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1 **Faunal mediated carbon export from mangroves in an arid area.**

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11

12 **Abstract**

13 The outwelling paradigm argues that mangrove and saltmarsh wetlands export much excess  
14 production to downstream marine systems. However, outwelling is difficult to quantify and currently  
15 40-50% of fixed carbon is unaccounted for. Some carbon is thought outwelled through mobile fauna,  
16 including fish, which visit and feed on mangrove produce during tidal inundation or early life stages  
17 before moving offshore, yet this pathway for carbon outwelling has never been quantified. We studied  
18 faunal carbon outwelling in three arid mangroves, where sharp isotopic gradients across the boundary  
19 between mangroves and down-stream systems permitted spatial differentiation of source of carbon  
20 in animal tissue. Stable isotope analysis (C, N, S) revealed 22-56% of the tissue of tidally migrating  
21 fauna was mangrove derived. Estimated consumption rates showed that 1.4% (38 kg C ha<sup>-1</sup> yr<sup>-1</sup>) of  
22 annual mangrove litter production was directly consumed by migratory fauna, with <1% potentially

23 exported. We predict that the amount of faunally-outwelled carbon is likely to be highly correlated  
24 with biomass of migratory fauna. While this may vary globally, the measured migratory fauna biomass  
25 in these arid mangroves was within the range of observations for mangroves across diverse  
26 biogeographic ranges and environmental settings. Hence, this study provides a generalised prediction  
27 of the relatively weak contribution of faunal migration to carbon outwelling from mangroves and the  
28 current proposition, that the unaccounted-for 40-50% of mangrove C is exported as dissolved  
29 inorganic carbon, remains plausible.

30 **Key words:** trophic relay; mangrove; carbon budget; outwelling hypothesis; mangrove litter; carbon  
31 flux; fish; food webs

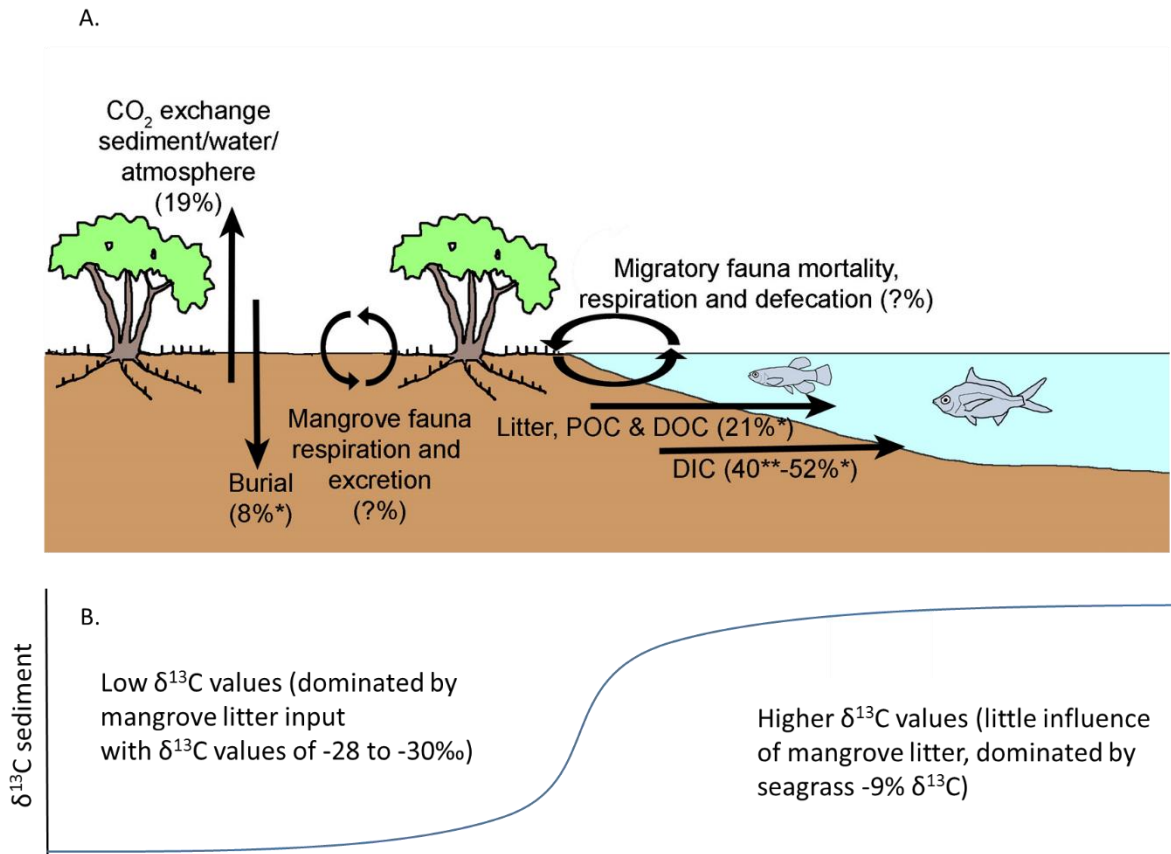
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### 33 **1. Introduction**

34 Mangrove forests are amongst the world's most productive marine ecosystems (Alongi 2014), with  
35 net primary productivity (NPP) in the order of 208 Tg C yr<sup>-1</sup> (Bouillon et al. 2008a). Mangrove forests  
36 achieve a steady state once the forest reaches maximum biomass at around 20-30 years through a  
37 constant process of mortality and renewal (Lugo 1980) so, assuming the living biomass is not becoming  
38 more carbon dense, then carbon has to be lost at a rate equal to the amount of carbon fixed as NPP.  
39 Hence this productivity is either retained within the mangrove forest, as a standing stock of live  
40 material such as wood, buried in sediments, or exported to neighbouring habitats as litter, particulate  
41 and dissolved organic carbon (POC and DOC) and dissolved inorganic carbon (DIC), or lost to the  
42 atmosphere (Bouillon et al. 2008a, Maher et al. 2013, Alongi 2014). The out-welling hypothesis argues  
43 that export of locally-derived POC and DOC is an important ecosystem function of mangroves, which  
44 drives detrital based food webs in adjacent coastal habitats (Odum 1968, Odum and Heald 1972).  
45 Export of mangrove carbon has been estimated to make a significant trophic contribution to adjacent  
46 ecosystems (Lee 1995, Jennerjahn and Ittekkot 2002, Dittmar et al. 2006, Abrantes et al. 2015). The  
47 theory of outwelling is supported by mass balance evaluations that show the amount of carbon fixed

48 by mangroves normally greatly exceeds the amount stored within the forest (Alongi 2014, Twilley et  
49 al. 2017), although the scale of outwelling varies considerably between forests (Guest and Connolly  
50 2004), due to differences in coastal geomorphology, tidal regimes, freshwater flow and productivity  
51 (Granek et al. 2009, Vaslet et al. 2012). In the 1990s, global estimates could account for 48% of the  
52 total global mangrove primary production (Figure 1) of  $218 \pm 72$  million tons C yr<sup>-1</sup>, by incorporating  
53 information on carbon burial, CO<sub>2</sub> efflux and carbon outwelled as leaf litter, POC and DOC; the  
54 remaining 52% was thought outwelled as DIC, albeit there was insufficient data to confirm this  
55 (Bouillon et al. 2008a). More recent assessments of DIC export at two sites in Australia (Maher et al.  
56 2013, Santos et al. 2019) supported the estimates of Bouillon et al. (2008a), although Alongi (2014)  
57 suggested that only 40% of NPP was exported as DIC. Here, we explore the extent to which faunal  
58 outwelling accounts for some of the un-explained losses in mangrove NPP.

59 While the outwelling of mangrove carbon as POC, DOC and DIC may represent an important tropic  
60 subsidy to other coastal habitats (Dittmar et al. 2006), the movement of fauna out of the mangrove,  
61 and their subsequent capture or predation, is an additional plausible direct mechanism for export of  
62 mangrove carbon, as well as a route for mangrove contribution to coastal food webs and fisheries.  
63 Fauna that feed in the mangrove during high tides and then move offshore to defecate and respire  
64 during low tide should also contribute to carbon outwelling (Figure 1). At present, however, there is  
65 little evidence to clarify what proportion of fauna-mediated export may benefit fisheries production  
66 (Saenger et al. 2013)



67

68 Figure 1: A.) Fate of mangrove primary production and importance of each component, as a  
 69 percentage of net mangrove primary productivity. Percentages are based on data in \* Bouillon et al.  
 70 (2008a) and \*\* Alongi (2014). B.) Isotopic profile of sediments across the transition from mangrove to  
 71 intertidal mudflats and seagrass beds, illustrating the retention of mangrove productivity within the  
 72 forest.

73 Adult and juvenile fauna use mangroves as spawning and feeding grounds and as a refuge from  
 74 predation (Saenger et al. 2013). Faunal outwelling occurs when mangrove carbon that has been  
 75 ingested by animals within the mangrove either directly, through eating mangrove leaves or indirectly  
 76 through eating fauna containing mangrove C, is then transferred out of the mangrove into  
 77 downstream/subtidal habitats. Two forms of direct faunal mediated mangrove outwelling have been  
 78 proposed, although we do not differentiate between them in the current study: ontogenetic  
 79 outwelling, where juveniles/larvae that have been sustained on mangrove production migrate out of  
 80 the mangroves as they mature; and trophic relay, where predators transfer mangrove carbon out of

81 the forest after feeding on mangrove-sustained prey (Kneib 1997, Connolly and Lee 2007). Indirect  
82 faunal outwelling includes the mangrove carbon assimilated by fauna feeding at the base of the food  
83 web transforming the refractory mangrove material into more labile carbon that may then be  
84 exported by transfer up the food chain or water mediated tidal export after mineralization.

