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

3 Bruno Welter Giraldes^{1*}, Mark Chatting¹ and David Smyth²

4
5 ¹ Environmental Science Center (ESC), Qatar University (QA), Doha - Qatar.

6 ² School of Natural and Built Environment, Queens University, Belfast, United Kingdom

7
8 *Corresponding author; E-mail: bweltermgiraldes@qu.edu.qa

9
10 **Abstract** This study presents the first documented observations of a brachyuran crab's proactive
11 fishing behaviour in conjunction with mangrove pneumatophores which are employed as prey-
12 localization devices. All ecological data were recorded in situ using simple behavioural
13 observations, visual census and field experiments. Field experiments were based on stimulus-
14 response and ecological surveys on random displacement. Assemblages of *Metopograpsus*
15 *messor* were observed daily performing a foraging/predatory tide-related cyclic behaviour
16 pattern in an arid mangrove ecosystem which experiences challenging environmental conditions.
17 Prey-localizing behaviour was observed during the flood tide when pneumatophore-borne
18 vibrations were used to identify potential prey. The prey simulation field experiment (where a
19 single pneumatophore was stimulated by knocking) showed that in >93% of instances a crab
20 approached the exact pneumatophore being stimulated. As water levels increased during the tidal
21 cycle *M. messor* was observed climbing pneumatophores. The crabs anchored themselves to the
22 pneumatophore just above the water level with their pereopods. The chelipeds were positioned
23 in a pincher-like trap, and remained in a 'capture-position' waiting for prey to move within
24 striking range. This characteristic fishing behaviour was performed daily by a population of *M.*
25 *messor*. Ecological observations suggest that both these predatory behaviours are associated with
26 the fish *Aphanius dispar dispar* in a direct prey–predator relation. Evidence suggests that these
27 fishing behaviours evolved due to characteristics within the *M. messor* phylogeny (foraging in
28 intertidal zones; daily displacement following tidal levels; high sensitivity to vibrations; and an
29 opportunist diet) and its associated environment (presence of pneumatophores and high
30 availability of a fish resource).

31

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

33

34 INTRODUCTION

35 The mangrove habitat of the western Arabian Gulf is a biologically extreme environment
36 typified by; a lack of freshwater input, extreme high-end temperature variations 35 to 50 °C and
37 salinities which can fluctuate between 35 and 65 ppt (Al-Maslamani *et al.*, 2013). Due this
38 extreme arid condition those mangrove forests can be considered ecologically unique. An
39 extreme ecosystem where the tree assemblages consist of only one species *Avicennia marina*
40 (Forssk.) Vierh. which forms the entire ecosystem (Abdel-Razik, 1991; Al-Khayat and Jones,
41 1999; Riegl and Purkis, 2012; Al-Maslamani *et al.*, 2013; Walton *et al.*, 2014). The arid
42 mangrove of the west coast of the Arabian Gulf can be considered as an ancient and well
43 established ecosystem, which is supported by a suite of endemic species confined to the specific
44 demographics and conditions created by *A. marina* (De Grave & Al-Maslamani, 2006; Al-
45 Maslamani *et al.*, 2013; Al-Maslamani *et al.*, 2015; Naderloo, 2017).

46 One of the most prevalent species associated with this mangrove environment is the tree climber
47 crab *Metopograpsus messor* (Forskål, 1775) a medium-sized crab native to the western Indian
48 Ocean and the Arabian/Persian Gulf (Naderloo, 2011). A Grapsidae crab which belongs to a
49 group of terrestrial tree climbers that are reported as occupying herbivores, detritivores and
50 omnivores niches within different trophic chains. It is considered a habitat-generalist and is
51 common in a variety of coastal habitats including muddy substrates, rocky shores and mangroves
52 (El-Sayed *et al.*, 2000; Linton and Greenaway, 2007; Poon *et al.*, 2010; Naderloo, 2011; Lee,
53 2015). The species is easily identifiable with naked eyes by its dark colored dashes and some
54 specimens with red chelae (Holthuis, 1977; Naderloo, 2011). The only species with those
55 characteristics recorded in the studied site (Naderloo, 2017).

