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The fishing behavior by *Metopograpsus messor* (Decapoda: Grapsidae) and the use of pneumatophore-borne vibrations for prey-localizing in an arid mangrove setting

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Abstract This study presents the first documented observations of a brachyuran crab's proactive fishing behaviour in conjunction with mangrove pneumatophores which are employed as prey-localization devices. All ecological data were recorded in situ using simple behavioural observations, visual census and field experiments. Field experiments were based on stimulus-response and ecological surveys on random displacement. Assemblages of Metopograpsus messor were observed daily performing a foraging/predatory tide-related cyclic behaviour pattern in an arid mangrove ecosystem which experiences challenging environmental conditions. Prey-localizing behaviour was observed during the flood tide when pneumatophore-borne vibrations were used to identify potential prey. The prey simulation field experiment (where a single pneumatophore was stimulated by knocking) showed that in >93% of instances a crab approached the exact pneumatophore being stimulated. As water levels increased during the tidal cycle M. messor was observed climbing pneumatophores. The crabs anchored themselves to the pneumatophore just above the water level with their pereiopods. The chelipeds were positioned in a pincher-like trap, and remained in a 'capture-position' waiting for prey to move within striking range. This characteristic fishing behaviour was performed daily by a population of M. messor. Ecological observations suggest that both these predatory behaviours are associated with the fish Aphanius dispar dispar in a direct prey–predator relation. Evidence suggests that these fishing behaviours evolved due to characteristics within the M. messor phylogeny (foraging in intertidal zones; daily displacement following tidal levels; high sensitivity to vibrations; and an opportunist diet) and its associated environment (presence of pneumatophores and high availability of a fish resource).

Key words: Behavioral ecology; Arabian Gulf; Decapod, Brachyura, Grapsoid; Arid ecosystem.

INTRODUCTION

The mangrove habitat of the western Arabian Gulf is a biologically extreme environment typified by; a lack of freshwater input, extreme high-end temperature variations 35 to 50 ^{0}C and salinities which can fluctuate between 35 and 65 ppt (Al-Maslamani *et al.*, 2013). Due this extreme arid condition_those mangrove forests can be considered ecologically unique. An extreme ecosystem where the tree assemblages consist of only one species *Avicennia marina* (Forssk.) Vierh. which forms the entire ecosystem (Abdel-Razik, 1991; Al-Khayat and Jones, 1999; Riegl and Purkis, 2012; Al-Maslamani et al., 2013; Walton et al., 2014). The arid mangrove of the west coast of the Arabian Gulf can be considered as an ancient and well stablished ecosystem, which is supported by a suite of endemic species confined to the specific demographics and conditions created by *A. marina* (De Grave & Al-Maslamani, 2006; Al-Maslamani *et al.*, 2013; Al-Maslamani *et al.*, 2015; Naderloo, 2017).

One of the most prevalent species associated with this mangrove environment is the tree climber crab *Metopograpsus messor* (Forskål, 1775) a medium-sized crab native to the western Indian Ocean and the Arabian/Persian Gulf (Naderloo, 2011). A Grapsidae crab which belongs to a group of terrestrial tree climbers that are reported as occupying herbivores, detritivores and omnivores niches within different trophic chains. It is considered a habitat-generalist and is common in a variety of coastal habitats including muddy substrates, rocky shores and mangroves (El-Sayed et al., 2000; Linton and Greenaway, 2007; Poon et al., 2010; Naderloo, 2011; Lee, 2015). The species is easily identifiable with naked eyes by its dark colored dashes and some specimens with red chelae (Holthuis, 1977; Naderloo, 2011). The only species with those characteristics recorded in the studied site (Naderloo, 2017).