85 Tree litter (leaves, fruits, etc) on average represents 31% of mangrove production (Bouillon et al.  
86 2008a) and its fate is central to unravelling mass-balance budgets. Some litter is exported directly on  
87 the tide (Boto and Bunt 1981) and the contribution of litter export to coastal food webs has been  
88 questioned, as mangrove litter has low nutritional value (high C:N ratios) and is highly refractory  
89 (Rodelli et al. 1984, Loneragan et al. 1997, Bouillon et al. 2002, Skov and Hartnoll 2002, Connolly et al.  
90 2005). Much litter is retained in the mangrove through herbivory, as many invertebrates are highly  
91 dependent on mangrove produce as a food source (eg. Rodelli et al. 1984, Chong et al. 2001, Walton  
92 et al. 2014). This is especially true of the old world mangroves in Indo-West Pacific biogeographic  
93 region (McIvor and Smith 1995, Lee 1998). Litter feeders and microbes process and nutritionally enrich  
94 litter transforming it to detritus, making it available for uptake by deposit and filter feeders  
95 (Poovachiranon et al. 1986, Skov and Hartnoll 2002). In turn, litter, detritus and filter feeders are  
96 consumed by tidal predators and thus litter may be indirectly exported through trophic relay (Lee  
97 1995), although this outwelling mechanism is rarely considered and has never been quantified.

98 The idea of faunal outwelling has been around for 50 years (Heald and Odum (1970), yet its  
99 significance to mangrove carbon budgets remains untested, probably because generating the  
100 evidential data is technically challenging. First, the abundance of migratory fauna per unit area of  
101 mangrove has to be estimated. This can be achieved catching fauna at the mangrove edge during the  
102 ebbing tide in water draining from a known area of mangrove (Thayer et al. 1987, Blaber and Milton  
103 1990, Barletta et al. 2003, Castellanos-Galindo and Krumme 2013, Shahraki and Fry 2016), although  
104 estimating the size of the catchment area can be difficult if the mangrove has complex drainage/creek  
105 morphology (Huxham et al. 2008). Secondly, the proportion of mangrove carbon in the tissues of

106 migratory fauna needs quantification. This step has been facilitated by the development of chemical  
107 tracers, such as stable isotopes and fatty acids, which utilize the principle of “you are what you eat”  
108 (eg. Rodelli et al. 1984, Meziane and Tsuchiya 2000). Thirdly, the tracers used to account for mangrove  
109 carbon should only be present inside the mangrove to ensure that the mangrove carbon in the fauna  
110 was acquired within the mangrove forest. Fourthly, the NPP of the site needs to be known. Typically,  
111 litter production is used as a proxy for NPP as this is simple to measure and typically accounts for 31%  
112 of NPP (Bouillon et al. 2008a).

113 We undertook the first empirical study of the role of aquatic faunal-mediated outwelling to mangrove  
114 carbon budgets and tested the hypothesis that outwelling by marine migratory faunal represents a  
115 significant component of mangrove productivity. Two estimates of outwelling were considered: (1)  
116 direct outwelling, that is mediated by feeding in mangrove forests at high tide by non-mangrove  
117 resident species, and their subsequent excretion or mortality in adjacent subtidal; and (2) indirect  
118 outwelling, represented by the proportion of the mangrove carbon food web that supports fauna  
119 migrating between the mangrove and down-stream habitats.

120

## 121 **2. Methods**

### 122 **2.1. Study Sites:**

123 We used arid mangroves in Qatar as an ideal system for studying faunal outwelling. Firstly, Qatar  
124 mangroves have gently sloping shorelines with relatively simplified systems of creeks and drainage  
125 channels that enables positioning of the traps and estimation of their catchment area. In arid  
126 mangroves outwelling to adjacent food webs is limited (Walton et al. 2014, Ray and Weigt 2018), as  
127 lack of rainfall greatly restricts flushing and the resulting outwelling of particulate organic material  
128 (POM) that is otherwise characteristic in wetter, tropical climates (Loneragan et al. 1997, Al-  
129 Maslamani et al. 2012, Al-Maslamani et al. 2013). The high retention of productivity within Qatar  
130 mangrove forests leads to a sharp isotopic boundary in sediments and sedentary fauna at the

131 seaward edge of forests, between a mangrove area which is depleted in  $^{13}\text{C}$ , and down-stream tidal  
132 flats and subtidal seagrass habitats, which are more enriched in  $^{13}\text{C}$  (Figure 1: Below)(Walton et al.  
133 2014). The low export of litter, and associated sharp isotopic boundary, makes Qatar mangroves  
134 ideal sites for investigating faunal mediated carbon export, as any mangrove carbon incorporated  
135 into the tissue of migratory fauna has to have been consumed within the mangrove area; it is  
136 unlikely to have been outwelled and consumed down-stream.

137

138 The study sampled the three largest mangrove forests in Qatar: Al Khor, West Al Dhakira and South Al  
139 Dhakira (Figure 2). These had 2m tidal ranges, silty sediments and mono-specific *Avicenna marina*  
140 stands. Trees ranged from ~5 m tall at the seaward fringe to stunted <1m mature trees at landward  
141 fringes (Chatting et al. 2020). Sites had a central tidal channel, but on either side were dominated by  
142 a flat substrate that drained evenly across the surface, except, where the gradient was slightly steeper  
143 and small channels (2-5 cm deep, <50 cm wide) formed. These flatter areas were selected for sampling,  
144 in order to represent the majority of the mangrove area. A broad, gently sloping mudflat exists to the  
145 west of the mangroves in Al Khor, with sediments similar to the mangrove. Non-mangrove intertidal  
146 areas at Al Dhakira sites were steep and relatively narrow. Subtidally, sites had patchy seagrass beds,  
147 mainly *Halodule uninervis*, with some *Halophila stipulacea* occasionally reaching intertidal areas close  
148 to the mangrove fringe (Walton et al. 2016). Anthropogenic impacts from fishing, tourism and sewage  
149 input is limited in these mangroves (Walton et al. 2016), they are protected with no fishing permitted  
150 under the Protected Area Management Plan 2008-2013 (SCENR 2007).

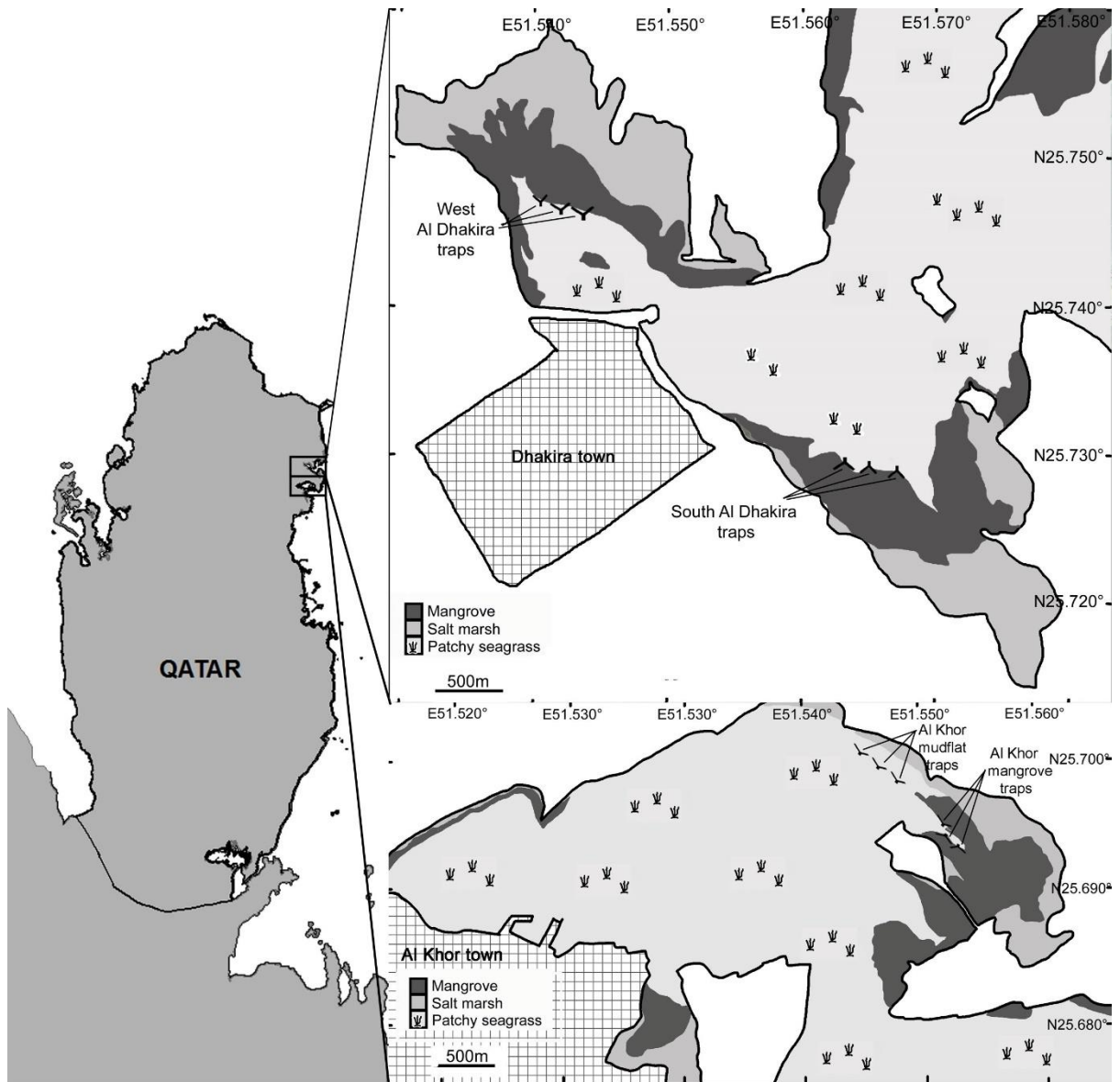
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152 **2.2. Sampling Design:** At each mangrove site three fyke nets (3mm mesh) were placed along the  
153 seaward mangrove fringe (Fig 3, S1. Table 1). Previous trials indicated 1mm was easily blocked and  
154 5mm mesh permitted smaller shrimp and fish to escape. All traps were at the same tidal elevation.  
155 Nets were 1m tall (well above high tide level) and with 5 m wings, resulting in a 5.8-9.2 m trapping



