 30 s, after which, the separator was raised.

Test Odor Preparation

Mussel Odor. Fresh green mussels *Perna viridis* were bought at Miagao Public Market and brought to the laboratory. After cleaning, the meat was removed from the shell. Approximately 20 g of green mussel were immersed in the header tank containing 20 L of filtered seawater. After 3 hours, the meat pieces were removed.

Snapper Odor. Chemical cues from an organism may be released through excreta or by skin secretion (Chivers & Smith 1998). For this test odor, a healthy juvenile red mangrove snapper *Lutjanus argentimaculatus* (total length = 12.70 cm) was obtained from Igang Marine Station of the Aquaculture Department of Southeast Asian Fisheries Development Center (SEAFDEC/AQD) in Nueva Valencia, Guimaras. Before the start of the experiment, the snapper was maintained and acclimated in a 30-L capacity holding tank for 3 days and fed to satiation. After acclimation in the laboratory, it was transferred and immersed in a 20-L capacity header tank for 3 h after which, the fish was removed from the header tank and returned to its holding tank.

Combination of Mussel Odor and Snapper Odor. The mixture of conflicting odors was prepared by soaking 10 g fresh green mussel meat in a 10-L capacity header tank. In a separate 10-L header tank, a juvenile snapper was placed. After 3 h, the mussel meat pieces and snapper were removed from the header tanks. Finally, both mussel odor and snapper odor solutions were mixed to produce a 20-L mixture.

Experimental Design

All tests were performed under red light between 2130H to 0300H, since the test animals are nocturnal feeders (Ratchford & Eggleston 1998). This is to minimize visual stimuli and disturbances during trials.

At the start of each test, ten blue swimming crab instars were randomly placed in the y-maze tank. Prior to each test, the test animals were conditioned for 30 min in the acclimation chamber.

The trial began after the barrier was removed and the blue swimming crab instars were allowed to freely respond to the introduced test odor. The responses of crab instars were documented using a video camera. The length of their stay to either left or right chamber was recorded and the average time spent by ten crabs for every trial was computed. The position of each crab instar was determined (i.e., position of the snout and/or chelae) and the number of crabs in each chamber was recorded (Monteclaro et al. 2014).

The duration of observation for each trial was 180 s. The location and number of the test animals in the y-maze were recorded every 30 s, where a total of six images per trial were produced. At the end of each test, crab instars were removed from the y-maze tank and were acclimated to holding tanks. The header and y-maze tanks were then drained, washed with laboratory detergent, refilled, and rinsed several times with seawater until the next test. All test animals were used only once.

Statistical Analyses

All tests were replicated six times. Two groups of animals were observed – those that actively moved upstream and those that did not attempt to move towards the trial area. The test animals that displayed interest, demonstrated avoidance, and/or moved towards the source of test odors were classified as 'trackers,' while those that did not show any movement and/or preferred to stay in the acclimation chamber were labeled as 'settlers'. The total number of crabs over six images per treatment was counted to determine the mean percentage in either left or right chamber of the y-maze tank over a 3-min run. The behavioral response of crab instars in a particular run was considered as a single replicate data for analysis. The time spent by crab instars in each chamber was also recorded. The percentage of settling and tracking crabs were transformed into arcsine √% for statistical analyses.

The percentage of settling and tracking crabs were determined using the formulae:

$$\%\ settling\ crab\ instars = \frac{number\ of\ crabs\ that\ did\ not\ show\ movement\ or\ stayed\ in\ acclimation\ chamber}{total\ number\ of\ crabs\ in\ the\ aquarium} \times 100 \quad (1)$$

$$\%\ tracking\ crab\ instars = \frac{number\ of\ crabs\ that\ avoided\ or\ tracked\ the\ odor\ source}{total\ number\ of\ crabs\ in\ the\ aquarium} \times 100 \quad (2)$$

Since the data collected were not normally distributed (Shapiro-Wilk's Test, $p<0.05$), the non-parametric Mann-Whitney U Test was used to compare the time spent by blue swimming crab instars in each independent lateral half of the y-maze. The Statistical Package for Social Sciences (SPSS) version 20 was used to analyze the data. All values were expressed as mean ± standard error of the mean (SEM).