The decapod species represent an integral component within the majority of marine trophic chains occupying different roles throughout its length, including as predators (Boudreau and Worm, 2012). Indeed, predatory behavior in decapods is commonly identified as active foraging, however there are no recorded observations of crabs presenting a proactive fishing behavior. In addition, accounts exist of terrestrial decapods using substrate-borne vibrations in predator avoidance and courtship (Christy, 1991; Hill, 2001; Koga *et al.*, 2001). However, the use of substrate-borne vibrations for prey-localization during foraging and fishing has not been documented (Brownell and Farley, 1979; Bell et al., 1991).

Therefore, this study aims to report the fishing behavior of *Metopograpsus messor* as witnessed in the arid mangroves of the western Arabian Gulf and their use of mangrove pneumatophore networks and substrate-borne vibrations for prey-localization. A list of the main component species and a discussion of the ecological drivers which may account for the observed behavior is also presented.

MATERIAL AND METHODS

Study area

Observations and records took place *in-situ* within the mangrove assemblages at Al-Khor (25^{o} 41' 29.2" N – 51^{o} 33' 15.7" E) and Al-Dhakira (25^{o} 45' 01.5" N – 51^{o} 32' 21.7" E) in the east coast of Qatar (Figure 1). The mangrove environment at these two sites was characterized by a riparian ecosystem formed as a result of hydrodynamic sculpting due to ebbing and flooding tides. The riparian corridors were fringed by pneumatophores of *A. marina* trees which grew along the boundaries of the channels (Figure 2). The study sites were visited every two months over a two-year period.

Fishing behavior and prey-localizing behavior

M. messor fishing and prey-localizing behavior was recorded with naked eyes and video camera using sampling behavioral rules as per Martin and Bateson (1986). Intertidal and subtidal observations were obtained at a distance of approximately 3-10m; using snorkeling dive when necessary. A total of 48 ecological observations were conducted to record and describe the proactive predatory fishing behavior and prey-localizing/foraging behavior. Surveys were performed throughout the tidal cycle, which was schematically divided in: Low Tide; Flood Tide start (intertidal flooded areas <5cm); Flood Tide (intertidal flooded areas >5cm); High Tide (water covering the pneumatophores). Aiming describe the relation of the fishing and prey-localizing behavior with the tide cycle it was recorded the position in the riparian zone where specimens of *M. messor* were observed: 1) hiding in cavities; 2) prey-localizing/foraging in the bottom; 3) fishing on pneumatophores; 4) climbing the mangrove trees.

Prey-localization experiment

During the observations for the fishing behavior it was documented small fish creating vibrations on pneumatophores during the ingression of the flooding tide (start). This was accompanied by specimens of *M. messor* moving in the direction of the vibration source. Based in this observation, a comparative *in-situ* assessment of tactile sensitivity in relation to pneumatophore vibration was designed to evaluate the contribution of substrate-borne vibrations in prey-localization. The experiment was recorded using video as per sampling rules described in Martin and Bateson (1986). The hypothesis being that the prey-localizing behavior of this crab was initiated and directed by pneumatophore-borne vibrations.

The experiment focused on stimuli-response. Small knocks were made against pneumatophores using a piece of wood to create small vibrations in a single pneumatophore trying to mimic and recreate those vibrations created by the small fish previously observed *in situ*. The experiment was replicated x 30 during the start of a flood tide. Before each experiment, observers remained motionless for five minutes, to allow crabs to get accustomed to their presence.

Ecological relations and implications with the described behaviors

Aiming understand the abiotic and biotic relation and implications with the observed behaviors: it was evaluated the frequency and abundance of *M. messor* and the composition and frequency of the main species possible related to these predatory behaviors; it was recorded all observed trophic inter and intra-specific associations; and it was recorded all higher records of temperature and salinity using probes and data loggers. For this ecological evaluation the riparian zone in the studied channels was schematically divided according with the position in the arid mangrove system with an open-water area close to the sea (Figure 2A, C) and a semi-confined-waters area in the peripheral mangrove zone, near the salt marshes (Figure 2B, D) including tide pools. This ecological evaluation took place during the flood tide because it is the tide moment where the prey-localizing and fishing behavior were observed. Voucher specimens of recorded species were collected and returned to the laboratory for taxonomic verification, preservation and collection cataloguing.