156 gape per trap, with gape variation due to wing placement. Bottom edges of nets were buried in the  
157 sediment. In West Al Dhakira and Al Khor fyke nets were set over small drainage channels (Figure 3).  
158 South Al Dhakira had no clear drainage channels and traps were randomly positioned along the  
159 mangrove edge. To simplify the estimation of the area from which water drained through each fyke  
160 net, nets were placed where the ebbing water flowed perpendicular to the mangrove edge. Prior  
161 trapping trials conducted in 2013-2016 indicated that small channels perpendicular to the shore line  
162 produced the least variable estimates of faunal density. Sampling took place on one spring-tide day  
163 in spring (29 April – 1 May 2017) and in the autumn (8 – 10 October 2017), to represent the spawning  
164 season and the appearance of juveniles in coastal habitats, respectively. These periods were selected  
165 to capture the maximum migratory biomass and was informed by the previous campaigns to traps fish  
166 detailed in Walton et al (2014) and the trial use of larger nets (30m) to block the larger mangrove  
167 channels, in addition to field observations of fish migratory pattern during our extended presence in  
168 the mangroves over a two year period. As the major spring tides occurred at night, fyke nets were set  
169 in the afternoon at low water and emptied the next morning at the following low water. Thus,  
170 sampling quantified mobile fauna using the mangrove during the nocturnal spring tide. During the  
171 second sampling, a mudflat site at Al Khor was also sampled, to evaluate whether migratory fauna  
172 were specific to mangroves or generalist fauna present in other intertidal habitats. Only Al Khor had a  
173 suitable mudflat site for sampling, with intertidal flats of the same intertidal height, slope and  
174 sediment characteristics as the mangrove.

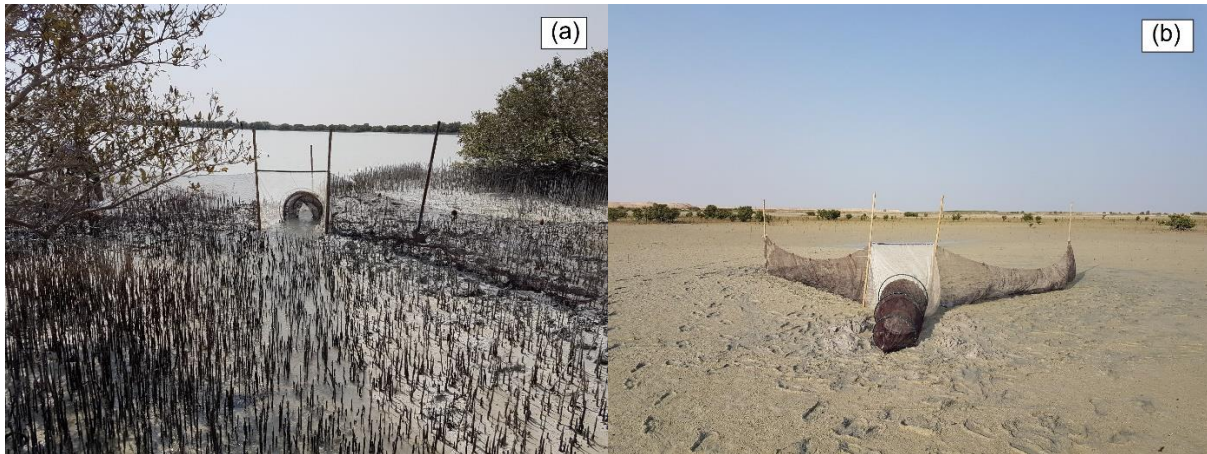
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176

177 Figure 2: Location of traps in the mangrove forests of Al Khor, West and South Al Dhakira.

178



179 Figure 3: Fyke nets placed across (a) a small mangrove drainage channel and (b) on the un-vegetated  
180 mudflat at Al Khor.

181 The catch, mainly fish and shrimp, was stored on ice until sorting. All species other than *Aphanius*  
182 *dispar* and *Gerres longirostris*, were separated out, counted and the total length and wet weight  
183 noted. The remaining catch of *A. dispar* and *G. longirostris* which formed 94% of the biomass was  
184 subsampled and each species weighed, measured and counted, and scaled up by the total biomass  
185 from that species to determine population structure. Fish biomass estimates from mangrove areas in  
186 October (n=9) were compared with those from mudflat areas (n=3) using a two sample T-test on  
187 normally distributed data. More detailed analysis of catch composition data is presented in  
188 Supplementary Material 1.

189

190 **2.3. Tracing the food source of fauna (trophic linkage).** Stable isotopes of C, N and S were used to  
191 assess the contribution of mangroves and alternative dietary sources to the tissues of migratory fauna.  
192 Muscle tissue was extracted (~1g dw/specimen) from 5 specimens per species per trapping event.  
193 Three potential food sources were sampled. Mangrove leaves were collected from 5 stations along  
194 seaward to landward transects through each of the 3 mangrove forests (For transect details see  
195 Chatting et al. 2020), seagrass leaves were collected from 12 stations across Al Khor and Al Dhakira  
196 bays. Yellow leaves (n = 5 per site) of the mangrove *Avicenna marina* and leaves of the seagrass

197 *Halodule uninervis* were cleaned under distilled water to remove encrusting organisms and sediment.  
 198 Phytoplankton (n = 3 samples) were collected at the bay mouths using a 50 µm phytoplankton net;  
 199 the sample were sieved and particles >100µm were excluded to minimise contamination by  
 200 zooplankton. Samples were dried (50°C, 48h), homogenised and weighed into tin cups (Elemental  
 201 Microanalysis Ltd.), before elemental analysis and isotope ratio mass spectrometry (EA–IRMS) by a  
 202 Europa Hydra 20/20 stable-isotope mass spectrometer were performed by Iso-Analytical Ltd. Isotopic  
 203 results are reported as δ values, where δ<sup>13</sup>C, δ<sup>15</sup>N and δ<sup>34</sup>S are equal to 1000 × [(R<sub>sample</sub> –  
 204 R<sub>standard</sub>/R<sub>standard</sub>) – 1], in which R<sub>sample</sub> and R<sub>standard</sub> equal the <sup>13</sup>C/<sup>12</sup>C, <sup>15</sup>N/<sup>14</sup>N and <sup>34</sup>S/<sup>32</sup>S ratios of  
 205 samples and standards, respectively. Laboratory standards, traceable to inter-laboratory comparison  
 206 standards distributed by the International Atomic Energy Agency (for further detail see  
 207 <http://www.iso-analytical.co.uk/standards.html>), were run interspersed with samples which resulted  
 208 in standard deviations of <0.4‰ for δ<sup>13</sup>C, <0.3‰ for δ<sup>15</sup>N and <0.3‰ for δ<sup>34</sup>S.

209

210 **2.4. Construction of carbon outwelling budget.** The amount of mangrove carbon consumed by  
 211 migratory aquatic fauna ( $MC_F$ , Kg C ha<sup>-1</sup> yr<sup>-1</sup>) was derived by Equation 1 (broadly based on consumption  
 212 models in Scheiffarth and Nehls (1997) and Walton et al. (2015)), which includes five main parameters,  
 213 the estimation of which are outlined in sections further down:


214 Equation 1. 
$$MC_F = \sum B \times Q/B \times pM \times DWt:WWt \times pMC_c$$

215

216 where  $B$  (kg ha<sup>-1</sup>) was the mean biomass of migratory aquatic species per catchment area of mangrove  
 217 forest;  $Q/B$  was the consumption rate per year by that biomass of fauna;  $pM$  was the proportion of  
 218 that food that was mangrove-derived; and  $MC_F$  estimates were converted to leaf dry weight using  
 219 0.342 (the mean dry weight to wet weight ratio (DWt:WWt) of yellow mangrove leaves (Fourqurean  
 220 and Schrlau 2003)) as  $Q/B$  is a WWt:WWt ratio; and  $pMC$  is the proportion of C in yellow mangrove

221 leaves (Mean C%±SE=39.7±0.47, n=11). The amount of carbon outwelled by fauna (FCO) was  
 222 estimated for each species using our Equation 2 and is formed of two parts excretion and mortality:

