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1 Snail leaps and bounds: Drivers of the diel movement pattern of a large invertebrate, the
2 Caribbean queen conch, in a marginal inshore habitat.

3

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23 **Abstract**

24

25 Understanding the relationship between animals' movement and their environment is crucial
26 for fisheries and species management. There is currently a lack of detailed information about
27 the movement of slow moving benthic species, especially for species of ecological or
28 commercial importance. Here we document the relationship between diel movement and
29 environmental parameters in a groundwater-fed coastal inlet for the queen conch (*Lobatus*
30 *gigas*, Linnaeus 1758), an important fisheries resources of the Caribbean region, using 3D
31 accelerometers and video cameras. Our results show immature queen conch ($n=9$) spend most
32 of their active time grazing, exhibiting two main distinct movements we characterise as a
33 'leap' and a 'drift' mostly used to access new foraging resources. When overturned, they
34 'flip', producing a movement with the highest acceleration recorded in order to limit
35 exposure and restore normal position. Movement patterns appear to be significantly affected
36 by the oxygen concentration in bottom water, with lower activity during low-oxygen levels in
37 the morning (probability of 0.75 to observe zero movement per hour) and maximum activity
38 during the afternoon when oxygen concentration is at its maximum (probability of 0.80 to
39 observe >10 movements per hour). Salinity and temperature had little effect on movement
40 patterns. Our results confirm that highly variable marginal habitats like groundwater-fed
41 inlets are suitable for juvenile conch growth and should be included in efficient conservation
42 plans.

43

44 **Key words:** movement recognition model, biologging, movement ecology, foraging
45 behaviour, marine ecology, endangered species, fisheries.

46 **Introduction**

47

48 Understanding the underlying behavioural reasons that explain why an animal moves is the
49 main challenge in movement ecology. Within a habitat, animal movement is driven by the
50 interaction of physiology, motion capacity, navigational capacity and environmental
51 parameters (Turchin 1998, Nathan 2008). By impacting the ability of an animal to move,
52 habitat quality is known to constrain species survival, reproduction, and population density as
53 an animal has to move to feed, reproduce, and avoid predators or other unfavourable
54 conditions (Turchin 1998, Nathan 2008). Large terrestrial and marine populations usually
55 thrive in high quality habitats, while in comparison, marginal habitats (i.e. low-quality
56 habitats) tend to be inhabited by smaller populations, and often require adaptation to specific
57 local conditions to be able to persist over time (Bridle and Vines 2007, Kawecki 2008).
58 However, marginal habitats can also offer protection against predators (Heithaus et al. 2007,
59 Heithaus and Dill 2002, Bonnot et al. 2016), dramatic stochastic environmental disturbances
60 (Crawford et al. 2018, Vrdoljak and Hart 2007) and can be used by animals to lower
61 interindividual competition (Duarte et al. 2017, Larson 1980).

62 While the movement pattern and behaviour of avian and terrestrial species in a range
63 of habitats is well studied (Milner-Gulland et al. 2011, Viswanathan 2011), information about
64 marine species remains comparatively more limited. The majority of the work on marine
65 species focuses on mid to long-range movement of fast-moving birds, mammals, or fishes
66 (Hussey et al. 2015). Comparatively the movement ecology of slow-moving benthic species
67 such as gastropods, is poorly understood despite some of these species being of high
68 ecological and commercial importance (Stoner et al. 1995, Leiva and Castilla 2001). Few
69 intertidal species (e.g. Lissmann 1945, Chelazzi et al. 1988, Little 1989, Rilov et al. 2005)
70 and subtidal species (e.g. Coates et al. 2013, Jolivet et al. 2015) have been studied. Obtaining

71 insights on the movement of slow moving benthic species is especially important in the
72 context of fisheries management and climate change, mainly because it helps to identify
73 important habitats involved in the different stages of a species life cycle (Grüss et al. 2011,
74 Ogburn et al. 2017). Determining how movement data can be used to support conservation
75 and management is a current key question in marine movement ecology (Hays et al. 2016).

76 One such slow moving marine gastropod, the queen conch (*Lobatus gigas*, Bouchet et
77 al. 2011) is one of the most important fishery resources in the Caribbean region. As a result,
78 fished populations have been in decline for more than two decades (Theile 2001, Acosta
79 2006, Stoner et al. 2012a). This species is considered endangered and has been registered
80 under Appendix II of the Convention on International Trade in Endangered Species of Wild
81 Fauna and Flora (CITES) since 1992 (Acosta 2006). Queen conch biology and ecology have
82 been extensively studied for decades (Randall 1964, Stoner 1989a, 1989b, Stoner et al. 1995,
83 2012b), including their home range (e.g. using acoustic telemetry, Glazer et al. 2003,
84 Delgado and Glazer 2007, Stieglitz and Dujon 2017). However relatively little is known
85 about their small-scale movement patterns, for which only short descriptions have been
86 provided, and without significant resolution to understand movement patterns in relation with
87 environmental drivers (Parker 1922).

88 In this study we established a library of small-scale queen conch movements using
89 video footage and recorded the corresponding acceleration signal with a three-dimensional
90 (3D) accelerometer. We then modelled the links between queen conch diel movement
91 patterns with potential environmental drivers (e.g. salinity, dissolved oxygen concentration,
92 temperature and time of day). We expected groundwater input to have an effect on dissolved
93 oxygen concentration which should also have an effect on queen conch diel movement
94 patterns. More specifically, based on the Stieglitz and Dujon (2017) preliminary study, we
95 hypothesised that queen conch exhibit lower activity when dissolved oxygen concentration is

96 low compared to periods of high oxygen concentration. Obtaining insights on queen conch
97 movement is especially important as this type of groundwater-fed marginal habitat (i.e.
98 estuarine coastal inlets) could provide an efficient refuge for near-shore populations and may
99 be able to contribute to an effective conservation management of this endangered and
100 socioeconomically highly valuable species (Stoner 2003, Grüss et al. 2011, Stieglitz and
101 Dujon 2017).

102

103 **Materials and methods**

104 **Study site**

105 Fieldwork was conducted in the coastal inlet of Xel-Ha (20.317° N, -87.358° E) on the west
106 coast of the Yucatan Peninsula (Mexico, Figure 1). The inlet was formed by karst dissolution
107 (Back et al. 1979, Stoessell et al. 1989) and is approximately 400 m long and 350 m wide
108 with a maximum depth of three meters (Stieglitz and Dujon 2017). The inlet is connected to
109 the Caribbean Sea by a 100-m wide channel. Xel-Ha receives considerable inputs of low-
110 salinity groundwater creating a permanent thermohaline stratification that can be easily
111 observed in the water column. In addition, the inlet is characterised by large diel variations in
112 concentrations of dissolved oxygen (Stoessell et al. 1989, Stieglitz and Dujon 2017). Bottom
113 substrates are mostly sandy, with small to large isolated rocks, bare sand, visible microalgal
114 mats or turtlegrass beds (*Thalassia testudium*, Stieglitz and Dujon 2017). A large population
115 of mostly juvenile queen conch inhabits the inlet (Valle-Esquivel 1998, Peel and Aldana
116 Aranda 2012). Xel-Ha is a private tourist park, and this population is protected from fishing.