All specimens observed were recorded using a timed-search visual census methodology, which incorporated walking in the intertidal zones and snorkeling in the channels for the underwater surveys. For most species the index was the frequency, where during the first 10 minutes the observed species were recorded in terms of presence or absence and were considered frequent. Thereafter only species not previously observed were recorded and considered as occasional. It was presented in this study only frequent species. *M. messor* beyond the frequency it was estimated the abundance, where all specimens were counted during the first 10 minutes. A total of 40 x 1-hr surveys where undertaken.

RESULTS

Mangrove Channels – Species composition and environmental characteristics

A high degree of variation was recorded in temperature and salinity comparing the water masses in the channels. The open-waters areas near the sea presented maximum temperature of 36^{o}C and Salinities of 50ppt, similar to that previously recorded in the extreme hot marine ecosystem in the region (Camp *et al.*, 2018). The semi-confined-waters areas in the end of the channels, on the periphery of the mangroves, it was recorded an even more extreme environmental conditions in both temperature >49 ^{o}C and salinity 75ppt.

The main component species observed in the riparian zone during the flood tide are presented in Table 1. The crab *M. messor* was frequent in all intertidal zone with > 100 specimens recorded in the first 10 minutes in all surveys. The small fish *Aphanius dispar dispar* (Rüppell, 1829) was dominant underwater within the subtidal zone (Figure 3B-E) and was observed in all channels in open-water areas and in semi-confined-waters areas, including in tidal pools. It was recorded invading the intertidal riparian zone during the start of the tidal influx when water levels were < 4cm (Figure 3B) and dominating the intertidal zone throughout the flooding tide (Figure 3C). Among decapods in the intertidal zone the purple crab *Eurycarcinus orientalis* A.Milne-Edwards, 1867 was frequent in the riparian zone of the open-water mangrove areas and occasional in the semi-confined-waters areas, particularly prevalent in flooded areas of >5cm (Figure 3F, G). The shrimp *Palaemon khori* De Grave & Al-Maslamani, 2006 was observed in high-density patches accommodating large assemblages in the riparian zone in all channels in open-water areas and in semi-confined-waters areas, including in tidal pools, (Figure 3D). However, its densities decreased in the intertidal riparian zone.

Fishing and prey-localizing behavior

The results of the observed displacement/position of *M. messor* according with the tide cycle is highlighted in the Figure 4A, where the great majority of the population of this species followed a displacement pattern according with the raise of the water level. Presenting in sequence, a prey-localizing behavior in the start of the flood tide and a fishing behavior in the rest of the flood tide, after the water level cover the entire body of *M. messor*.

During the low tide *M. messor* was virtually absent in the riparian zone, hidden in burrows of other crabs in the substrate (Figure 4A). Prior to the flooding tide *M. messor* was observed moving out of the burrows along the riparian zone to start prey-localizing (Figure 5A); like a bioindicator indicating the start of the flood tide even before the water raise became visible. Crabs within the riparian zone initially displayed prey-localizing (foraging) behavior (Figure 5A) when the water is just in a small layer invading the mangrove. But as the tide rises a bit more *M. messor* starts to climb *A. marina* pneumatophores. They positioned themselves above the surface of the water and adopted a readiness stance to commence fishing (Figure 5D). This was identified by the crabs anchoring themselves to the roots with their pereiopods and positioning their chelipeds in a pincher-like trap, remaining motionless and waiting for prey to move within striking range (Figure 5E). *M. messor* displayed a high level of tactile sensitivity to stimuli on the water surface and was recorded attempting to capture anything within range of its chelipeds. The crab was observed capturing actively moving fish in its chelipeds retaining the prey in a vice like grip until all movement had ceased (Figure 5F). Sequential prey-localizing and fishing behavior in the flood tide were recorded during all observations during the study (Figure 5D-F). *M. messor* specimens were witnessed congregating on the trunks and branches of *A. marina* at a height consistent with the water level during the peak of high tide when the riparian zone was totally flooded (Figure 4A).