223 Equation 2. 
$$FCO = MC_f \times 0.9 \times T_{RE} + \sum (B \times Mort_{yr} \times DWt:WWt \times pM \times pFC)$$

224 

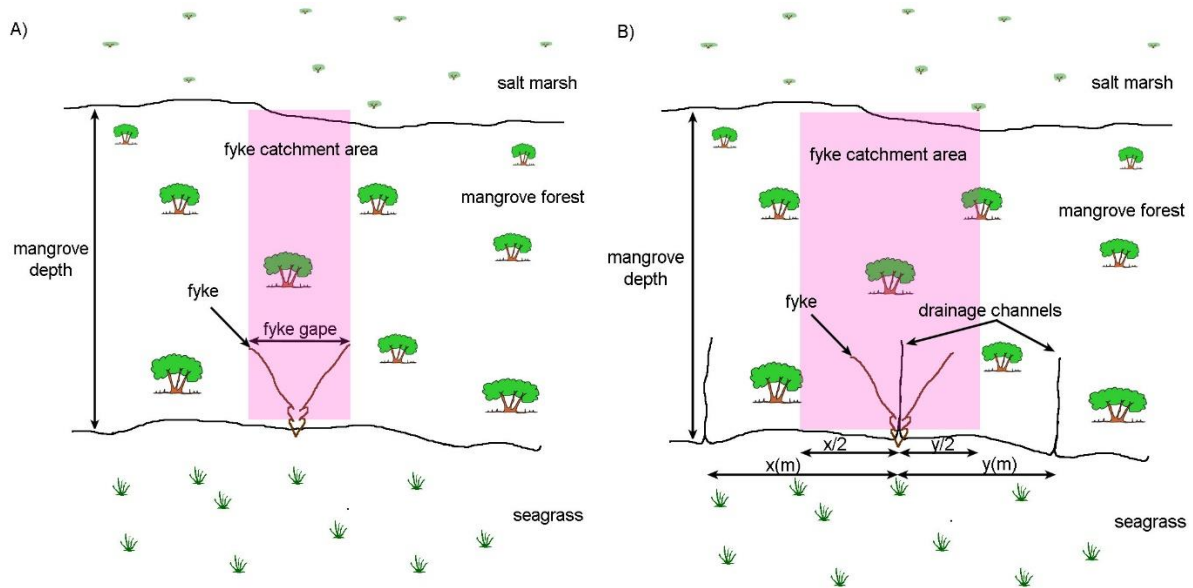
225 Excretion Mortality

226 Where  $T_{RE}$  was the proportion of the time migratory fauna spent outside the mangrove respiring and  
 227 excreting (estimated at 60% - see below section 2.4.5) and 0.9 the trophic transfer efficiency (Pauly  
 228 and Christensen 1995); while  $pFC$  is the proportion of C in the fauna from the isotopic analysis,  
 229  $DWt:WWt$  is the wet to dry weight ratio of 0.226 (unpublished data) and  $Mort_{yr}$  was the annual  
 230 mortality rate, as estimated using literature values for instantaneous mortality for each species. We  
 231 assumed that mortality of fauna was predominantly outside the mangrove, as mangroves are  
 232 considered a refuge from predation.

233

234 **2.4.1. Faunal biomass per catchment area,  $B$  ( $kg\ ha^{-1}$ ):** Faunal biomass values from fyke-net catches  
 235 ( $kg$  wet weight), were expressed relative to an estimate of the catchment area. In Qatar the relatively  
 236 homogenous mangrove surface and simple drainage facilitates estimates of catchment area. The  
 237 method for calculation of the catchment area for each fyke net depended on the presence or absence  
 238 of drainage channels in the sampling area. Where no drainage channels were present (South Al  
 239 Dhakira), the catchment area equalled the gape width of the fyke net multiplied by the mangrove  
 240 depth (the distance between the seaward and landward mangrove forest boundaries (Fig 4a). Where  
 241 the net straddled a channel, the catchment area equalled the mangrove depth multiplied by half the  
 242 distance between the trapped drainage channel and the adjacent drainage channels on each side (ie.  
 243  $x/2+y/2$ . Figure 4b). The logic of the latter was that adjacent channels had similar sizes (confirmed by  
 244 visual inspection) and thus were likely to have equal shares in the catchment area between them.

245



246 Figure 4: Diagrammatic representation of the catchment area (shaded) for fyke-nets placed without  
 247 (a) and with (b) a drainage channel.

248

249 **2.4.2. Food Consumption rate,  $Q/B$  ( $\text{yr}^{-1}$ ):** Body weight has been used to estimate daily energy  
 250 expenditure in birds and animals (eg. Nagy 1987). Here, the amount of food ingested, expressed as a  
 251 proportion of the consumer's biomass ( $Q/B$ ), was estimated using a combination of body weight and  
 252 the aspect ratio of the caudal fin (following Palomares and Pauly 1998), in the equation

253 Equation 3 
$$\log Q/B = 7.964 - 0.204 \log W^\infty - 1.965 T' + 0.083 A + 0.532 h + 0.398 d$$

254 where  $W^\infty$  was the asymptotic weight (g),  $T'$  was the mean annual water temperature ( $27.05^\circ\text{C}$ )  
 255 expressed as 1000/Kelvin (Kelvin =  $^\circ\text{C} + 273.15$ ),  $A$  was the caudal fin aspect ratio,  $h$  and  $d$  represented  
 256 the type of food consumed (if herbivore  $h=1, d=0$ ; if detritivore  $h=0, d=1$ ; and if carnivore  $h$  and  $d=0$ ),  
 257 with fish dietary habits derived from  $\delta^{15}\text{N}$  values (see trophic level estimates below). Caudal fin aspect  
 258 ratio was estimated with Image J (version 1.51j8) to measure the caudal fin area and height, on images  
 259 obtained from FishBase (2019).  $Q/B$  values of 21.9 and  $10.75 \text{ yr}^{-1}$  were used for crustaceans and other  
 260 rare fish species (<1% of the total biomass), respectively, with values derived from the mangrove  
 261 studies of Wolff et al. (2000) and Vega-Cendejas and Arreguin-Sánchez (2001).

262

263 **2.4.3. Proportion of faunal diet that was mangrove derived,  $\rho M$ :** The source of carbon assimilated in  
264 faunal tissues were derived from stable isotopes of  $^{13}C$ ,  $^{15}N$  and  $^{34}S$ . For the four species that  
265 individually represented >1% of the caught biomass (combined they composed 98% of the biomass),  
266 the contribution of primary producers to faunal tissues was estimated using the Bayesian isotopic  
267 mixing model mixSIAR (Stock and Semmens 2013). For the remaining 16 species, which individually  
268 formed <1% of the trapped biomass, the combined average dietary contribution of mangroves, as  
269 estimated by the mixing model, was used. The MixSIAR model was selected as it incorporates the  
270 isotopic variability in the sources and consumers, as well as the uncertainty of the trophic  
271 discrimination factor (Stock and Semmens 2013). MixSIAR was run in JAGS and called through R (R  
272 Core Development Team, 2016) and the 'MixSIAR' package (Stock and Semmens 2013). The models  
273 were run with no informative priors and specified both residual and process error. Mangrove site was  
274 entered as a random effect. The longest Markov Chain Monte Carlo settings were used: chains = 3,  
275 chain length = 1,000,000, burn-in rate = 500,000 and thinning rate = 500, as this produces the best  
276 convergence on the true posterior distribution for each variable (Stock and Semmens 2013).  
277 Convergence was evaluated by Gelman-Rubin diagnostics (Gelman and Rubin 1992). The trophic level  
278 of a consumer was estimated using 2.3‰ for the first trophic step above the mean  $\delta^{15}N$  values of the  
279 primary producers and an additional 2.9‰ for each higher trophic level (McCutchan et al. 2003, Shang  
280 et al. 2008, Walton et al. 2014). To account for the isotopic discrimination that occurs between primary  
281 producers and primary consumers trophic enrichment factors ( $\pm 1SD$ ) of  $0.5 \pm 1.32\text{‰}$ ,  $2.3 \pm 1.54\text{‰}$  and  
282  $0.5 \pm 0.52\text{‰}$  were applied and for subsequent trophic steps values of  $1.3 \pm 0.85\text{‰}$ ,  $2.9 \pm 1.24\text{‰}$  and  
283  $0.5 \pm 0.52\text{‰}$  were used for C, N and S respectively (McCutchan et al. 2003). Microphytobenthos (MPB)  
284 was not included in isotopic mixing models, as it was present in very low concentrations ( $\sim 0.1\%$  of  
285 sediment carbon, Chatting unpublished data) and as MPB  $\delta^{13}C$  values of 29-26‰ indicated that  
286 mineralised mangrove carbon was incorporated into MPB (David et al. 2019).

287

288 **2.4.4. Estimation of mangrove-derived biomass consumed,  $MC_F$ :** The amount of mangrove biomass  
289 that was consumed either directly by the migratory fauna, or indirectly by all the organisms that form  
290 the base of the food web on which the migratory fauna feed.

291 **a) Direct consumption:** The annual consumption of mangrove derived carbon (Direct  $MC_F$   
292 estimated using Equation 1) eaten by the migratory fauna feeding either on mangrove  
293 biomass or fauna that contain mangrove carbon (part of indirect consumption)

294 **b) Indirect consumption:** The annual mangrove carbon consumed by herbivores and  
295 detritivores at the base of the food web that supports the migratory fauna. It is an estimate  
296 of the biomass of mangrove primary production supporting each of mobile faunal species,  
297 assuming 10% transfer between trophic steps (Pauly and Christensen, 1995) using the  
298 equation

$$299 \text{ Indirect } MC_F = \text{Direct } MC_F \times 10^{(TL-2)}$$

300 where TL equates to trophic level. A proportion of the indirect consumption will end up being  
301 ingested by the migratory fauna.