56 The decapod species represent an integral component within the majority of marine trophic
57 chains occupying different roles throughout its length, including as predators (Boudreau and
58 Worm, 2012). Indeed, predatory behavior in decapods is commonly identified as active foraging,
59 however there are no recorded observations of crabs presenting a proactive fishing behavior. In
60 addition, accounts exist of terrestrial decapods using substrate-borne vibrations in predator
61 avoidance and courtship (Christy, 1991; Hill, 2001; Koga *et al.*, 2001). However, the use of

62 substrate-borne vibrations for prey-localization during foraging and fishing has not been
63 documented (Brownell and Farley, 1979; Bell et al., 1991).

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

69

70 MATERIAL AND METHODS

71 Study area

72 Observations and records took place *in-situ* within the mangrove assemblages at Al-Khor (25°
73 41' 29.2" N – 51° 33' 15.7" E) and Al-Dhakira (25° 45' 01.5" N – 51° 32' 21.7" E) in the east
74 coast of Qatar (Figure 1). The mangrove environment at these two sites was characterized by a
75 riparian ecosystem formed as a result of hydrodynamic sculpting due to ebbing and flooding
76 tides. The riparian corridors were fringed by pneumatophores of *A. marina* trees which grew
77 along the boundaries of the channels (Figure 2). The study sites were visited every two months
78 over a two-year period.

79

80 Fishing behavior and prey-localizing behavior

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

92

93 **Prey-localization experiment**

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

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

108

109 **Ecological relations and implications with the described behaviors**

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

122 All specimens observed were recorded using a timed-search visual census methodology, which
123 incorporated walking in the intertidal zones and snorkeling in the channels for the underwater

124 surveys. For most species the index was the frequency, where during the first 10 minutes the
125 observed species were recorded in terms of presence or absence and were considered frequent.
126 Thereafter only species not previously observed were recorded and considered as occasional. It
127 was presented in this study only frequent species. *M. messor* beyond the frequency it was
128 estimated the abundance, where all specimens were counted during the first 10 minutes. A total
129 of 40 x 1-hr surveys were undertaken.

130

131 **RESULTS**

132 **Mangrove Channels – Species composition and environmental characteristics**

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

139 The main component species observed in the riparian zone during the flood tide are presented in
140 Table 1. The crab *M. messor* was frequent in all intertidal zone with > 100 specimens recorded in
141 the first 10 minutes in all surveys. The small fish *Aphanius dispar dispar* (Rüppell, 1829) was
142 dominant underwater within the subtidal zone (Figure 3B-E) and was observed in all channels in
143 open-water areas and in semi-confined-waters areas, including in tidal pools. It was recorded
144 invading the intertidal riparian zone during the start of the tidal influx when water levels were <
145 4cm (Figure 3B) and dominating the intertidal zone throughout the flooding tide (Figure 3C).
146 Among decapods in the intertidal zone the purple crab *Eurycarcinus orientalis* A.Milne-
147 Edwards, 1867 was frequent in the riparian zone of the open-water mangrove areas and
148 occasional in the semi-confined-waters areas, particularly prevalent in flooded areas of >5cm
149 (Figure 3F, G). The shrimp *Palaemon khori* De Grave & Al-Maslamani, 2006 was observed in
150 high-density patches accommodating large assemblages in the riparian zone in all channels in
151 open-water areas and in semi-confined-waters areas, including in tidal pools, (Figure 3D).
152 However, its densities decreased in the intertidal riparian zone.

153

154 **Fishing and prey-localizing behavior**

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

160 During the low tide *M. messor* was virtually absent in the riparian zone, hidden in
161 burrows of other crabs in the substrate (Figure 4A). Prior to the flooding tide *M. messor* was
162 observed moving out of the burrows along the riparian zone to start prey-localizing (Figure 5A);
163 like a bioindicator indicating the start of the flood tide even before the water raise became
164 visible. Crabs within the riparian zone initially displayed prey-localizing (foraging) behavior
165 (Figure 5A) when the water is just in a small layer invading the mangrove. But as the tide rises a
166 bit more *M. messor* starts to climb *A. marina* pneumatophores. They positioned themselves
167 above the surface of the water and adopted a readiness stance to commence fishing (Figure 5D).
168 This was identified by the crabs anchoring themselves to the roots with their pereiopods and
169 positioning their chelipeds in a pincher-like trap, remaining motionless and waiting for prey to
170 move within striking range (Figure 5E). *M. messor* displayed a high level of tactile sensitivity to
171 stimuli on the water surface and was recorded attempting to capture anything within range of its
172 chelipeds. The crab was observed capturing actively moving fish in its chelipeds retaining the
173 prey in a vice like grip until all movement had ceased (Figure 5F). Sequential prey-localizing and
174 fishing behavior in the flood tide were recorded during all observations during the study (Figure
175 5D-F). *M. messor* specimens were witnessed congregating on the trunks and branches of *A.*
176 *marina* at a height consistent with the water level during the peak of high tide when the riparian
177 zone was totally flooded (Figure 4A).