A general overview about the relationship between flood tide, prey-localizing and fishing behavior and the main species observed is illustrated in Figure 6. Which documents in the first instance (Figure 6A) of the low tide that most specimens of *M. messor* are absent or hidden from view. However once flood tide begins (Figure 6B) the population of *M. messor* move out from the other crabs' burrows and adopt a prey-localizing behavior. Once shoals of *A. d. dispar* start to invade the intertidal zone *M. messor* adopt a fishing stance (Figure 6C), as water levels rise *M. messor* starts active fishing behavior which is accompanied by *E. orientalis* moving out of its burrows to begin a predatory hunt.

Observed trophic relationships with *M. messor*

As the flood tide began to ingress, several specimens of *M. messor* were observed holding *A. d. dispar* in their chelipeds (Figure 5B). Some individuals of *M. messor* were recorded with *P. khori* clasped in their chelipeds (Figure 5C) and some with small specimens of *M.messor* demonstrating cannibalistic behavior. The purple crab *E. orientalis* was recorded prey-localizing and preying on *M. messor* once the flooding tide was underway (Figure 3G).

Pneumatophore-borne vibrations and prey-localizing

Experiments to evaluate *M. messor* response to pneumatophore-borne vibrations showed that in >93% of the replicate specimens could locate the exact pneumatophore being stimulated (Figure 4B). Interestingly, some replicates recorded an accumulation of specimens identifying the pneumatophore-borne vibrations. However, when a group was present, only the largest specimen reached the vibration source (Figure 7). When large specimens with red chelae was present the other individuals avoid approaching the vibration source even though the stimuli had been recognized. This priority in capture the available food and the distance that was always maintained between smaller and larger individuals is highlighting the intraspecific competition and a hierarchy relation within the population of this species (Figure 7A-D). The high percentage response from *M. messor* revealed the crab is equipped with acute tactile sensitivity awareness which effectively identified pneumatophore movements as indicators of active prey. In addition, the use of a piece of wood to create the vibration means that olfactory and visual cues can be excluded as triggers in prey-localization.

This experiment suggests a direct trophic relation of *M. messor* with the fish *A. d. dispar*, as all observations in the study recorded shoals of *A. d. dispar* producing vibrations as they accessed the mangrove channels during the start of the tidal influx (Figure 3B). Suggesting also a direct relation of the fishing behavior establishment with the high frequency of *A. d. dispar* and related to the daily displacement of *M. messor* during the tidal influx.

DISCUSSION

Trophic relationships related to the fishing and prey-localizing behavior

The trophic relationship observed in this study identified a unique trait associated with *M. messor* as the crab is generally considered an opportunist detritivore, herbivore and omnivore but not an active predator (El-Sayed et al., 2000). Indeed, the results of this study highlights that the prey-localizing and fishing predatory behaviours are not just opportunistic behaviours of few specimens but a stablished pattenr for the entire population. A special condition not recorded for other Grapsid crabs (Fratini et al., 2000; Linton and Greenaway, 2007; Poon et al., 2010; Lee, 2015). *M. messor* was observed predating not only on *A. d. dispar* but also on the shrimp *P. khori* and smaller *M. messor* demonstrating that the crab is more of a generalist predator rather than a specialist (El-Sayed et al., 2000; Walton et al., 2014). It is possible, a genetic trait has dominated this specific population of *M. messor* to evolve from opportunistic foragers to generalist hunters/fishers. It is important to highlight that this an important record of a terrestrial crab performing in a predatory manner over a vertebrate.