302 An average mangrove litter production estimate for these three mangrove sites of  $6847 \text{ kg ha}^{-1}$   
303  $\text{yr}^{-1}$  (Chatting pers. comm.), the equivalent of  $2718 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  (using the below yellow leaf  
304 carbon content estimate), was used to covert dry wieght consumption estimates to  
305 percentage of mangrove litter production. All estimates were converted to C using the C to  
306 dry weight ratio of 0.397 derived from the carbon content of oven dried yellow *A. marina*  
307 leaves.

308 **2.4.5. Proportion of time fauna spend outside the mangrove,  $T_{RE}$ :** The mean tidal height of the lower  
309 mangrove fringe was measured using DGPS during spring tides in February 2016 and found to be 0.2m  
310 above mean tide. Tidal charts were used to estimate the proportion of the day when the tidal level



311 was below this mean tidal level of 0.2m, this was regarded as the time when fauna are all clear of the  
312 mangrove.

313

### 314 3. Results

315 The catchment area that drained through each of the traps varied from just over one hectare for the  
316 traps in West Al Dhakira to under a tenth of hectare for one of the traps in Al Khor. Species  
317 compositions and biomass varied markedly between mangrove and the mudflat, but not between  
318 mangrove sites: Area-adjusted catches indicated that ~ 3 times more fish (by biomass) used the  
319 mangroves than the mudflat area, with pooled mangrove catches significantly higher than mudflat  
320 catches (t-test, on October data only:  $T = -2.72$ ,  $P = 0.026$ ,  $DF = 8$ )(Table 1). Mangrove traps caught in  
321 total 74.49 kg (74,420 individuals) in May and 76.42 kg (79,290 individuals) in October and 1.19 kg  
322 (340 individuals) on the mudflat (see Supplementary information table 2 for further information).  
323 Sampled individuals ranged in size from ~1cm for the smallest *Palaemon khorii* to 34cm for a garfish  
324 (*Belone belone*) with the majority of the catch 2-7cm in length. On average ( $\pm$ SE), mangrove forests  
325 were visited by ~ 14 kg ha<sup>-1</sup> of fish and crustaceans during a single tide; 97 $\pm$ 2% of that was fish, and  
326 78 $\pm$ 3% was the Arabian pupfish *A. dispar*. The other major contributors were the strongspine  
327 silverbiddy *Gerres longirostris* (16 $\pm$ 3%), the milkfish *Chanos chanos* (2 $\pm$ 1%) and the shrimp *Palaemon*  
328 *khorii* (3 $\pm$ 2%). In contrast crustaceans formed 70 $\pm$ 19% of the smaller mudflat catches, with the blue  
329 swimming crab *Portunus pelagicus* forming 69 $\pm$ 19% of the biomass. For details on areas trapped, catch  
330 biomass, biodiversity and non-parametric statistical tests used to detect differences, see  
331 supplementary material S1.

332 Table 1: Faunal biomass (kg ha<sup>-1</sup>) caught at mangrove and mudflat sites (mean $\pm$ SD, n = 3 fyke nets/site).

Site	May	October
Al Khor mangrove (n=3)	12.26 $\pm$ 6.40	16.21 $\pm$ 17.98

South Al Dhakira mangrove (n=3)	12.16 ± 6.78	10.23 ± 9.33
West Al Dhakira mangrove (n=3)	17.14 ± 1.35	16.50 ± 2.19
Al Khor mudflat (n=3)		4.49 ± 1.15
Combined average of all mangrove areas (n=9)	13.85 ± 5.32	14.32 ± 10.64

---

333

334 **3.1. Consumption rate** (Q/B, yr<sup>-1</sup>): The three major fish species, *A. dispar*, *G. longirostris*, and *C.*  
335 *chanos*, consumed 52.2, 16.8 and 27.8 times their body mass per year, respectively, estimated using  
336 the body mass and caudal fin ratios. Literature derived values of Q/B of 21.9 and 10.75 were used for  
337 *P. khor*i and the less frequently occurring (<1% of biomass) species (Vega-Cendejas and Arreguin-  
338 Sánchez 2001).

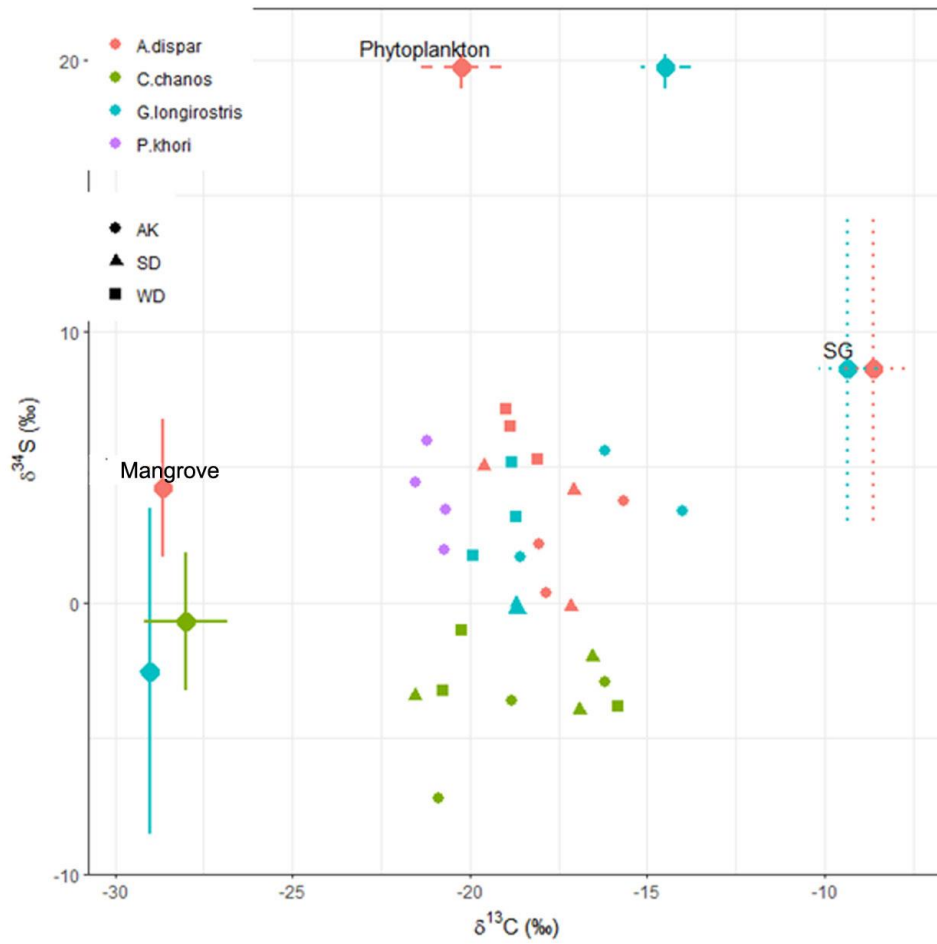
339

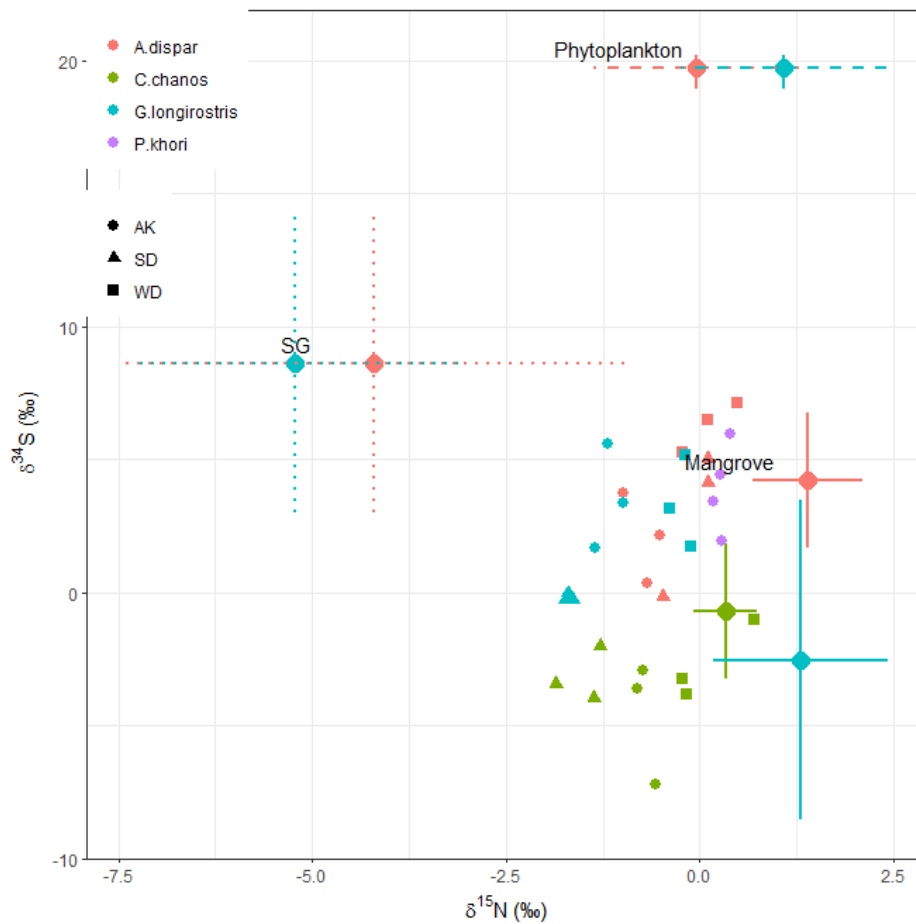
340 **3.2. Mangrove derived dietary proportion and trophic level:** Primary producers had distinct  $\delta^{13}\text{C}$  and  
341  $\delta^{34}\text{S}$  values, averaging -28.6‰ and 0.3‰ for mangrove (yellow leaves), -16.4‰ and 19.2‰ for  
342 phytoplankton and -9.1‰ and 8.6‰ for seagrass, respectively (Figure 5). However, only seagrass  $\delta^{15}\text{N}$   
343 values of -4.9‰ were well separated from the other two primary producers: mangroves (1.1‰) and  
344 phytoplankton (0.7‰). Of the consumers *P. khor*i was the most depleted in  $^{13}\text{C}$  at -18.4‰, *C. chanos*  
345 the most depleted in  $^{34}\text{S}$  at -2.7‰, while *G. longirostris* was the most enriched in  $^{15}\text{N}$  at 7.2‰. The  $\delta\text{N}$   
346 values of the main consumers, relative to those of the primary producers, showed the trophic level  
347 (TL) of the dominant species ranged from omnivores to carnivores (*C. chanos* – TL 2.6, *A. dispar* - TL  
348 3.3, *P. khor*i - TL 3.5, *G. longirostris* – TL 4.0). The higher the trophic level, the larger the amount of  
349 primary production required to support the consumer (Pauly and Christensen 1995).