117 **Tagging and observation of movement**

118 Queen conch were tagged using a VEMCO prototype tri-dimensional accelerometer
119 (12 cm long, 35 g mass in air with battery) with a 10 Hz acquisition frequency. To minimise

120 animal disturbance, a diver carefully fixed the accelerometer onto the top of the apex of the
121 tagged individual in an arbitrary position using a plastic collar (typically behind the larger,
122 upfront row of spines), and without moving or removing the animal from its environment
123 (Figure 2). In addition, a small 5 cm long and 2 cm wide orange fishing float fixed at the
124 extremity of a ca 20 cm string was attached to the collar to visually help locating the animal
125 in the inlet. The total weight of the apparatus was <70 g in air thus of a negligible weight in
126 water when attached to a shell range of 0.5 to 1.5 kg (Stieglitz and Dujon 2017). All queen
127 conch resumed movement and foraging within 15 minutes after deploying the tag. In April
128 2011, four individuals (C1 to C4) were equipped with the accelerometer and continuous 3D
129 acceleration was recorded for approximately 48 hours for each animal, effectively recording a
130 cumulative time series over a duration of ca. 8 days (Table 1). In April 2012, five additional
131 queen conch were monitored for four to nine hours each (S1 to S3, J1 and J2, Table 1), and
132 their movements were concurrently recorded with two GoPro video cameras placed at
133 approximately 50 cm distance from the animal. Cameras were carefully moved and replaced
134 when the tagged conch was outside of the field of view or when camera memory was full. An
135 ethogram was then constructed based on visual examination of these video records. The video
136 records show no evidence of the tagged individuals attempting to remove their apparatus.
137 Similarly, based on the video footage and the movement of the float there was no evidence
138 that the individuals experienced strong currents (the float was almost always directly
139 vertically above the animal). The five April 2012 queen conch were a mix of immature
140 subadults (S1 to S3) and juveniles (J1 and J2, Table 1, Stoner et al. 2012, Boman et al. 2018).
141 We have no size measurement of the queen conch observed in April 2011 but we
142 nevertheless assume their day-to-day behaviour is similar to those observed in April 2012, as
143 they were representative of Xel-Ha population in this period (Table 1, Peel and Aldana
144 Aranda 2012, Stieglitz and Dujon 2017).

145 **Acceleration and movement analysis**

146 Acceleration time series were first carefully calibrated to take into account the position of the
147 device on the queen conch shells (see Supplementary Methods 1). Then the static component
148 of the acceleration time series (equal to 1 g) was removed by applying an order four low pass
149 Butterworth filter with a 4 Hz cut-off frequency on each acceleration axis (following Shepard
150 et al. 2008a). After filtering, the Overall Dynamic Body Acceleration (ODBA, expressed in
151 g), corresponding to the combined dynamic acceleration induced around the centre of an
152 animal's mass during a movement was calculated as (equation 1):

153
$$(1) ODBA (g) = \sqrt{a_x^2 + a_y^2 + a_z^2}$$

154 With a_x the calibrated and filtered acceleration on the surge (the front-back axis), a_y on the
155 sway axis (the left-right axis) and a_z on the heave axis (the vertical axis). The typical
156 accelerometer noise, most likely due to waves and manual calibration, was inferior to 0.01 g.
157 Therefore, the queen conch were considered moving when the ODBA was > 0.01 g during
158 >0.2 seconds and confirmed using video records (Figure 3).

159 All of the movements identified on the video records were classified as either 'leap',
160 'flip' or 'drift', and matched with their corresponding acceleration signal. We expected the
161 'flip' to be a relatively rare event. Therefore, to ensure we adequately captured this
162 movement type we manually overturned J2 and recorded the way that individual restored its
163 natural position ten times (Table 1). Manual overturning was performed at the very end of the
164 video recording session before carrying J2 to the laboratory for calibrating the accelerometer
165 axes. A suite of simple descriptors was subsequently calculated for each movement (Table 2).
166 These descriptors were then used to build a flexible discriminant linear model to
167 automatically classify the different movement types (R 'mde' package Hastie et al. 1994,
168 Hastie and Tibshirani 2013). Finally, this model was applied to the 48-hour time series data
169 recorded in April 2011 to classify the movements of the four individuals for which there were

170 no video recordings available. All calculations were performed in R software (Version 3.2.3,
171 R Development Core Team 2013).

172 **Relationship between queen conch movement and environmental parameters.**

173 To investigate if queen conch diel movement is influenced by ambient environmental
174 parameters, dissolved oxygen concentration, salinity and temperature at the sea floor of the
175 inlet were recorded at hourly intervals, using a pre-calibrated YSI multiprobe. The probe was
176 deployed within a few metres distance of the animal subjects. This data was obtained during
177 the April 2011 session for the animals C1 to C3, but not for C4 due to probe maintenance.

178 Movement data was first aggregated by calculating the number of movements
179 detected over a one-hour period. Then, logistic regression models were used to explore any
180 possible relationship between environmental parameters and queen conch movement (Zuur et
181 al. 2009). More specifically we linked the probability to observe 0, ≥ 1 , ≥ 10 and ≥ 25
182 movement per hour (termed as N_{mov} and representing 21 %, 79 %, 42 % and 20 % of the
183 cumulative videos duration respectively) to hourly measurements of salinity, temperature,
184 dissolved oxygen concentration and the time of day. Odds ratios were used to compare the
185 relative odds of the occurrence of the outcome of interest (here the different levels of N_{mov}).
186 If the odds ratio equals one, the exposure to an environmental parameter does not affect
187 movement, if <1 exposure is associated with a lower probability of occurrence of the
188 outcome, and if >1 exposure is associated with a higher probability of occurrence of the
189 outcome (see, Szumilas 2010). Throughout the manuscript all means are reported as (mean \pm
190 *sd*) except for the logistic regression results which are reported as (mean \pm *se*).

191 **Results**

192 **Description of movement types**

193 Three different types of movements were identified from the recorded video data and termed
194 as ‘leap’, ‘drift’ and ‘flip’ (Figure 3,4). Four different phases of the leaping movement can be
195 identified (see Figure 3a, 4a, Electronic supplement 1): From a resting position (L1) the
196 queen conch lifts the shell lip, (L2) using foot contraction the animal propels the shell
197 forward, (L3) the lip falls back on the sediment with gravity (L4). This movement is
198 expressed chiefly in changes of sway and surge. Typical maximum ODBA acceleration is
199 around 0.3 g and mean ODBA over a full movement cycle is 0.05 ± 0.03 g. Mean duration of
200 a leap movement is 2.4 ± 0.8 seconds.

201 The drift movement corresponds to small movements a queen conch makes to rotate
202 the shell to access new areas close by (Figure 3b, 4b, Electronic supplement 2). This
203 movement is performed in one step (D2) and can be either a left or right turn. It has low
204 acceleration values, with maximum ODBA values often <0.1 g (mean ODBA = 0.02 ± 0.01
205 g). Mean duration of a drifting movement is 2.1 ± 0.7 seconds.

206 Queen conch encountering a slope or an obstacle (e.g. a rock or another queen conch)
207 can sometimes lose their balance and their shell can turn upside down or fall on its side. The
208 aperture of the shell is then oriented sideward or toward the sea surface. To restore their
209 natural position, the queen conch flip their shell by first extruding their foot out of the shell
210 (F1) to take support on the sea floor. Then an abrupt contraction of the foot muscle results in
211 a rotation of the shell (F2, F3; Figure 3c, 4c, Electronic supplement 3). If the aperture is not
212 facing the sea floor after a first flip, the animal will repeat this movement until the shell is in
213 the correct position. The flip is the movement with the highest acceleration values observed,
214 with a recorded maximum ODBA greater than 1 g, a mean ODBA equal to 0.23 ± 0.09 g, and
215 a mean duration of 1.8 ± 0.7 seconds. Flips also produce the greatest recorded acceleration on

216 the heave axis. While ten of those flips were artificially induced by manually overturning J2
217 and orienting the aperture toward the sea surface, a natural overturn was recorded on video,
218 when an untagged queen conch on a rocky slope collided with the monitored animal.

219 Under certain conditions, queen conch bury themselves in the sediment, and buried
220 queen conch are sometimes observed in the inlet. Burying behaviour was not observed during
221 our recordings. Similarly, mating behaviour was not observed. These two behaviours are
222 likely to produce distinct acceleration patterns different to those observed here but are either
223 rare or confined to periods outside of the observation period and thus not included in the
224 ethogram.