Another inter-linked trophic relationship was that of the purple crab *E. orientalis* which actively hunted *M. messor*. Species at the genus *Eurycarcinus* are recognized predators of other crab species in mangrove environments (Dahdouh-Guebas *et al.*, 1999; Fratini *et al.*, 2000) and apparently this is the case of *E. orientalis* in the studied arid mangrove. Possibly *E. orientalis* is not an exclusive predator of *M. messor* however the availability and abundance of the prey turned these species closely trophic-related (prey-predator). The fact that *E. orientalis* emerged from its burrows after a significant layer of water had flooded the intertidal zone, is probably related to its gill adaptations in avoiding desiccation. But certainly, the presence of a predator underwater is a stimulus for a mass displacement of *M. messor* climbing the pneumatophores. This trophic connection between *A. d. dispar*, *M. messor* and *E. orientalis* is supported by nitrogen isotope δ 15N analysis (see Walton et al., 2014). The high densities of *P. khori* along the fringe of the riparian zone (Figure 3D) initially suggested a direct trophic web relation with *A. d. dispar* and *M. messor* as the species share a specific habitual niche (Figure 3D). However, isotope analysis revealed that *P. khori* is not a main prey item for *A. d. dispar* or *M. messor,* as no correlated δ 15N isotope values were reported (see Al-Maslamani *et al.*, 2013; Walton *et al.*, 2014). Although, it may be that the trophic relation between *P. khori* and *M.messor* and other species in this riparian habitat is accounted for at the planktonic stages. As the endemic shrimp is described as a plankton feeder (Al-Maslamani et al. 2013) and a large constituent of the *A. d. dispar* diet is also plankton (Keivany and Ghorbani 2012).

An interesting observation in this study was the social hierarchy within *M. messor,* whereby large *alpha* specimens had priority in capturing prey, (Figure 7) and with smaller individuals even allowing larger specimens primacy in locating vibrations. The smaller crabs (M1 and M3 in Figure 7) were visibly avoiding any inter-species competition. Similar behavior has been reported in other grapsid species (Nara et al., 2006) but not for *M. messor*. The observed cannibalism of smaller *M. messor* by the larger *alphas* highlights the voracity of this hierarchical social standing (El-Sayed et al., 2000; Walton et al., 2014). In addition, the red chelae described for this species (Holthuis, 1977; Naderloo, 2011) was only observed in large specimens and could be related to the individuals hierarchical position. Undeniably, more behavioral questions related to this unique mangrove habitat and its associated inhabitants have been raised. Particularly in the population dynamics of this crab, the correlation of its color patterns and the diet composition in relation to hierarchical position. Furthermore, *M. messor* occurs in different regions and habitats of the Gulf and Indian ocean (Naderloo, 2017) and is invasive in Hawaii (Paulay, 2007) and behavioral studies comparing this species in different regions may highlight what is characteristic of the species and what is regional adaptations.