RESULTS

Percentage of Settlers and Trackers in Test Odors

As soon as the barrier was removed, the blue swimming crab instars started to move around the y-maze. During the test, all animals were monitored and their responses to the test odors were recorded. In the control tests, 100% of the test animals behaved as trackers. The percentage of trackers on the right side of the chamber (52.00 ± 0.65 %) had no significant difference with that on the left side (48.00 ± 0.65 %) (Mann-Whitney U Test, p=0.934) (Fig. 2). These suggest that the animals did not show any bias to any of the two chambers in the aquarium and that behavioral responses in succeeding tests must be an outcome to the test odors used.

When mussel odor was presented on one side and seawater on the other side of the maze, the percentage of settlers on both sides did not differ significantly (Mann-Whitney U Test, p=0.138) (Fig. 3). In contrast, the percentage of trackers in the mussel odor stream was significantly higher (87.00 ± 0.42 %) than those that stayed in the control seawater (10.00 ± 0.52 %). In addition, a significant majority of crabs were able to locate the mussel odor source (Mann-Whitney U Test, p=0.003) than merely settling down in the chamber. The test animals appeared to have initiated foraging response as indicated by crabs that directed their chelae towards their mouth area. These results showed that hatchery-reared blue swimming crab instars have the ability to identify and search possible food odors.

The introduction of snapper odor elicited avoidance by the test animals. When exposed to the snapper odor, crab instars were observed to cease movement and frequently extended one or both chelae upwards. The settlers preferred to stay in the control chamber (13.00 ± 0.49 %) (Mann-Whitney U Test, p=0.022). Most trackers (87.00 ± 0.42 %) also preferred to stay in the control chamber (Mann-Whitney U Test, p=0.002) (Fig. 4). It is possible that crab instars have identified the snapper odor as a novel one, which caused the test animals to suppress their movement. This is a possible response to decrease vulnerability towards a potential danger.

When given a choice between mussel odor and snapper odor, settlers chose to stay in the mussel odor stream (17.00 ± 0.67 %) (Mann-Whitney U Test, p=0.022). Trackers also actively located the source of the mussel odor stream (83.00 ± 1.43 %) (Mann-Whitney U Test, p=0.022) (Fig. 5). These results further validate the earlier findings that hatchery-reared crab instars seem to have the ability to search for food odors and avoid cues associated with unfamiliarity or variation.

Crab settlers did not discriminate between the mussel odor-snapper odor mixture (2.00 ± 0.17 %) and control seawater (25.00 ± 0.96 %) (Mann-Whitney U Test, p=0.05). In contrast, most trackers stayed in the control chamber (70.00 ± 1.00 %) than in the odor mixtures

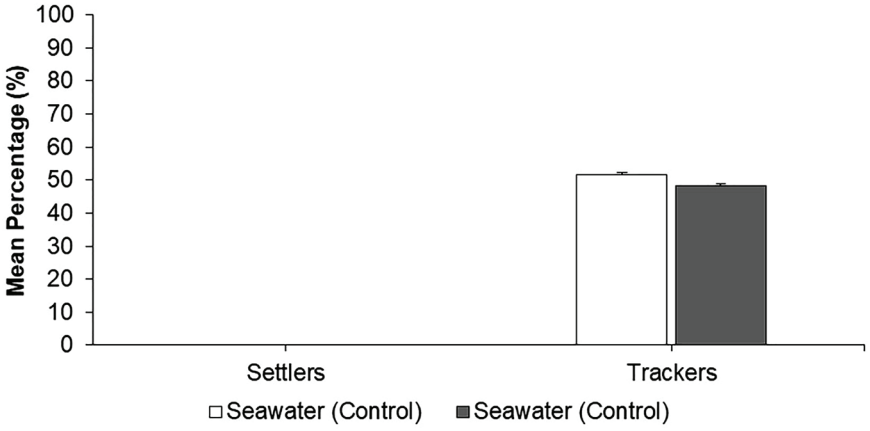

Figure 2. Percentage of crab instar settlers and trackers in the y-maze during control tests where only seawater (control) was placed in the chambers, n=60. SW, seawater. Values are expressed as mean ± SEM. Letter notations indicate significant difference ($p<0.05$) between the two test odors.