350 *G. longirostris* and *A. dispar* used different sources of primary productivity, with the latter much more  
351 reliant on phytoplankton-derived productivity than the former (Figure 6). The Bayesian mixing models  
352 indicate that the mean ( $\pm 1\text{SD}$ ) mangrove contribution to animal tissue was 40‰ ( $\pm 13$ ) for *A. dispar*,

353 43‰ ( $\pm 13$ ) for *G. longirostris*, 51‰ ( $\pm 18$ ) for *C. chanos*, 57‰ ( $\pm 9$ ) for *P. khoris* and 22‰ ( $\pm 7$ ) for the  
354 pooled remaining species (Figure 6).

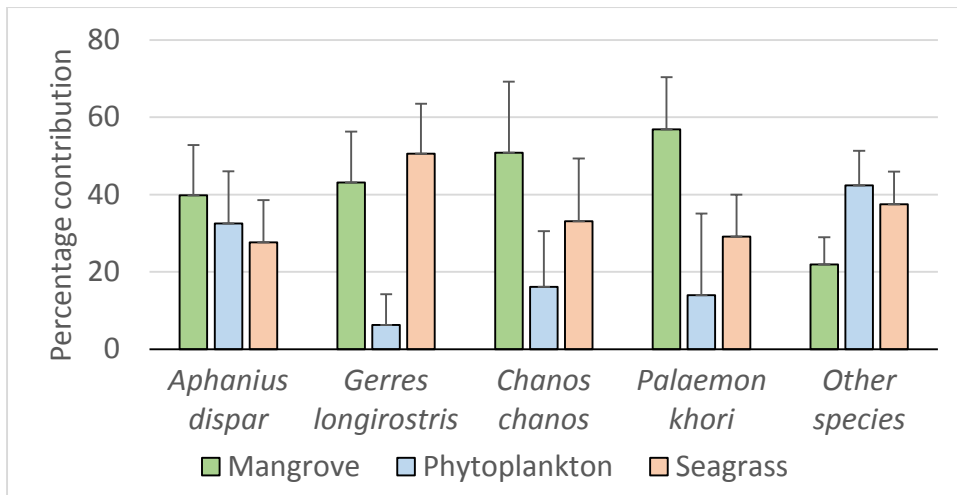
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356 Figure 5: Stable isotope values (‰) of carbon and sulphur ( $\delta^{13}\text{C}$ ,  $\delta^{34}\text{S}$ ) (above) and nitrogen and  
 357 sulphur ( $\delta^{15}\text{N}$ ,  $\delta^{34}\text{S}$ ) (below) for *A. dispar*, *G. longirostris*, *C. chanos*, *P. khorii* (corrected for isotopic  
 358 discrimination) and primary producers (mangrove, seagrass (SG) and phytoplankton) in the sampled  
 359 mangrove areas of Al Khor (AK in red), West Al Dhakira (WD in blue) and South Al Dhakira (SD in green),  
 360 Qatar

361



362

363 Figure 6: Mean percentage of diets originating from the primary producers (mangrove, seagrass (SG)  
 364 and phytoplankton) in the 3 sampled habitats for *A. dispar*, *G. longirostris*, *C. chanos*, and *P. khori* and  
 365 the other 14 minor species that formed <2% of the total biomass, estimated using the Bayesian model  
 366 mixSIAR. Error bars represent 1 standard deviation from the mean.

367

368 **3.3. Biomass consumed.**

369 Direct consumption (Direct MC<sub>F</sub>): On average ( $\pm 1SD$ )  $35 \pm 33$  and  $2 \pm 3$  kg (C) ha<sup>-1</sup>yr<sup>-1</sup> of mangrove  
 370 carbon were consumed by the two main species *A. dispar* and *G. longirostris* (Table 2). Table 2 shows  
 371 the steps by which the annual consumption of mangrove material by migratory fauna is estimated.  
 372 Faunal biomass is derived from fyke net catches, daily consumption rates of the biomass are based on  
 373 the Q/B estimated from Equation 3. To reiterate, the proportion of the consumption that originated  
 374 from mangrove production was estimated from the proportion of mangrove derived carbon in the  
 375 sampled fauna (from the isotopic modelling and assumed assimilation and ingestion rates were  
 376 similar) and extrapolated to a yearly rate. These estimates of mangrove consumption as wet weight  
 377 were then converted to dry weight using a value of 0.342, the dry to wet weight ratio of yellow  
 378 mangrove leaves determined by Fourqurean and Schrlau (2003), and finally to carbon using our value  
 379 of 39.7% as carbon content of yellow mangrove leaves.

380 In total,  $37.7 \pm 32.8 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  of mangrove material or  $1.4 \pm 1.2\%$  of the annual (C) litter production  
 381 was directly consumed by the migratory fauna and, thus, available for export (Table 2).  
 382 Indirect consumption (Indirect  $\text{MC}_F$ ): Significantly more,  $928 \pm 698 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  of mangrove  
 383 production, was on average ( $\pm\text{SD}$ ) processed by the food web that supported the migratory fauna  
 384 (indirect consumption). Thus,  $34.1\%$  ( $=0.928 \times 100 / 2.72 \text{ t C ha}^{-1} \text{ yr}^{-1}$ ) of the leaf litter produced in these  
 385 mangroves passed through the food web that supported the migratory fauna, assuming a mean  
 386 annual litter production of  $2.72 \text{ t C ha}^{-1} \text{ yr}^{-1}$  for Qatar mangroves. Of this only 4% (Direct consumption  
 387 =  $37.7 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ ) were passed on to the migratory fauna.

388 Litter production has been estimated to account for 31% of mangrove net primary production (MNPP)  
 389 (Bouillon et al. 2008a), and these consumption values therefore represent 0.4% ( $=1.4\% \times 0.31$ ) and  
 390 10.6% of mangrove net primary production, for direct and indirect consumption respectively.

391

	<i>A. dispar</i>	<i>G. longirostris</i>	<i>C. chanos</i>	<i>P. khori</i>	Minor sp.
Fish biomass ( $\text{Kg wet wt ha}^{-1}$ )	11.92 $\pm$ 7.1	1.98 $\pm$ 1.4	0.28 $\pm$ 0.52	0.24 $\pm$ 0.59	0.27 $\pm$ 0.06
Consumption by fish ( $\text{Kg ha}^{-1}\text{d}^{-1}$ )	1.73 $\pm$ 1.1	0.09 $\pm$ 0.1	0.02 $\pm$ 0.04	0.01 $\pm$ 0.04	0.01 $\pm$ 0.002
Annual mangrove consumed (kg wet $\text{t ha}^{-1}\text{yr}^{-1}$ )	254.22 $\pm$ 240.5	15.83 $\pm$ 19.3	3.95 $\pm$ 8.7	2.78 $\pm$ 7.2	0.64 $\pm$ 0.3
Annual mangrove consumed (kg dry $\text{wt ha}^{-1}\text{yr}^{-1}$ )	86.94 $\pm$ 82.3	5.41 $\pm$ 6.6	1.35 $\pm$ 3.0	0.95 $\pm$ 2.5	0.22 $\pm$ 0.1

Annual mangrove consumed (kg (C) ha <sup>-1</sup> yr <sup>-1</sup> )	34.52±32.6	2.15±2.6	0.54±1.2	0.38±0.98	0.09±0.05
Percentage of mangrove litter directly consumed by migratory fauna (%)	1.27±1.2	0.08±0.1	0.02±0.04	0.01±0.04	0.003±0.002
Indirect annual consumption of mangrove biomass (kg (C) ha <sup>-1</sup> yr <sup>-1</sup> )	672.56±636.4	234.41±285.3	2.24±5.0	13.04±33.9	5.37±2.9

392 Table 2: Estimation of the mean (±SD) proportion of mangrove litter production consumed and  
393 potentially outwelled by migratory fauna.

394

395 **3.4. Proportion of time fauna spend outside the mangrove T<sub>RE</sub>:** The mean height of the mangrove  
396 fringe was 0.2m above mean tide level with the water level high enough to enter the mangroves on  
397 average 40% of the time, so conversely the mangrove were dry 60% of the time forcing the fauna into  
398 subtidal habitats. A T<sub>RE</sub> of 60% of the time was used to calculate the amount of respiration/excretion  
399 that occurred outside the mangroves.