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

186 **Observed trophic relationships with *M. messor***

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

192
193 **Pneumatophore-borne vibrations and prey-localizing**

194 Experiments to evaluate *M. messor* response to pneumatophore-borne vibrations showed that in
195 >93% of the replicate specimens could locate the exact pneumatophore being stimulated (Figure
196 4B). Interestingly, some replicates recorded an accumulation of specimens identifying the
197 pneumatophore-borne vibrations. However, when a group was present, only the largest specimen
198 reached the vibration source (Figure 7). When large specimens with red chelae was present the
199 other individuals avoid approaching the vibration source even though the stimuli had been
200 recognized. This priority in capture the available food and the distance that was always
201 maintained between smaller and larger individuals is highlighting the intraspecific competition
202 and a hierarchy relation within the population of this species (Figure 7A-D). The high percentage
203 response from *M. messor* revealed the crab is equipped with acute tactile sensitivity awareness
204 which effectively identified pneumatophore movements as indicators of active prey. In addition,
205 the use of a piece of wood to create the vibration means that olfactory and visual cues can be
206 excluded as triggers in prey-localization.

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

212
213 **DISCUSSION**

214 **Trophic relationships related to the fishing and prey-localizing behavior**

215 The trophic relationship observed in this study identified a unique trait associated with *M.*
216 *messor* as the crab is generally considered an opportunist detritivore, herbivore and omnivore but

217 not an active predator (El-Sayed et al., 2000). Indeed, the results of this study highlights that the
218 prey-localizing and fishing predatory behaviours are not just opportunistic behaviours of few
219 specimens but a stablished pattenr for the entire population. A special condition not recorded for
220 other Grapsid crabs (Fratini et al., 2000; Linton and Greenaway, 2007; Poon et al., 2010; Lee,
221 2015). *M. messor* was observed predating not only on *A. d. dispar* but also on the shrimp *P.*
222 *khori* and smaller *M. messor* demonstrating that the crab is more of a generalist predator rather
223 than a specialist (El-Sayed et al., 2000; Walton et al., 2014). It is possible, a genetic trait has
224 dominated this specific population of *M. messor* to evolve from opportunistic foragers to
225 generalist hunters/fishers. It is important to highlight that this an important record of a terrestrial
226 crab performing in a predatory manner over a vertebrate.

227 Another inter-linked trophic relationship was that of the purple crab *E. orientalis* which
228 actively hunted *M. messor*. Species at the genus *Eurycarcinus* are recognized predators of other
229 crab species in mangrove environments (Dahdouh-Guebas *et al.*, 1999; Fratini *et al.*, 2000) and
230 apparently this is the case of *E. orientalis* in the studied arid mangrove. Possibly *E. orientalis* is
231 not an exclusive predator of *M. messor* however the availability and abundance of the prey
232 turned these species closely trophic-related (prey-predator). The fact that *E. orientalis* emerged
233 from its burrows after a significant layer of water had flooded the intertidal zone, is probably
234 related to its gill adaptations in avoiding desiccation. But certainly, the presence of a predator
235 underwater is a stimulus for a mass displacement of *M. messor* climbing the pneumatophores.
236 This trophic connection between *A. d. dispar*, *M. messor* and *E. orientalis* is supported by
237 nitrogen isotope $\delta^{15}\text{N}$ analysis (see Walton et al., 2014). The high densities of *P. khori* along
238 the fringe of the riparian zone (Figure 3D) initially suggested a direct trophic web relation with
239 *A. d. dispar* and *M. messor* as the species share a specific habitual niche (Figure 3D). However,
240 isotope analysis revealed that *P. khori* is not a main prey item for *A. d. dispar* or *M. messor*, as
241 no correlated $\delta^{15}\text{N}$ isotope values were reported (see Al-Maslamani *et al.*, 2013; Walton *et al.*,
242 2014). Although, it may be that the trophic relation between *P. khori* and *M.messor* and other
243 species in this riparian habitat is accounted for at the planktonic stages. As the endemic shrimp is
244 described as a plankton feeder (Al-Maslamani et al. 2013) and a large constituent of the *A. d.*
245 *dispar* diet is also plankton (Keivany and Ghorbani 2012).