225

226 **Building a statistical model for movement recognition**

227 The flexible discriminant model was built from a total of 463 movements from the 2012
228 video and accelerometer records (403 leaps, 50 drifts and 10 flips, Table 1, Figure 5). Five
229 descriptors ($\text{Mean}_{\text{ODBA}}$, Mean_{Z^2} , T , Mean_{Y^2} , Mean_{X^2}) allowed 95 % of movements to be
230 correctly identified. $\text{Mean}_{\text{ODBA}}$ alone allowed 89 % of movements to be correctly identified
231 because of the considerable differences in acceleration ranges between the different
232 movement types. Other descriptors did not significantly improve the model performance (<
233 0.01 % improvement). The 25 out of 463 (6%) misclassified movements are leaps predicted
234 as drifts (16 movements) and drifts predicted as leaps (nine movements, Figure 5).

235 **Application of movement recognition model**

236 The application of the model to the 48-hour time series data (without video recordings)
237 confirms queen conch predominantly perform leaps, which represents 90 to 95 % of the
238 recorded movements (Figure 6). Drifts represent between 5 to 10 % of total movements.
239 Video recordings confirmed that leaps and drifts are strongly related to grazing behaviour,
240 clearly identifiable by the movement of the proboscis at the surface of the sediment. Three
241 naturally produced flips were observed, all with a smaller maximum ODBA (0.34, 0.31 and
242 0.44 g) compared to the flips recorded by manually overturning the queen conch. This
243 suggests the natural overturns were not complete (e.g., if a queen conch slipped on the edge
244 of a rock or a slope). Incomplete turnover requires smaller movements to restore a standard
245 position.

246 **Relationship between queen conch movement and environmental parameters.**

247 Ambient dissolved oxygen concentration ranged from 3.2 mg L⁻¹ to 9.7 mg L⁻¹ (mean: 5.6 ±
248 1.3 mg L⁻¹) following a daily cycle with a minimum concentration in the early morning hours
249 and a maximum concentration in the middle of the afternoon, typical for stratified estuarine
250 conditions (Figure 6a). Bottom salinity ranged between 19 and 33 (mean: 24.5 ± 2.8),
251 following a tidal cycle (Figure 6b). Bottom temperature variations were small and ranged
252 between 25.5°C and 28.6 °C (mean: 26.8 ± 0.5 °C) (Figure 6c).

253 Overall, salinity and temperature had little effect on the number of movements
254 recorded per hour (Table 3). The models including salinity and temperature were not
255 significant while the model including the time of day were significant but with odd ratios
256 close to one (indicating little effect on the number of movements per hour). Dissolved oxygen
257 concentration was the environmental parameter explaining most of the queen conch activity
258 pattern with the highest odds ratio (Table 3). The probability to observe ≥1, ≥10 and ≥25
259 movements per hour increased with the dissolved oxygen concentration (odd ratios of 3.0, 1.8

260 and 1.2 respectively, Table 3, Figure 7). During late morning and early afternoon activity
261 increased until reaching a maximum around 4:00 pm when dissolved oxygen concentration is
262 the highest (Figure 6a). In parallel, the probability of observing no movement during a one-
263 hour period decreased significantly (odd ratio of 0.3) with increased dissolved oxygen
264 concentration. A reduction of activity (almost no movements) was observed around 6:00-7:00
265 am, corresponding to the ambient dissolved oxygen minimum and was associated with a
266 probability to observe no movement during a one-hour period close to 0.75 (Figure 6a, Figure
267 7).

268 **Discussion**

269 **Model performance**

270 Most queen conch daily activity is spent on grazing. Movement is mainly composed of leaps
271 interspaced with drifts. Flips are relatively rare occurrences. We showed that a simple model
272 can be trained to classify those movement types with high performance. Only 6 % of
273 movements were misclassified by the predictive model. Upon closer inspection, leap and drift
274 misclassifications were mainly due to a small rotation component (smaller than drifts) of the
275 shell during some leap movements. Video records show those misclassified movements are
276 clearly leaps occurring mostly on small local slopes, resulting in the distribution of the leap
277 descriptor to overlap with the distribution of the drift movement descriptors. The low error
278 rate of the model is acceptable and does not influence the ecological interpretation of queen
279 conch movement (both leaps and drifts are mostly used to graze). Overall, queen conch
280 movements are simple compared with those of animals like sharks, sea turtles, sea birds or
281 marine mammals (e.g. Shepard et al. 2008b, Wilson et al. 2008, Dujon et al. 2018) or even
282 other marine benthic invertebrates (e.g. Robson et al. 2012, Jolivet et al. 2015). This
283 simplicity allows models to be built that offer a very good representation of ‘day-to-day’
284 movement behaviours on the time scales of observation while more complex movement

285 patterns would require advanced signal processing tools such as wavelet analysis and similar
286 methods (e.g., Sakamoto et al. 2009, Whitney et al. 2010). Our simple method is easy to
287 implement and to extend to new field sites and organisms (for example one of the other
288 several species of fished gastropods or more broadly on large slow moving benthic marine
289 species, Leiva and Castilla 2001).

290 **3D accelerometry for studies of the movement ecology of marine snails**

291 The two main limiting factors of this work were (1) the memory capacity of the device,
292 which limited the recording time to 48 h with a 10 Hz acquisition frequency which does not
293 allow long term monitoring of queen conch; and (2) the need to recapture the queen conch at
294 the end of recording to download the data. Recently, higher performing accelerometers and
295 bio-loggers have become available which overcome these limitations for future studies
296 (Evans et al. 2013, Hussey et al. 2015).

297 By attaching the accelerometer to the shell, only movement resulting from foot
298 muscle contraction was registered. When the shell is not moving, most of the body movement
299 is restricted to moving the proboscis, especially during grazing. These body movements were
300 not recorded but are a very important part of the animal's biology, as they allow the
301 individual to feed. Energy production, oxygen consumption and movement are highly inter-
302 related (Schmidt-Nielsen 1971, Garland Jr 1983) and acceleration has been shown to be a
303 proxy of oxygen consumption and physiology of a large range of taxa (Halsey and Shepard
304 2009), such as bivalves (Robson et al. 2012), marine mammals (Jeanniard-du-Dot et al.
305 2017), amphibians (Halsey and White 2010) and marine birds (Murchie and Cooke 2011). In
306 the case of marine benthic species, a careful calibration between acceleration and oxygen
307 consumption could be used to provide an estimation of animal metabolism.

308 Queen conch spend most of their active periods grazing. This feeding and associated
309 energy expenditure is necessary to support their fast growth rates of body and shell and can

310 represent, depending on species, 75 % to 410 % of the energy invested in somatic growth and
311 6 % of the total respiratory losses (Palmer 1992). Currently, relatively little information is
312 available on queen conch physiology and oxygen consumption. The analyses of the co-
313 variations of activity and environmental parameters presented herein document that the
314 immature queen conch is able to deal with considerable variations in oxygen concentration
315 and salinity, and is still able to graze efficiently to sustain its growth, confirming preliminary
316 investigations (Stieglitz and Dujon 2017). This suggests physiological adaptations to the
317 quasi-estuarine habitat which is atypical for this species considered to be marine (Bridle and
318 Vines 2007, Kawecki 2008).

319 Queen conch is only one of several large marine snails in tropical and temperate waters and
320 relatively very little is known to date about the behaviour of such species, many of which are
321 important fisheries resources and play an important role in ecosystems (Stoner 1989b, Stoner
322 et al. 1995, Leiva and Castilla 2001). Successful conservation management of endangered
323 species critically depends on a good understanding of the species' movement and of their
324 interactions with the environment (Grüss et al. 2011, Ogburn et al. 2017) and we showed that
325 3D accelerometry is a powerful approach to obtain valuable insights for understanding the
326 fundamental ecology of marine snails.