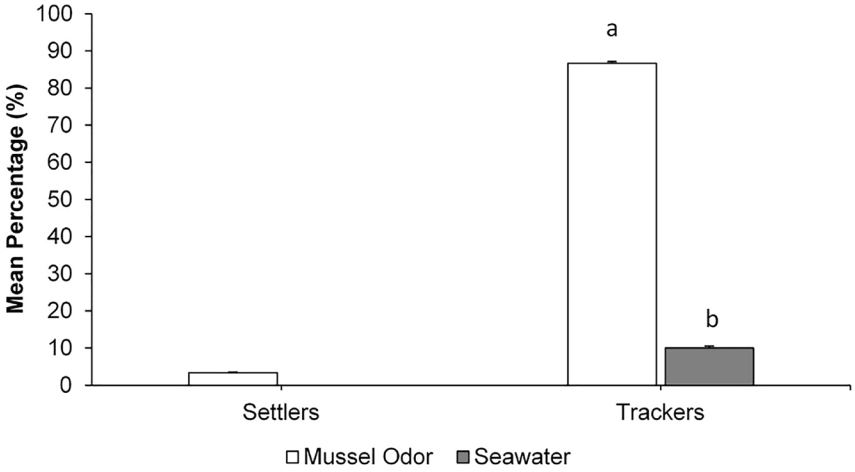

Figure 3. Percentage of crab instar settlers and trackers in the y-maze tank in response to mussel odor, n=60. MO, mussel odor (white bars); SW, seawater (gray bars). Values are expressed as mean ± SEM. Letter notations indicate significant difference (p<0.05) between the two test odors.

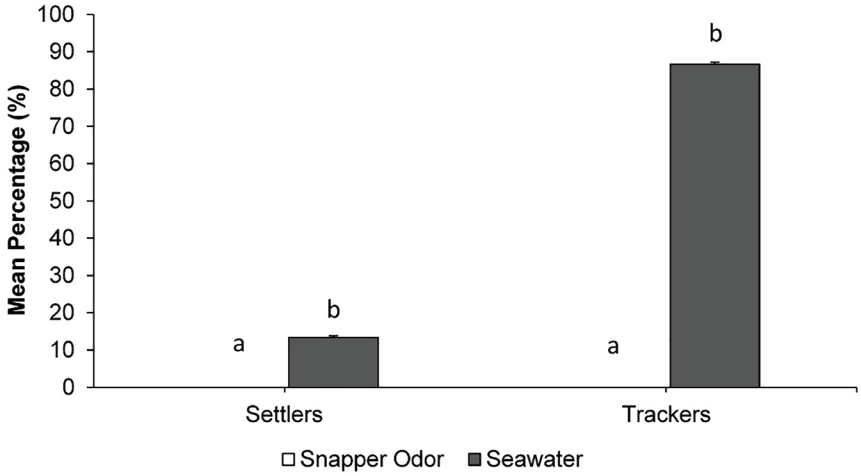

Figure 4. Percentage of crab instar settlers and trackers in the y-maze tank when snapper odor was introduced, n=60. SO, snapper odor (white bars); SW, seawater (gray bars). Values are expressed as mean ± SEM. Letter notations indicate significant difference (p<0.05) between the two test odors.

(3.00 ± 0.21 %) (Mann-Whitney U Test, p=0.003) (Fig. 6). These suggest that although most of the crab instars get attracted when presented singly with mussel odor, they prefer to avoid the same when it is combined with snapper odor.

Time Spent by Crab Instars in Test Odors

Table 1 shows the amount of time spent by crab instars in control and in different test odor cues. The time spent by crab instars within the two lateral halves with control seawater (left chamber = 78.29 ± 6.44 s and right chamber = 77.79 ± 6.59 s) had no significant difference (Mann-Whitney U Test, p=0.88). This further suggests that the crab instars did not demonstrate preference to any of the two lateral halves.

Crab instars significantly spent more time in the mussel odor stream (73.87 ± 7.64 s) (Mann-Whitney U Test, p=0.001) than in control seawater (38.66 ± 8.90 s). In contrast, the introduction of snapper odor caused little or no exploration of crab instars around the snapper odor stream (29.68 ± 6.32 s) (Mann-Whitney U Test, p=0.021).

When presented simultaneously, the test animals spent more time in the mussel odor stream (75.38 ± 6.63 s) than