246 An interesting observation in this study was the social hierarchy within *M. messor*,
247 whereby large *alpha* specimens had priority in capturing prey, (Figure 7) and with smaller

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

261

262 **Evolutionary considerations about the Fishing and prey-localizing behaviors**

263 The extremes in salinity and temperature experienced in the western Arabian Gulf during the
264 summer months have been comprehensively documented, typifying this marine region as an
265 extreme hot environment (Riegl & Purkis, 2012; Ibrahim Al-Maslamani *et al.*, 2015; Giraldes *et*
266 *al.*, 2016; Camp *et al.*, 2018). However, the conditions recorded in the peripheral zone of this
267 mangrove ecosystem is beyond the extreme hot and saline conditions previously recorded, and
268 the adaptations for surviving these conditions are yet to be described. Species such as *P. khor*
269 and *A. d. dispar* not only survive in these water conditions but flourish. It was recorded in this
270 study that those species flourish including in peripheral areas in the mangrove with water
271 temperature >49 °C and salinity 75; an amazing evolutionary adaptation to survive in a very
272 extreme hot ecosystem. This high density of *P. khor*, endemic to the studied ecosystem (De
273 Grave and Al-Maslamani, 2006; Al-Maslamani et al., 2013), suggests that this arid mangrove is
274 indeed an ancient and isolated well-established extreme hot ecosystem. An ancient and isolated
275 characteristic that is supported by the presence of endemic gastropod species such as *Pirenella*
276 *conica* (Blainville, 1829), *Clypeomorus bifasciata persica* (Houbrick, 1985), *Echinolittorina*
277 *arabica* (El Assal, 1990), *Mitrella blanda* (Sowerby, 1844), and *Priotrochus kotschy* (Philippi,
278 1849), indigenous to the western Arabian Gulf (Al-Maslamani *et al.*, 2015) and commonly

279 observed in the studied mangrove (BWG pers. observ.). Fossil records indicate that the
280 speciation of these gastropods took place some 6000 years ago when extreme saline lakes
281 dominated the region (Houbrick, 1985; Reid, Dyal and Williams, 2010; Stewart et al., 2011;
282 Williams et al., 2011; Al-Maslamani et al., 2015). The presence of an ecosystem with endemic
283 species which evolved under these arid conditions presents evidence to support that the current
284 mangrove ecosystem has existed since this geological period. Therefore, the interspecific relation
285 of the species associated to the recorded behaviors in this mangrove ecosystem, maybe have
286 been undergoing a process of evolutionary adaptations since this geological epoch. Forcing
287 evolutionary interspecific relations with the only few component species adapted to survive in
288 this very extreme temperature environment. In other words, the unique fishing behavior and the
289 pneumatophore-borne vibration for prey-localizing which is demonstrated by *M. messor* may
290 have developed out of necessity during an aeon of isolation within a very extreme environment.
291 Where an opportunist omnivore species became an active predator.

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

309 phenotypic behavior related to the arid mangrove environment plus the phylogenetic
310 characteristics inherited by *M. messor*.

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

333

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340

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

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

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

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

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

473 **Figure 6** Relations linkage with the fishing behaviour displayed by *Metopograpsus messor* on
474 the flood tide; with the observed position of each species: *M. messor* in the foraging/prey-

475 localizing and fishing behaviour; *A. d. dispar*; *E. orientalis*; and *P.khori*. (A) in the low tide; (B)
476 at the beginning of the flood tide with just a small layer of water; (C) in the sequential flood tide
477 progression.

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

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