400

#### 401 **3.5. Faunal Carbon Outwelling (FCO)**

402 The amount of faunally outwelled carbon (FCO) estimated from Equation 2 is composed of two parts,  
403 excretion/respiration and mortality. Outwelling due to carbon excretion/respiration was estimated  
404 assuming that 90% of the food ingested is later respired or excreted, based on the 10% assimilation  
405 rate of Pauly and Christensen (1995). Therefore of the 38 kg C ha<sup>-1</sup> yr<sup>-1</sup> of mangrove material directly  
406 consumed, 34 kg C ha<sup>-1</sup> yr<sup>-1</sup> is lost through excretion/respiration but only 60% is lost outside the  
407 mangrove while the tide is out and is thus estimated to be 20.8±18.0 kg C ha<sup>-1</sup> yr<sup>-1</sup> or 0.8% of leaf litter  
408 production. Mean outwelling of mangrove biomass from mortality of migratory species, is estimated  
409 at 0.48±27 kg C ha<sup>-1</sup> yr<sup>-1</sup> or 0.02% of leaf litter production. This was based on annual mortality rates

410 (derived from instantaneous mortality rates) that ranged from > 90% for *A. dispar* and *P. khori* to 40%  
411 for larger-sized minor species and C percentages with a range of 44-46% obtained from the isotope  
412 analysis.

413

#### 414 **4. Discussion**

415 This study provides a first estimate of the proportion of mangrove productivity that is outwelled by  
416 migratory fauna. The idea that fauna are a significant pathway for the movement of carbon out of  
417 mangroves was first suggested by Beever et al. (1979) after describing the outwelling of larvae from  
418 mangrove resident crabs. Later, Lee (1995) hypothesised that faunal outwelling of mangrove-derived  
419 carbon maybe an important and neglected pathway of mangrove C export, and the idea has since  
420 been reiterated (eg. Connolly and Lee 2007, Bouillon and Connolly 2009, Saenger et al. 2013), but its  
421 significance has never been quantified until now.

422 For Qatari mangroves direct consumption of mangrove carbon by all fauna that move in and out of  
423 the mangroves with the tides was very minor, at  $37.7 \pm 32.8$  kg (C)  $\text{ha}^{-1} \text{yr}^{-1}$  or 1.4% of mangrove litter  
424 production, suggesting mobile fauna have a relatively insignificant role in the consumption of  
425 mangrove production. Estimates of faunally induced outwelling of that consumed mangrove material  
426 resulting from Equation 2 were only  $20.8$  kg C  $\text{ha}^{-1} \text{yr}^{-1}$  (equivalent to  $0.77 \pm 0.66$  % of mangrove litter  
427 production or 0.26% of mangrove NPP). This faunal carbon export had two modes: the excretion and  
428 respiration of fauna during the period when the mangrove forest was dry; and from the mortality of  
429 migratory fauna, that we assumed occurred outside the mangrove. Our estimates of the mangrove  
430 carbon both consumed and outwelled by migratory fauna are 30 to 50 times smaller than estimates  
431 for C outwelled to neighbouring habitats as POC ( $1312$  and  $1187$  kg C  $\text{ha}^{-1} \text{yr}^{-1}$ ) and DOC ( $1500$  and  
432  $2029$  kg C  $\text{ha}^{-1} \text{yr}^{-1}$ ) (Bouillon et al. 2008a, Alongi 2014, respectively).

433 Our estimate for indirect consumption, that part of the mangrove productivity that is consumed by  
434 the food web supporting the migratory fauna, is much more significant, accounting for 34.1% of the



435 mangrove litter production or 10.6% of NPP, however it is unclear how much is outwelled. Other  
436 studies have shown the importance of fauna in processing mangrove carbon, in a review Lee (1998)  
437 reported high densities of grapsid crabs could process all the litter in some Indo-Pacific mangroves  
438 resulting in the retention of mangrove material within the forest. Similarly in Northern Australia  
439 isopod densities of >7000 individuals m<sup>-2</sup> producing faecal pellets at a maximal rate of 4 g C m<sup>-2</sup> d<sup>-1</sup> and  
440 was equivalent to litter production rates (Poovachiranon et al. 1986). In Qatar only 4.1% of this indirect  
441 consumption is passed up the food web to the migratory fauna and just 2.2% faunally outwelled, with  
442 the rest likely recycled or ending in the DIC, DOC or POC pathways. Previous studies of the same  
443 systems have found evidence of only limited biogeochemical outwelling (Walton et al. 2014), yet  
444 present results show that a significant proportion of migratory faunal biomass is derived from  
445 mangrove production and in agreement with findings across a wide range of mangroves (Hemminga  
446 et al. 1994, Primavera 1996, Abrantes and Sheaves 2009, Al-Maslamani et al. 2012, Al-Maslamani et  
447 al. 2013, Walton et al. 2014).

448 The propagation of errors through our model has resulted in large standard deviations about the mean  
449 values, most of which come from variation in catches and the uncertainty around the estimates for  
450 mangrove dietary proportion from the isotope modelling. Biomass estimates were especially varied  
451 between traps in the autumn sampling of the Al Khor and South Al Dhakira mangroves, in contrast to  
452 the traps in West Al Dhakira where estimates of biomass were remarkably consistent, this was likely  
453 due to changes in drainage patterns or the presence of a larger more mobile predator eliciting an  
454 evasion response from the smaller species. Invariably, traps will underestimate fish abundance.  
455 However, when compared to other studies (Table 3) our study showed some of the tightest estimates  
456 of biomass variation including those conducted in the mangroves of neighbouring Iran (Shahraki and  
457 Fry 2016). Sampling seasons were selected based on observations of when the highest numbers of  
458 fish are seen at the mangrove fringe, these coincide with spring spawning season in the Gulf  
459 (Sivasubramaniam and Ibrahim 1982) and the appearance of juveniles in the autumn. These sampling  
460 times were similar to those of Shahraki and Fry (2016) although our second sampling was performed

461 later in the year as our aim was to estimate peak fish abundance so as to be able to estimate the  
462 maximum amount of carbon outwelling due to faunal movement. Our estimates do not attempt to  
463 include other methods of faunally induced outwelling resulting from sedentary or resident mangrove  
464 fauna such as the release of eggs/larvae or the outwelling of excretory products as detailed in Beaver  
465 et al. (1979) although some of this is captured through our indirection consumption estimates. These  
466 traps with 3 mm mesh were selected as mesh size is a balance between capturing relevant sized  
467 organisms and the allowing the free passage of water to prevent net avoidance by the target species.  
468 Trap size was based on previous trapping trials using both non quantitative smaller fyke nets reported  
469 in (Walton et al. 2014) and large larger nets employed across major drainage channels, where water  
470 pressure caused sub-net erosion regardless of measures taken. We did not try to assess organisms  
471 smaller than the 3mm mesh size, which may have included both larval stages and zooplankton.  
472 Zooplankton has been found to feed mostly on phytoplankton in mangrove areas (Bouillon et al. 2000,  
473 Chew et al. 2012) indicating a limited role in the outwelling of mangrove material. Our biomass  
474 estimates are from fairly pristine arid mangroves that have been protected under the Protected Area  
475 Action Plan 2008-2013 (SCENR 2007). Nutrient inputs to our sites are also limited, as water from waste  
476 water treatment plants are used for inland irrigation and only a small amount of nutrient enrichment  
477 was detected in the west of Al Khor bay, furthest from the studied mangroves (Walton et al. 2016).  
478 While the mangroves are currently surrounded by substantial amounts of sabkha/salt marshes in  
479 which to expand as climate change causes sea level to rise, this situation could be jeopardised by  
480 future coastal developments.

481 Our estimates of Q/B of 10 to 52 fall within the range estimated for marine fish of 1-115 and are close  
482 to the only mangrove associated species *Signus canalicutatus* that has a Q/B of 61.7 (Palomares and  
483 Pauly 1998). The highest consumption rates were calculated for *A. dispar* which would have significant  
484 positive impact on the resulting mangrove consumption estimates and hence faunal outwelling. We  
485 reran the analysis using a Q/B of 23.7, which assumes *A. dispar* to be a carnivore, and not an omnivore

486 as indicated by the isotope data, and this led to a fall in the proportion of mangrove litter production  
487 consumed by the migratory fauna from 1.4% to 0.7%.