Evolutionary considerations about the Fishing and prey-localizing behaviors

The extremes in salinity and temperature experienced in the western Arabian Gulf during the summer months have been comprehensively documented, typifying this marine region as an extreme hot environment (Riegl & Purkis, 2012; Ibrahim Al-Maslamani *et al.*, 2015; Giraldes *et al.*, 2016; Camp *et al.*, 2018). However, the conditions recorded in the peripheral zone of this mangrove ecosystem is beyond the extreme hot and saline conditions previously recorded, and the adaptations for surviving these conditions are yet to be described. Species such as *P. khori* and *A. d. dispar* not only survive in these water conditions but flourish. It was recorded in this study that those species flourish including in peripheral areas in the mangrove with water temperature >49 ^{o}C and salinity 75; an amazing evolutionary adaptation to survive in a very extreme hot ecosystem. This high density of *P. khori,* endemic to the studied ecosystem (De Grave and Al-Maslamani, 2006; Al-Maslamani et al., 2013), suggests that this arid mangrove is indeed an ancient and isolated well-established extreme hot ecosystem. An ancient and isolated characteristic that is supported by the presence of endemic gastropod species such as *Pirenella conica* (Blainville, 1829), *Clypeomorus bifasciata persica* (Houbrick, 1985), *Echinolittorina arabica* (El Assal, 1990), *Mitrella blanda* (Sowerby, 1844), and *Priotrochus kotschyi* (Philippi, 1849), indigenous to the western Arabian Gulf (Al-Maslamani *et al.*, 2015) and commonly observed in the studied mangrove (BWG pers. observ.). Fossil records indicate that the speciation of these gastropods took place some 6000 years ago when extreme saline lakes dominated the region (Houbrick, 1985; Reid, Dyal and Williams, 2010; Stewart et al., 2011; Williams et al., 2011; Al-Maslamani et al., 2015). The presence of an ecosystem with endemic species which evolved under these arid conditions presents evidence to support that the current mangrove ecosystem has existed since this geological period. Therefore, the interspecific relation of the species associated to the recorded behaviors in this mangrove ecosystem, maybe have been undergoing a process of evolutionary adaptations since this geological epoch. Forcing evolutionary interspecific relations with the only few component species adapted to survive in this very extreme temperature environment. In other words, the unique fishing behavior and the pneumatophore-borne vibration for prey-localizing which is demonstrated by *M. messor* may have developed out of necessity during an aeon of isolation within a very extreme environment. Where an opportunist omnivore species became an active predator.

The present study demonstrates the high vibration sensitivity of *M. messor* for prey-localizing. An use of substrate-borne vibration that is intensively used for several arthropods (Brownell and Farley, 1979; Bell et al., 1991; Christy, 1991; Hill, 2001; Koga et al., 2001) including for prey-localizing. The present study also demonstrates the relation of different feeding behavior and prey-localizing with the natural daily displacement of *M. messor* following the water level according with the tidal cycle. A behavioral displacement within the Grapsoid crabs phylogeny (Lee, 2015), which is present in several intertidal crabs in a convergent evolution of tree climbers in mangrove ecosystems (Fratini *et al.*, 2005). In the arid mangroves of Qatar in a habitat dominated by inter-connected pneumatophore webs it would appear that these vibration sensors have been utilized out of necessity as prey-localization tools. In other words, the evolved fishing behavior of *M. messor* may be considered as a higher complexity behavior of the prey-localizing behavior; and the prey-localizing behavior a higher complexity of the foraging behavior reported for the other omnivorous Grapsoid crabs (Fratini et al., 2000; Linton and Greenaway, 2007; Poon et al., 2010; Lee, 2015). A fishing and prey-localizing behavior that are consequence of tidal related displacement of tree climber crabs and it vibration sensitivity skill in an habitat with a pneumatophore web (Abdel-Razik, 1991; Al-Khayat and Jones, 1999; Riegl and Purkis, 2012; Al-Maslamani et al., 2013; Walton et al., 2014). A phenotypic behavior related to the arid mangrove environment plus the phylogenetic characteristics inherited by *M. messor.*

The large abundance of it primary prey resource *A. d. dispar* certainly is another contributing environmental factor in this predatory evolutionary adaptations of *M. messor*. The daily feeding runs by the fish on the flooding tide reinforcing the importance of the crabs early positioning on the pneumatophores prior to water influx. These intertidal feeding forays by fish are a common phenomenon in mangroves worldwide and also influence the behavior of associated predators (Robertson and Duke, 1990; Krumme, 2004). However, in this case, the small body mass of *A. d. dispar* permits it to swim in shoals in extremely shallow water, thereby producing vibrations which are transferred through the pneumatophores which act as stimuli for the highly tactile sensitive *M. messor*. The experiment performed during this study demonstrated that *M. messor* were able to locate a single pneumatophore stimulated vibration which was created to mimic the disturbance produced by *A. d. dispar*. Suggesting a direct prey-predator linked trophic relationship (Abrams, 2000). A similar prey-predator association has been described for other grapsoid crabs in other regions (Sheaves and Molony, 2000) but in this case the behavior is based on the *Avicennia marina* pneumatophore web. In addition, the opportunist generalist diet of the tree climber crab supports the theory of a direct evolutionary relation may have occurred as a result of the high abundance of *A. d. dispar* in the intertidal zone. The large abundance of *A. d. dispar* and *M. messor* recorded in this study strongly suggest a direct and successful trophic relation between them and the predatory behavior described in this study certainly is related to the dominance of these species. However, further research would be necessary to assess if the fishing behavior is a genetically evolved characteristic of a specific local population. Particularly as this brachyuran crab species is not exclusive to the mangroves but occurs in other habitats within the Arabian Gulf (Naderloo, 2011).