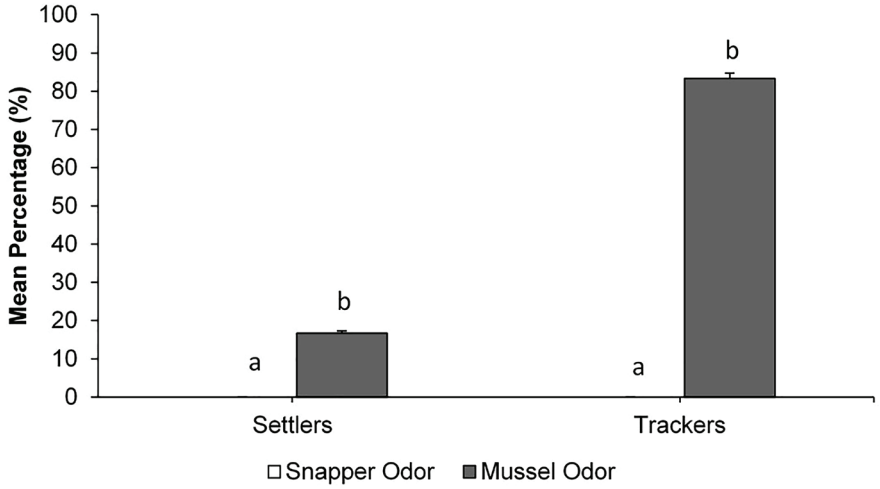

Figure 5. Percentage of crab settlers and trackers between the mussel odor and snapper odor in the y-maze tank, n=60. SO, snapper odor (white bars); MO, mussel odor (gray bars). Values are expressed as mean ± SEM. Letter notations indicate significant difference (p<0.05) between the test odors.

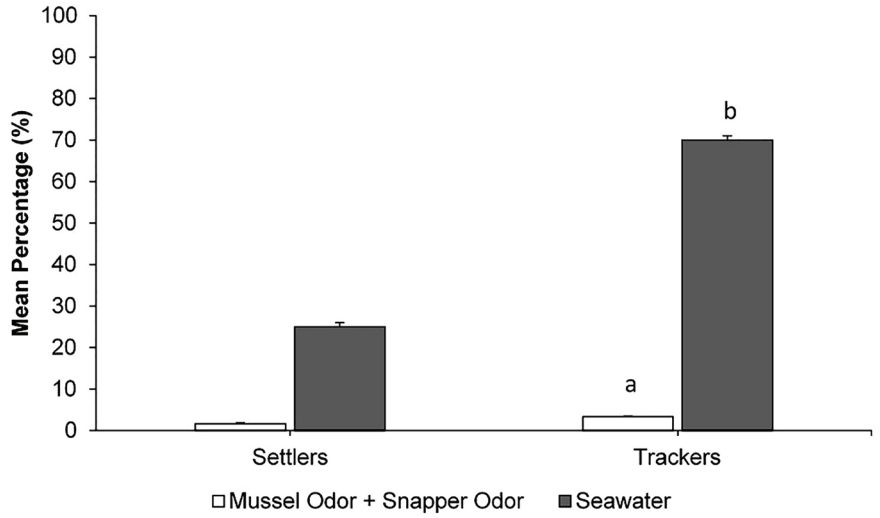

Figure 6. Percentage of crab instar settlers and trackers in the y-maze in response to conflicting odors (mixture of mussel and snapper odors), n=60. MO + SO, mussel odor + snapper odor (white bars); SW, seawater (gray bars). Values are expressed as mean ± SEM. Letter notations indicate significant difference (p<0.05) between the two test odors.

in the snapper odor (15.00 ± 4.65 s) (Mann-Whitney U Test, p=0.00). But when presented with a combination of mussel and snapper odors, crab instars spent longer time in control seawater (77.91 ± 7.49 s) than in the mussel odor-snapper odor mixture (45.57 ± 7.36 s) (Mann-Whitney U Test. p=0.004). These results further validate the earlier findings that blue swimming crabs – even at their early life stages – have the ability to detect odors, both favorable and not, and can respond accordingly. Furthermore, they seem to have the ability to evaluate the risks associated with conflicting odors.

DISCUSSION

The capacity of animals reared in a hatchery, especially during the early life stages, to evaluate the different processes in the natural environment such as predator-prey relationship and habitat selection is largely unknown. In an environment where both threat (e.g., predation risk) and

Table 1. Average time spent by crab instars in control and in different odor cues in the y-maze tank, n=60. Values are presented as mean ± SEM. Letter notations denote significant difference ($p < 0.05$) between the two test odors.

Test Solution*		Time spent (s)
Control	SW	77.79 ± 6.59
	SW	78.29 ± 6.44
MO vs SW	MO	73.87 ± 7.64^a
	SW	38.66 ± 8.90^b
SO vs SW	SO	29.68 ± 6.32^a
	SW	51.91 ± 7.53^b
MO + SO vs SW	MO + SO	45.57 ± 7.36^a
	SW	77.91 ± 7.49^b
SO vs MO	SO	15.00 ± 4.65^a
	MO	75.38 ± 6.63^b

*Seawater (SW); Mussel Odor (MO); Snapper Odor (SO)

reward (e.g., food and/or shelter) are present, this study assessed the risk-sensitivity of hatchery-raised animals, which are largely sheltered and well-provided with care.