327 **Ecological significance of queen conch movements**

328 The accelerogram and video footages revealed queen conch perform leaps for long distance
329 movement, and drifts to rotate their shell. Both movement types are used to access new
330 foraging resources. Drifts are also used to find a better balance on slopes and rocks, or when
331 colliding with other queen conch. Contrary to most gastropods, members of the *Strombus*
332 genus do not crawl (Parker 1922, Lissmann 1945, Randall 1964, Little 1989). Occurrence of
333 flip movements is rare but very important (around one flip every 1000 movements); a queen

334 conch must be able to return to its resting shell position when overturned, in order to avoid
335 exposure to attack by a predator or, considering a longer period, to dying from starvation.

336 At least two known behavioural patterns (burial and mating) along with other
337 potential behaviours associated with reproduction or ontogenetic habitat shift were not
338 observed in this study. Here, the implications of those two movement with respect to shell
339 acceleration are briefly discussed. Hesse (1979) describes the burying of queen conch as a
340 succession of side to side foot movements and a pushing into the sand with the proboscis.
341 Based on these observations, acceleration records of burying behaviour should be comparable
342 to several drift movements, and should follow each other closely. Robertson (1959)
343 describes queen conch mating as the introduction of the male's contractile, black, spade-like
344 verge through the syphonal notch of the female. If both snails' shells are immobile, it may be
345 difficult to record and discriminate this behaviour in accelerometer studies.

346 **Temporal pattern of queen conch movement and response to environmental conditions**

347 In Xel-Ha inlet, the water column is permanently stratified due to the inflow of low-salinity
348 groundwater (Back et al. 1979, Stoessell et al. 1989, Stieglitz and Dujon 2017). Typical for
349 such estuarine conditions, oxygen exchange between the atmosphere and bottom water is
350 inhibited by this stratification, and large diurnal bottom oxygen variations persist (Borsuk et
351 al. 2001, Samal et al. 2006). During the day, the dissolved oxygen concentration increases
352 due to photosynthetic processes, and night-time oxygen consumption by benthic and pelagic
353 organisms lead to low-oxygen or hypoxic condition during the morning hours.

354 Most publications refer to the queen conch as a neritic animal mostly found on reefs and sea
355 grass beds (see Stoner 2003 and references therein). We consider Xel-Ha as a marginal
356 habitat for this marine species, because substantial variations in environmental conditions
357 caused by the continuous groundwater inflow persist that are not usually observed in the
358 species' typical marine habitat (Stoner 2003, Kawecki 2008, Stieglitz and Dujon 2017).Our

359 results provide some elements of an answer to the question of how queen conch adapt to
360 those estuarine conditions. We showed that activity patterns of the queen conch follow the
361 diurnal variations of dissolved oxygen concentration. During low-oxygen periods queen
362 conch limit energetic expenses by suspending movement and grazing. Conversely queen
363 conch exhibited the greatest amount of activity during periods of ample oxygen supply. In
364 contrast, despite considerable diurnal variations in ambient salinity, the animals' activity
365 appears to be little affected by this variation on a day to day time scale. On the one hand this
366 is perhaps surprising given that the queen conch is considered a marine (i.e. not estuarine)
367 species and has an hemolymph composition close to sea water (Colin 1967), yet on the other
368 hand, some molluscs have the ability to withstand variations in ambient salinity by storing
369 hyperosmotic hemolymph within the vascular system (Little 1981).

370 Despite being of lower quality, marginal habitats can play a role in the persistence of
371 species in situations where the core habitat is under substantial disturbance and where most of
372 the individuals inhabiting this key area are under threat of disappearing (e.g. roadside
373 grassland for native bees, Hopwood 2008; areas of low soil fertility and unsuitable for
374 farming for African mammals, Happold 1995 forest habitat for the European bison, Kerley et
375 al. 2012). In the case of the queen conch the main threats are the degradation of the core
376 habitats (e.g. nurseries and breeding grounds) by human activities and the removal of a large
377 proportion of mature individuals due to overfishing (Stoner and Ray-Culp 2000, Theile 2001,
378 Stoner 2003, Acosta 2006, Stoner et al. 2012b). Our result show the queen conch spend most
379 of its time foraging, which is key for sustaining the fast growth rates measured in this
380 groundwater-fed marginal habitat (Valle-Esquivel 1998, Peel and Aldana Aranda 2012). This
381 also suggests the groundwater-fed coastal areas of the Yucatan peninsula could play a role in
382 the conservation of the queen conch while the issues of core habitats degradation and
383 overfishing are being resolved.

384 In summary, environmental parameters, specifically the ambient oxygen
385 concentration can have an important impact on queen conch behaviour, and despite the
386 periodic low oxygen concentrations experienced in this inlet, which affect movement for food
387 intake, this habitat is a productive nursery ground with growth rates observed similar to those
388 habitats in fully-marine conditions (Valle-Esquivel 1998, Peel and Aldana Aranda 2012).

389

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403

404 **Author contribution**

405 TCS conceived the study; AMD and EA conducted the fieldwork. AMD carried the
406 calibration study and analysed the data. DW provided technical assistance with the
407 accelerometer prototype data processing. AMD and TCS led the writing with input from DW.

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- 605

606 **Figures**

607 **Figure 1:** Location of the ground-water-fed Xel-Ha inlet (represented by a black square) on
608 the Yucatan Peninsula (Mexico).

609

610 **Figure 2:** Photography of a queen conch (*Lobatus gigas*) carrying a 3D accelerometer (back
611 cylinder in A) recording the shell movements (in B) in Xel-Ha inlet in 2012. The proboscis
612 (showed by the red arrow in C) extrudes from the shell during grazing and its movement is
613 not recorded by the accelerometer.

614

615 **Figure 3:** The three main movements of the queen conch (*Lobatus gigas*) and its typical
616 accelerograms: (a) leap - the most frequent movements mainly used for grazing and long-
617 distance travels, (b) drift - used to rotate the shell to access close areas of sediment and (c) flip
618 - made when the conch shell is overturned. Note the scale differences on the y-axis for the three
619 movement types.

620

621 **Figure 4:** Visual representation of the three-main type of queen conch (*Lobatus gigas*)
622 movement: (a) the leap, (b) the drift, (c) the flip. The section, L1 to L4, D1 to D2 and F1 to
623 F4 correspond to the same naming on Figure 3.

624

625 **Figure 5:** Visual representation of the flexible discriminant model built using the acceleration
626 time series and video record of the five 2012 individuals. Five descriptors were retained to
627 build the model: $\text{Mean}_{\text{ODBA}}$, Mean_{Z^2} , T , Mean_{Y^2} and Mean_{X^2} . The leaps (white circles, $n =$
628 403), drifts (black circles, $n = 50$) and flips (white squares, $n = 10$) are relatively well
629 discriminated with an error rate of less than 6 % (leaps predicted as drift, $n = 16$ as grey
630 circles and drifts predicted as leaps, $n = 9$ as grey squares).