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Figure 1. Map of the survey sites at Al-Khor and Al-Dhakira, Qatar. Highlighting the mangrove areas; the salt marshes and high densities of the mangrove tree *Avicennia marina;* and the entrance of the channels at the studied riparian zone.

Figure 2. Images of the studied mangrove, with (A) the entrance of the channels in the open-water areas near the sea; (B) the end of the channels in the semi-confined-waters areas in the peripheral mangrove zone, near the salt marshes; and the studied riparian zone (C) in open-water areas and (D) the semi-confined-waters areas.

Figure 3. Images of observation within the studied mangrove; (A) the riparian zone dividing the intertidal zone above and the subtidal zone in flood. With shoals of *A.d.dispar* invading the intertidal zone (B) with a shallow layer of water < 4cm and (C) with a higher water level > 5cm ; and in the subtidal zone during the low tide (D) among the shrimp *P.khori* and (E) a shoal in shallow tide pools. Also, the illustration of *E. orientalis* within the flooded intertidal zone foraging/prey-localizing (M) with a vivid color and (N) a pale colored specimen after the capture of *M. messor* (arrow pointing the prey).

Figure 4. Ecological data; (A) the percentage of specimens of *Metopograpsus messor* (hiding in cavities, walking in the bottom, climbing the pneumatophores and climbing the tree), during the low tide, the flood tide (in the start) and after raise some centimeter (flooding the intertidal) and the high tide (with the pneumatophores totally flooded); (B) the percentage of times that *M. messor* identified or not identified the vibration stimuli in the pneumatophore.

Figure 5 Images of the two observed behaviors displayed by *Metopograpsus messor*: the foraging/prey-localizing behavior at the start of the flood tide with (A) the specimens concentrated in the riparian zone (B) after the capture of a fish *A.d.dispar* and (C) a shrimp *P.khori*. The fishing behavior on the flood tide after a heightened water level with (D) the specimens concentrated in the riparian zone (E) a specimen in the "fishing position" and (E) after the capture of a fish.

Figure 6 Relations linkage with the fishing behaviour displayed by *Metopograpsus messor* on the flood tide; with the observed position of each species: *M. messor* in the foraging/prey-localizing and fishing behaviour; *A. d. dispar; E. orientalis;* and *P.khori*. (A) in the low tide; (B) at the beginning of the flood tide with just a small layer of water; (C) in the sequential flood tide progression.

Figure 7. Images in sequential moments A, B, C and D, illustrating the "knocking experiment" to evaluate the "vibration sensibility", when using a wooden stick as stimuli [St.] and selecting a single pneumatophore [Pn], vibrations were created simulating a fish with a specific knocking-spot [KS]. In the first moment (A) four *Metapograpsus messor* [M1-4] were in the visual field near the knocking spot; in the second moment (B) the fifth specimen [M5] with a reddish chela appeared in the visual field; in the third moment (C) while specimens [M1-3] kept observing and the M4 moves far from the visual field, the fifth specimen [M5] arrives at approximately the knocking spot; in the fourth moment (D) the reddish chela [M5] reach the knocking-spot and try to catch the stick while two others [M1 and M3] carefully approximate.