As young individuals, crab instars were fed with crushed commercial crab feed pellets and must have been naïve to mussel odor prior their use in these tests. Despite this, hatchery-reared crab instars showed attraction towards mussel odor and exhibited food searching behavior, which suggest that they are able to associate the odor with food. In the wild, crab species have been reported to prey upon bivalves (Brown et al. 2011; Capelle et al. 2016) with mussels as the main diet of blue swimming crabs (Ingles 1996). The introduction of mussel odors might have induced their innate olfactory learning, maximizing their foraging efficiency under a 'risk-free' condition.

The crab instars responded differently to snapper odor. The general reaction was either indifference or alarm and the absence of food searching behavior. These responses suggest potential avoidance that leads to the reduction of energy expense and forage. The avoidance response of blue swimming crab instars to snapper odor may be a compromise behavior (Dill 1987). In the safety of the hatchery where instars never had the chance to interact with predators, the snapper odor is a novel molecule. The absence of encounter with such odors during their ecological time (lifetime) may result in the lack of accurate information that may be used by the animals for possible foraging opportunity. This adaptive behavior is expected in an environment with a predation threat where a larger organism, although not known, is likely to be a predator (Brown & Chivers 2005). For example, odor cues from both native (warmouth, *Lepomis gulosus*) and non-native (African jewelfish, *Hemichromis letourneuxi*) predators triggered antipredator responses (e.g., cessation of movement) to Eastern mosquitofish, flagfish, and riverine grass shrimp (Dunlop-Hayden & Rehage 2011). For brachyuran crabs, snappers have been reported as major predators in the wild (Svane & Cheshire 2005; Sheaves 2009; Usmar 2012). Thus, a recognition pattern that is genetically compelled (Wisenden 2014) and reflected through evolutionary history could also influence how an animal responds to predator odors.

While crab instars actively tracked the mussel odor stream when presented singly, they exhibited reduced movement and restrained tracking speed when the mussel odor was mixed with snapper odor. In the present study, the mussel odor-snapper odor mixture was regarded by test animals as unattractive. The test animals seemed to consider the conflicting odors as a putative deterrent mixture and chose not to trace the source even with the presence of mussel odor.

The risk aversion displayed by blue swimming crab instars shows a powerful effect where the mussel cue was overruled by snapper odor. This supports the life-dinner principle (Dawkins & Krebs 1979) where the act of feeding is suspended because the high probability of vulnerability and death overrides the urge to locate the high resource area (i.e., food, shelter). This is often known as trade-offs, which occurs during decision-making in animals. The foraging behavior of an individual contributes to the fitness of the next generation. Thus, the animal's understanding of stimuli present in the environment is important during food search and their ability to survive and reproduce. This is why repeated experience is also important to enhance the capability of an organism to recognize prey, forage, and evaluate the perceived predation risk appropriately (Brown et al. 2003).

The results of this study may have valuable implication in the behavioral conditioning of hatchery-reared organisms before their release in the wild. The presence of suitable stimuli such as rearing techniques and hatchery substrata (Le Vay et al. 2007) at appropriate stages of development is important and should be equated to the level of its wild counterparts. In the presence of a predator, the degree of response of an individual should be calibrated to the degree of potential threat; that some prey species must be trained only to metabolites of specialist predators (Chivers & Smith 1998). This is to avoid unnecessary responses of an organism towards novel or unusual chemical cues that could compromise their foraging time and mate location. This will also effectively reduce cannibalism and promote high survival and faster growth of juveniles.

The results provided firm evidence that hatchery-reared

blue swimming crab instars have the innate capability to distinctly identify attractive and aversive odors. By sufficiently exposing them to an unacceptable level of risk or uniform blends of risk-reward compounds, they have the ability to weigh varying contingencies that could either provide them with reliable information on food availability and/or familiarity to possible predator cues. Future studies may use this as a framework to address vital issues such as ecological and evolutionary consequences of varying chemical cue concentrations, the diversity of chemical cues as released by predators in the environment and ontogenetic effects to prey population.

CONCLUSION

Hatchery-reared blue swimming crab instars have the ability to evaluate when and where to spend their energy without compromising survival. They also have the capacity to evaluate consequences of food and alarm odors. The research findings suggest that the behavioral quality of these organisms appears to be maximized, efficient, and well-conditioned enough for release in the natural environment.

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