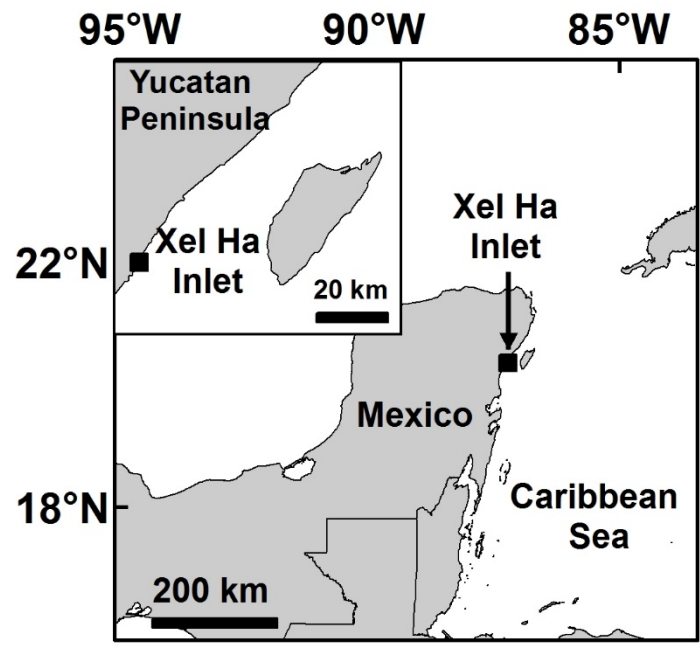
631

632 **Figure 6:** (a-c) Overall Dynamic Body Acceleration (ODBA, in g) records of four queen conch
633 (*Lobatus gigas*) recorded over a period of eight consecutive days in April 2011. Each vertical
634 bar indicates a conch movement and its associated ODBA (leap as grey bar, drift has black
635 bar). White circles represent flip movements. Movements were classified using the flexible
636 discriminant model. Dashed vertical lines indicate the start and end of each individual conch
637 record. No data was recorded during the period marked with a \emptyset . In (a) oxygen, (b) salinity and
638 (c) temperature variations are represented as solid black lines. Oxygen concentration follows a
639 diel pattern (mg L^{-1}), while the salinity and temperature ($^{\circ}\text{C}$) follow a tidal pattern.

640

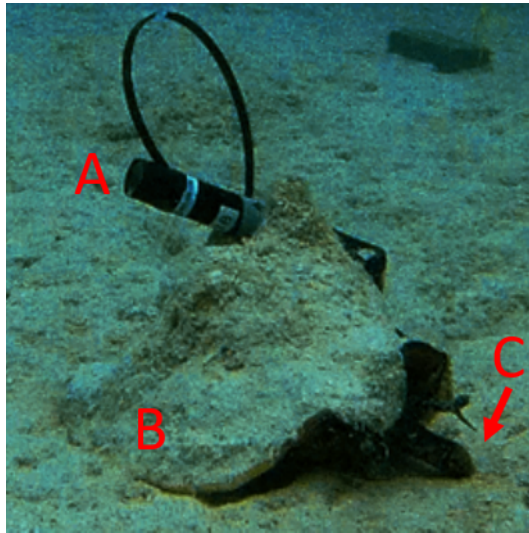
641 **Figure 7:** Probability curves of the logistic regression models linking the probability of
642 observing: (a) no movement ($N_{mov} = 0$, middle black line), (b) at least one movement ($N_{mov} \geq$
643 1, middle black line) (c) at least ten movements ($N_{mov} \geq 10$, middle black line) and (d) at least
644 25 movement ($N_{mov} \geq 25$, middle black line) per hour in function of the dissolved oxygen
645 concentration. Grey dashed lines represent the 95% confidence interval for each model.

646 **Figure 1**



647

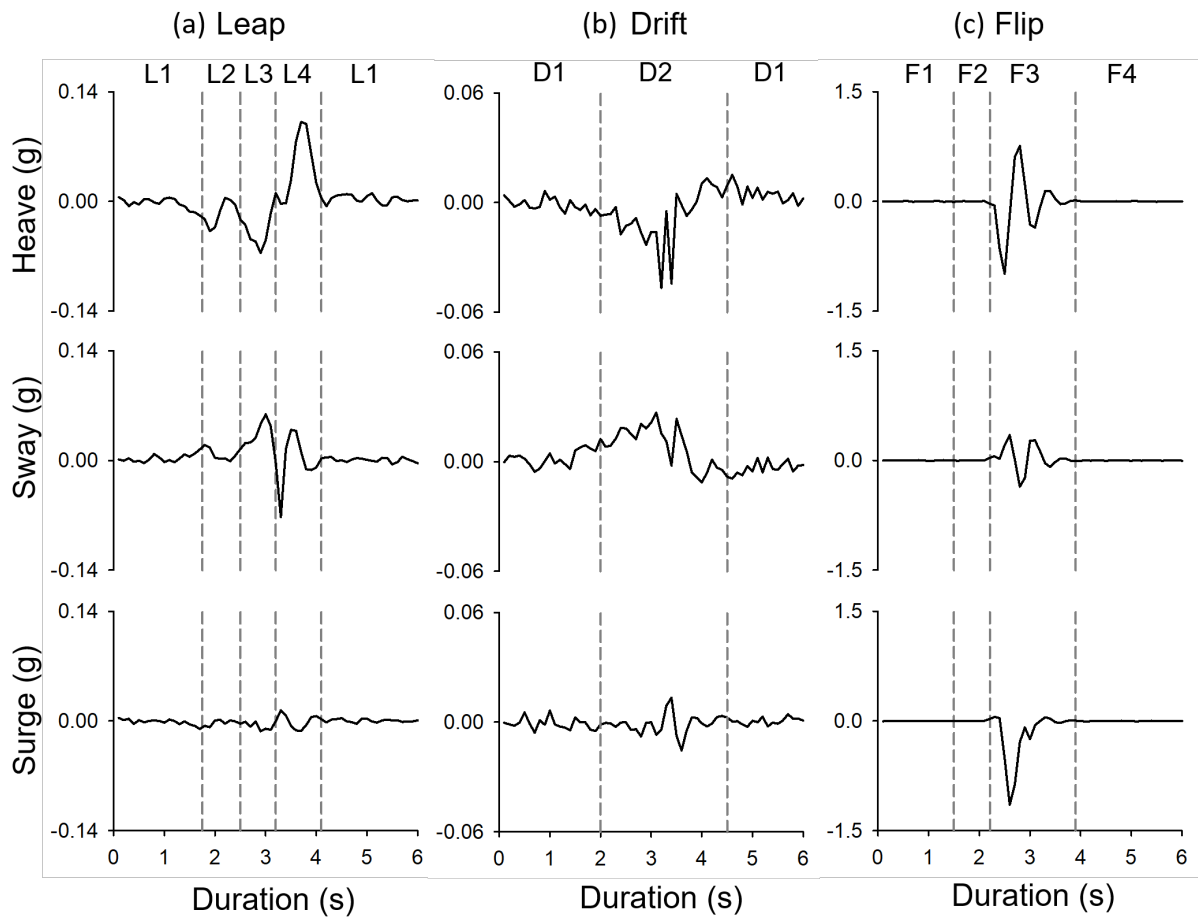
648 **Figure 2:**



649

650

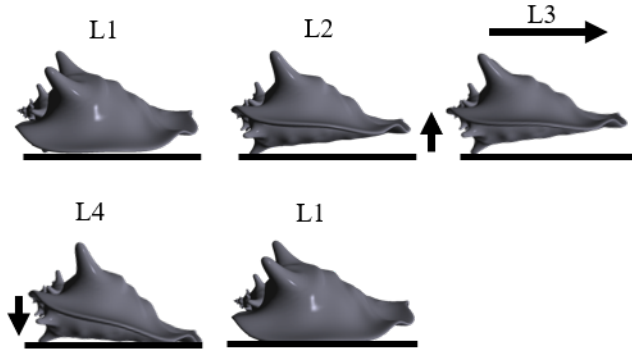
651 **Figure 3:**



652

653

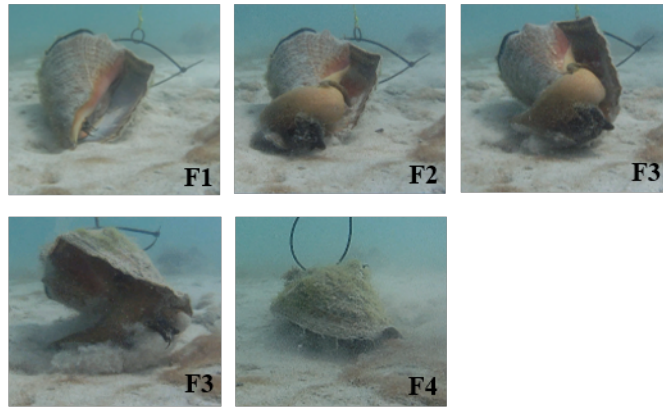
(a) Leap



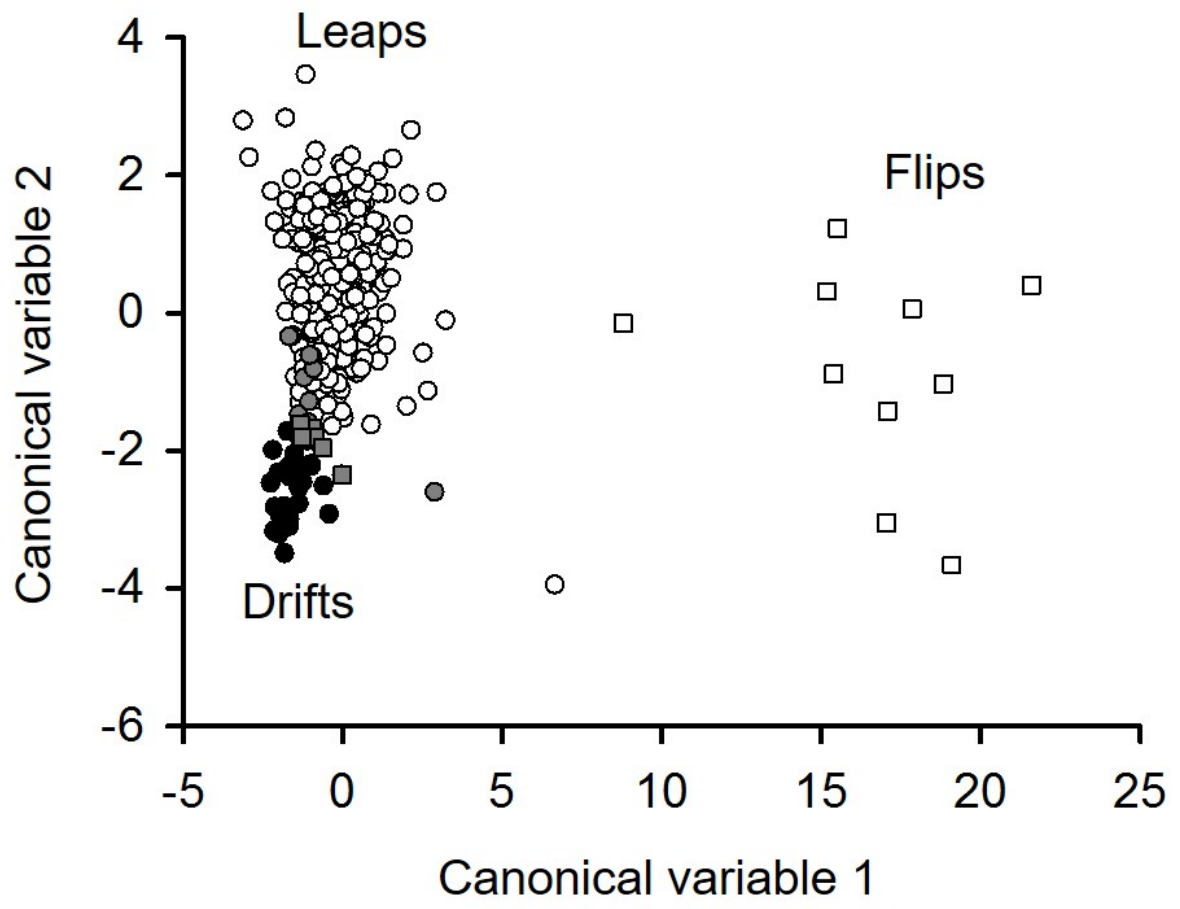
(b) Drift



(c) Flip

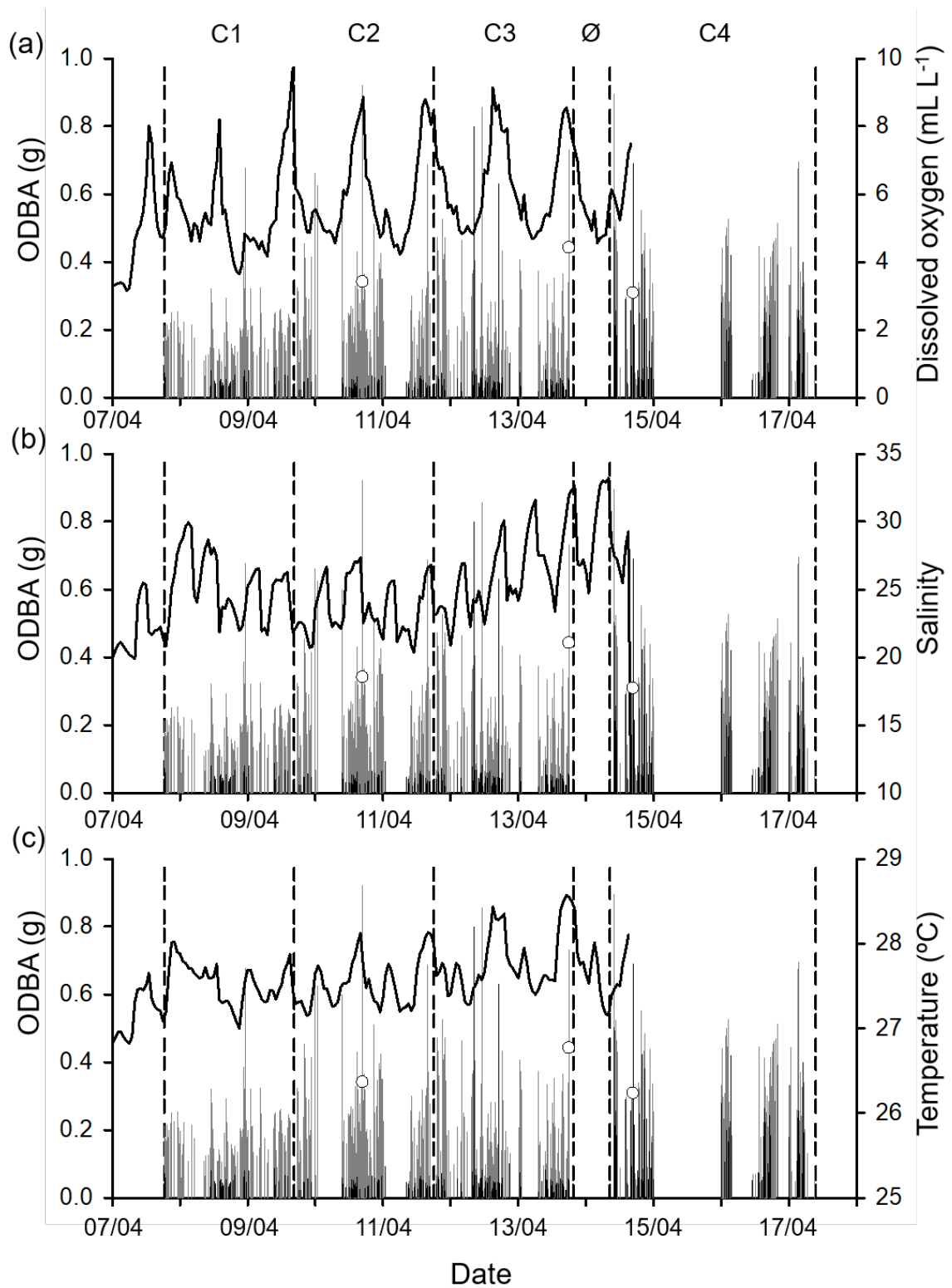


657 **Figure 5:**



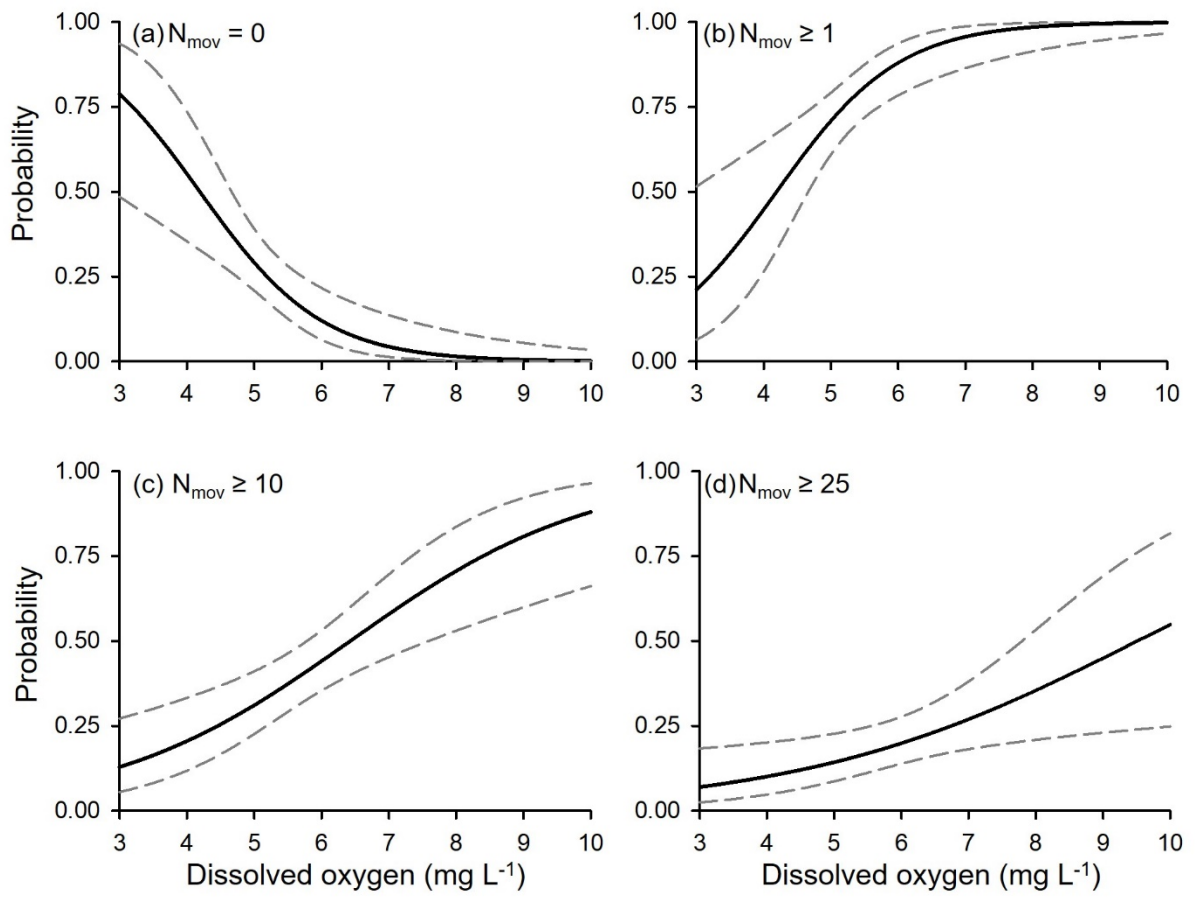
658

659 **Figure 6:**



660

661 **Figure 7:**



662

663 **Table 1:** Summary of the classified movements broken down by type for the nine queen
664 conch tagged with a 3D accelerometer. The first five queen conch in the table were used to
665 build the flexible discriminant model. The numbers between brackets correspond to the
666 number movements observed on the video and that were used to build the model. This model
667 was subsequently applied to the last four queen conch for which video recordings were not
668 available. For those individuals, the numbers in the leap, drift and flip column correspond to
669 the number of predicted movements.

| Conch ID | Syphonal length and lip width (mm) | Tag length (% of syphonal length) | Video Recorded | No of Leaps | No of Drifts | No of Flips | Total | Record duration (hh:mm) |
|----------|------------------------------------|-----------------------------------|----------------|-------------|--------------|-------------|-----------|-------------------------|
| S1 | 176 - 4 | 68% | Yes | 102 (63) | 14 (12) | 0 | 116 (65) | 7:25 |
| S2 | 212 - 11 | 57% | Yes | 154 (101) | 2 (2) | 0 | 156 (103) | 1:10 |
| S3 | 210 - 5 | 57% | Yes | 205 (47) | 33 (10) | 0 | 238 (57) | 9:15 |
| J1 | 180 - 0 | 67% | Yes | 198 (59) | 34 (13) | 0 | 232 (62) | 9:15 |
| J2 | 198 - 0 | 61% | Yes | 410 (133) | 16 (13) | 10 (10) | 436 (146) | 3:30 |
| C1 | - | - | No | 578 | 39 | 0 | 617 | 45:10 |
| C2 | - | - | No | 739 | 69 | 1 | 809 | 48:30 |
| C3 | - | - | No | 821 | 109 | 1 | 931 | 47:20 |
| C4 | - | - | No | 1116 | 94 | 1 | 1211 | 48:35 |

670

671 **Table 2:** List of descriptors calculated using the acceleration time series of the three types of
672 movements (leap, dript and flips) classified from the queen conch video records. The
673 descriptors were used to build a flexible discriminant analysis to discriminate between the
674 movements of queen conch for which no video recordings were available.
675

| Notation | Descriptor |
|---------------|---|
| E_x | Surge signal energy (g^2) |
| E_y | Sway signal energy (g^2) |
| E_z | Heave signal energy (g^2) |
| E_{ODBA} | ODBA signal energy (g^2) |
| Max_x | Surge acceleration maximum (g) |
| Max_y | Sway acceleration maximum (g) |
| Max_z | Heave acceleration maximum (g) |
| Max_{ODBA} | Maximum ODBA of the movement (g) |
| $Mean_x$ | Mean surge acceleration (g) |
| $Mean_y$ | Mean sway acceleration (g) |
| $Mean_z$ | Mean heave acceleration (g) |
| $Mean_{ODBA}$ | Mean ODBA (g) |
| $Mean_{x^2}$ | Mean squared surge acceleration (g^2) |
| $Mean_{y^2}$ | Mean squared sway acceleration (g^2) |
| $Mean_{z^2}$ | Mean squared heave acceleration (g^2) |
| T | Movement duration (s) |

676

677 **Table 3:** Logistic regression models exploring the relationship between the probability of
678 observing a given number of movements per hour ($N_{\text{mov}} = 0$, $N_{\text{mov}} \geq 1$, $N_{\text{mov}} \geq 10$, $N_{\text{mov}} \geq 25$)
679 and the environmental parameters (DO: dissolved oxygen concentration, S: salinity, T :
680 temperature, Tod : time of day). The odd ratio and AIC were only reported when the model
681 was statistically significant.

| Model | β | SE | p-value | Odds ratio | AIC |
|--|---------|-------|---------|------------|-------|
| $N_{\text{mov}} = 0 \sim \text{DO}$ | -1.101 | 0.314 | < 0.001 | 0.3 | 125.1 |
| $N_{\text{mov}} \geq 1 \sim \text{DO}$ | 1.101 | 0.314 | < 0.001 | 3.0 | 125.1 |
| $N_{\text{mov}} \geq 10 \sim \text{DO}$ | 0.558 | 0.155 | < 0.001 | 1.8 | 175.3 |
| $N_{\text{mov}} \geq 25 \sim \text{DO}$ | 0.397 | 0.163 | 0.01 | 1.2 | 134.1 |
| $N_{\text{mov}} = 0 \sim \text{S}$ | 0.067 | 0.082 | 0.41 | - | - |
| $N_{\text{mov}} \geq 1 \sim \text{S}$ | -0.067 | 0.082 | 0.41 | - | - |
| $N_{\text{mov}} \geq 10 \sim \text{S}$ | -0.023 | 0.069 | 0.74 | - | - |
| $N_{\text{mov}} \geq 25 \sim \text{S}$ | 0.005 | 0.085 | 0.95 | - | - |
| $N_{\text{mov}} = 0 \sim \text{T}$ | -1.275 | 0.787 | 0.12 | - | - |
| $N_{\text{mov}} \geq 1 \sim \text{T}$ | 1.275 | 0.787 | 0.11 | - | - |
| $N_{\text{mov}} \geq 10 \sim \text{T}$ | 1.064 | 0.585 | 0.07 | - | - |
| $N_{\text{mov}} \geq 25 \sim \text{T}$ | 0.600 | 0.680 | 0.38 | - | - |
| $N_{\text{mov}} = 0 \sim \text{Tod}$ | -0.183 | 0.043 | < 0.001 | 0.8 | 119.6 |
| $N_{\text{mov}} \geq 1 \sim \text{Tod}$ | 0.183 | 0.042 | < 0.001 | 1.2 | 168.9 |
| $N_{\text{mov}} \geq 10 \sim \text{Tod}$ | 0.082 | 0.027 | < 0.001 | 1.1 | 177.4 |
| $N_{\text{mov}} \geq 25 \sim \text{Tod}$ | 0.061 | 0.032 | 0.054 | - | - |

| | | | | | | |
|--|------|--------|-------|---------|-----|-------|
| $N_{\text{mov}} = 0 \sim \text{Tod} + \text{DO}$ | Tod: | -0.142 | 0.043 | < 0.001 | 0.9 | 112.7 |
| | DO: | -1.011 | 0.395 | 0.01 | 0.4 | |
| $N_{\text{mov}} \geq 1 \sim \text{Tod} + \text{DO}$ | Tod: | 0.142 | 0.043 | < 0.001 | 1.1 | 112.7 |
| | DO: | 1.01 | 0.269 | 0.01 | 2.7 | |
| $N_{\text{mov}} \geq 10 \sim \text{Tod} + \text{DO}$ | Tod: | 0.065 | 0.029 | 0.01 | 1.1 | 172.1 |
| | DO: | 0.421 | 0.162 | 0.01 | 1.5 | |
| $N_{\text{mov}} \geq 25 \sim \text{Tod} + \text{DO}$ | Tod: | 0.041 | 0.035 | 0.25 | - | - |
| | DO: | 0.318 | 0.174 | 0.07 | - | - |

682

683 **Figure captions:**

684

685 **Figure 1:** Location of the ground-water-fed Xel-Ha inlet (represented by a black square) on
686 the Yucatan Peninsula (Mexico).

687

688 **Figure 2:** Photography of a queen conch carrying a 3D accelerometer (back cylinder in A)
689 recording the shell movements (in B) in Xel-Ha inlet in 2012. The proboscis (showed by the
690 red arrow in C) extrudes from the shell during grazing and its movement is not recorded by
691 the accelerometer.

692

693 **Figure 3:** The three main movements of queen conch and their typical accelerograms: (a)
694 leap - the most frequent movements mainly used for grazing and long-distance travels, (b)
695 drift - used to rotate the shell to access close areas of sediment and (c) flip - made when the
696 conch shell is overturned. Note the scale differences on the y-axis for the three movement
697 types.

698

699 **Figure 4:** Visual representation of the three-main type of queen conch movement: (a) the
700 leap, (b) the drift, (c) the flip. The section, L1 to L4, D1 to D2 and F1 to F4 correspond to the
701 same naming on Figure 3.

702

703 **Figure 5:** Visual representation of the flexible discriminant model built using the acceleration
704 time series and video record of the five 2012 individuals. Five descriptors were retained to
705 build the model: MeanODBA, MeanZ², T, MeanY² and MeanX². The leaps (white circles, n =
706 403), drifts (black circles, n = 50) and flips (white squares, n = 10) are relatively well

707 discriminated with an error rate of less than 6 % (leaps predicted as drift, n = 16 as grey
708 circles and drifts predicted as leaps, n = 9 as grey squares).

709

710 **Figure 6:** (a-c) Overall Dynamic Body Acceleration (ODBA, in g) records of four queen
711 conch recorded over a period of eight consecutive days in April 2011. Each vertical bar
712 indicates a conch movement and its associated ODBA (leap as grey bar, drift has black bar).
713 White circles represent flip movements. Movements were classified using the flexible
714 discriminant model. Dashed vertical lines indicate the start and end of each individual conch
715 record. No data was recorded during the period marked with a \emptyset . In (a) oxygen, (b) salinity
716 and (c) temperature variations are represented as solid black lines. Oxygen concentration
717 follows a diel pattern (mg L^{-1}), while the salinity and temperature ($^{\circ}\text{C}$) follow a tidal pattern.
718

719 **Figure 7:** Probability curves of the logistic regression models linking the probability of
720 observing: (a) no movement ($N_{\text{mov}} = 0$, black line), (b) at least one movement ($N_{\text{mov}} \geq 1$,
721 upper black line) (c) at least ten movements ($N_{\text{mov}} \geq 10$, middle black line) and (d) at least
722 25 movement ($N_{\text{mov}} \geq 25$, middle black line) per hour in function of the dissolved oxygen
723 concentration. Grey dashed lines represent the 95% confidence interval for each model.

724 **Supplementary Methods 1**

725 A 3D accelerometer typically records acceleration in its own orthonormal coordinate system.
726 If fixed arbitrarily on the animal the accelerometer axes will not be aligned with the
727 orthonormal Earth system, which is ideally used to interpret the movement in a commonly
728 used framework, distinguishing surge (x axis, forward/backward), sway (y axis, sideways)
729 and heave (z axis, up/down). We thus need to transform the raw acceleration into the Earth
730 system using a 3D rotation matrix. To build this matrix, the rotation angles, θ_x , θ_y and θ_z
731 around the three axes of the accelerometers were determined by performing a calibration
732 procedure. At the end of each *in-situ* recording session, the animal was removed from the
733 water, carried carefully to the laboratory and laid on a horizontal surface. A succession of
734 forward, downward and up/down movements (corresponding to movements following the
735 axis of the earth orthonormal system) was then manually performed. In order to minimise the
736 effect of handling of the animal on its movement behaviour, this calibration which required
737 removal of the animal from the water was performed post-observation. We then extracted the
738 points with the maximum acceleration corresponding to these calibration movements and
739 applied an axis-angle methodology to determine the angles of the rotation matrix and convert
740 the data to the Earth system. The data obtained contains a static acceleration component, due
741 to gravity, equal to 1 g and a dynamic acceleration component, equal to zero, when the
742 animal is immobile and equal to the acceleration measured at the animal's centre of mass
743 during a movement.

744 **Electronic supplements**

745 **Electronic supplement 1.** Example of a queen conch performing a leap.

746

747 **Electronic supplement 2.** Example of a queen conch performing a drift.

748

749 **Electronic supplement 3.** Example of a manually overturned queen conch performing a flip
750 to restore standard position.