488 We used isotopes rather than stomach contents to determine contribution of mangrove carbon to the  
489 diet, as the carbon present in tissues of mobile fauna represent food that has been assimilated over a  
490 period of weeks and hence will include periods where access to the mangrove might be limited.  
491 Isotopic values of primary producers (mangrove, seagrass and phytoplankton) were similar to those  
492 of other studies with the exception of the depleted  $\delta^{15}\text{N}$  values of *H. uninervis* (Newell et al. 1995,  
493 Bouillon et al. 2008b, Walton et al. 2014), however previous research has shown these values  
494 widespread in these bays (Walton et al. 2016). We included sulphur isotopes to increase the isotopic  
495 distance between primary producers as recommended by Connolly et al. (2004). Mangrove and  
496 phytoplankton have similar  $\delta^{15}\text{N}$  and only differ by  $\sim 10\text{‰}$   $\delta^{13}\text{C}$ , but phytoplankton is enriched in  $^{34}\text{S}$  by  
497 17‰. Isotopic Bayesian mixing models showed the 4 species with the highest biomass were much  
498 more reliant on mangrove production for their nutrition 40–57% compared with 20% for the less  
499 abundant “minor” species. Moreover these 4 species showed strong attachment to the mangroves  
500 having a biomass at least 10 fold higher in the October mangrove than mudflat catches perhaps  
501 indicating that the higher biomass is related to feeding activity Whereas many of the minor species  
502 such as *Portunus pelagicus*, *Terapon jarbua*, *Platycephalus indicus*, and *Sillago sihama* were also found  
503 in mudflat catches suggesting more widespread use of coastal habitats. Further evidence of the  
504 distinct and significant differences in the species composition of catches from mangroves and mudflats  
505 are provided by PCoA and PERMANOVA analysis (S1.). We modelled the source contribution of  
506 mangroves to the tissue of migratory fauna, based on using yellow mangrove leaves but omitted MPB  
507 from the analysis to simplify the otherwise complicated isotopic influences between mangrove litter,  
508 MPB and sediment. We feel justified in this approach, because the biomass and productivity of MPB  
509 is very low in Qatar and the carbon incorporated into the MPB is of mangrove in origin (Davis et al.  
510 2009, Walton et al. 2014). Further discussion of the interpretation of the isotopic evidence related to  
511 MPB is presented in the supplementary material (S2). The isotope Bayesian mixing models suggested

512 that the contribution of mangrove carbon to the tissue of the migratory fauna ranged from 21 to 58%,  
513 with *P. khori* most reliant on the mangroves as a carbon source. The high reliance of *P. khori* on  
514 mangrove material as a dietary source is likely due to its strong attachment to the mangroves, it is a  
515 mangrove resident that has never been found in catches over the surrounding mudflat/seagass beds  
516 (Al-Maslamani et al. 2013).

517 Mangroves are found intertidally between mean sea level and high water, although these vary with  
518 location (Ellison 2009). In Qatar, mangroves are found 0.2 m above mean sea level, and from tidal  
519 charts we estimated that the mangroves were dry for 60% of the time when migratory fauna are  
520 forced out of the mangrove, where they continue to respire and excrete mangrove-sourced nutrients.  
521 We found that of the mangrove material consumed, 34 kg C ha<sup>-1</sup> yr<sup>-1</sup> (i.e. 90% from Pauly and  
522 Christensen 1995) is lost through excretion/respiration but only 60% is lost outside the mangrove  
523 while the tide is out and is thus estimated to be 20.8±18.0 kg C ha<sup>-1</sup> yr<sup>-1</sup> or 0.8% of leaf litter production.  
524 We assumed that this carbon loss was lost in proportions equal to that of the carbon composition of  
525 the migratory fauna, so that the tissue and excretion of *A. dispar* had a carbon content of 40%  
526 mangrove, 32% phytoplankton and 28% seagrass. The increase in metabolism after eating, known as  
527 specific dynamic action, indicates that respiration rates are not uniform (Jobling 1981). Similarly  
528 digestion times and assimilation efficiency, as mangrove carbon is regarded as especially refractory  
529 (Rodelli et al. 1984) may result in the unequal release of consumed material in neighbouring habitats.  
530 The impact of this could be explored further however it is unlikely to significantly increase the  
531 proportion mangrove carbon outwelled by fauna.

532 The values reported for outwelled POC and DOC of around 30% each of leaf litter production (Bouillon  
533 et al. 2008a), are much larger than our estimates of outwelled C in fish biomass (mortality estimates).  
534 However mangrove carbon outwelled as fish tissue, may be of much greater importance to coastal  
535 food webs than DOC or POC, as it directly enters at a high trophic level through predation; fish biomass  
536 in the present study had an average trophic level of ~3. Hence, while faunal-mediated direct export of

537 mangrove matter might be a small fraction of primary productivity, it may be much more significant  
538 to coastal fisheries than carbon outwelled as DIC, POC and DOC that has to pass through various  
539 trophic levels, before being incorporated into an exploitable species, with the potential associated  
540 trophic transfer loss by two orders of magnitude (Pauly and Christensen 1995). Moreover, while  
541 mangrove POC is highly refractory with high C:N ratios of 20 -30 (Canfield et al. 2005) but enriched  
542 compared to recently fallen leaf litter (Mean C:N  $\pm$  1SD = 93.7  $\pm$  9.8 unpublished data), mangrove  
543 carbon outwelled as mortality of fish biomass has a C:N of 4.2 to 5.1 that is more easily assimilated by  
544 consumers. In the studied mangroves (201 ha), the total outwelling associated with the mortality of  
545 the migratory fauna is equivalent to 96 kg of mangrove C yr<sup>-1</sup> or 947 kg yr<sup>-1</sup> of mangrove derived fish  
546 biomass wet weight. If commercial species were preying directly on the this outwelled mangrove fish  
547 biomass, this small area of mangrove may support commercial fish catches of 95 kg yr<sup>-1</sup>, using the 10:1  
548 trophic efficiency ratios of Pauly and Christensen (1995). However this does not consider the greater  
549 quantities of carbon outwelled through respiration and excretion by the mobile fauna.

550 The amount of the mangrove litter that is consumed is related to the biomass of the migratory fauna.  
551 *A. dispar* formed 80% of the biomass and is responsible for 91% of the mangrove carbon consumed  
552 (Table 3), the proportions are not equal as this species also had the highest consumption rate. We  
553 highlighted earlier, the impact of reducing consumption rates of *A. dispar* from 52 to 24, on the  
554 decreased mangrove consumption by the migratory fauna. The other important factor influencing  
555 mangrove consumption is the dietary reliance on mangrove as estimated by isotopic modelling, the  
556 biomass and consumption rates of *P. khori* and minor species are similar but isotopic values of *P. khori*  
557 suggest 57% of its diet is mangrove derived compared to the 22% of minor species resulting in  
558 consumption rates of mangrove that are much greater (Table 3). Our faunal biomass sampling  
559 indicates that arid mangroves support similar richness of migratory fauna to other mangroves (Table  
560 3). The differences in species composition and biomass found between the Al Khor mudflat and our  
561 experimental mangrove forest sites suggests that the faunal outwelling is specific to mangrove sites  
562 and not generalized coastal outwelling. To determine if the lack of rainfall at the current sites might

563 have some influence on the biomass of migratory fauna, and hence one of the most important factors  
564 in faunal consumption and outwelling of mangrove carbon, we compiled data from other studies that  
565 estimated mobile faunal biomass from around the world (Table 3). We used Pearson's correlation  
566 analysis to examine strength and direction of any relationship between logged biomass of mobile  
567 mangrove fauna with annual rainfall, logged total mangrove area, logged mean trap catchment area,  
568 and species numbers using the values given in Table 3. We found no relationships between faunal  
569 biomass and annual rainfall, nor with mangrove area, nor mean trapped area, nor the number of  
570 species ( $p>0.05$ ). Of course it is likely that other factors such as mangrove productivity, retention of  
571 productivity within the mangrove, and the amount bioprocessed within the mangrove, as well as  
572 faunal biomass in surrounding habitats will be important in influencing the biomass of mobile faunal  
573 that feeds in the mangrove forests. Hence, there may well be differences between old and new world  
574 mangrove due to the feeding traits of the mangrove fauna that can impact energy flow (McIvor and  
575 Smith 1995, Lee 1998). As the biomass of migratory faunal does not relate to aridity, we cautiously  
576 suggest that the results of the current study ought to be applicable to other higher rainfall areas.  
577 Rainfall-generated wash out of particulate mangrove carbon can lead to less defined isotopic  
578 boundaries, so that it becomes impossible, using stable isotopes, to determine whether mangrove  
579 carbon in mobile fauna is outwelled or derives from the ingestion of previously outwelled mangrove  
580 material. However in old world mangroves where the leaf litter is highly processed (McIvor and Smith  
581 1995, Lee 1998) and there is a large biomass of migratory fauna a correspondingly great proportion of  
582 the mangrove carbon may be faunally outwelled. However we suggest that migratory faunal biomass  
583 and amount (not proportion) of mangrove C exported by this faunal group are likely to be correlated.

584 Table 3: Estimates of fish biomass and number of species reported in mangrove forests around the  
585 world with estimates of total mangrove area, sampled mangrove area and annual rainfall. Sampling  
586 gears both measure density though by catching fauna from a known area of mangrove. Block nets by  
587 blocking the seaward migration of fauna during the ebbing tide, and enclosure nets are nets raised at  
588 high tide that enclose an area of mangrove.

Location and habitat	Total Mangrove Area (ha)	Annual rainfall (mm)	Trap catchment area (m <sup>2</sup> )	Sampling gear	No. spp.	Biomass mean $\pm$ SD (g m <sup>-2</sup> )	Source
Bahía Málaga, Pacific Columbia	4400	7399	6245	Block net	50	0.851 $\pm$ 1.194	Castellanos-Galindo and Krumme (2013)
Caeté Estuary, North Brazil	9900 <sup>(1)</sup>	2545	5896	Block net	49	2.1	Barletta et al. (2003)
Everglades National Park, USA	144447 <sup>(2)</sup>	1520	42	Block net and rotenone	63	14	Thayer et al. (1987)
Solomon Islands, Pacific Ocean	64200 <sup>(3)</sup>	3541 <sup>(4)</sup>	83.6	Block net and rotenone	85	11.6 $\pm$ 12.4	Blaber and Milton (1990)
Moreton Bay, Eastern Australia	15200 <sup>(5)</sup>	1008	3340	Enclosure net	41	25.3 $\pm$ 20.4	Morton (1990)
Embley River, Northern Australia	8300	1787	585	Enclosure net	55	3.9	Vance et al. (1996)
Pagbilao Bay, Philippines	110.7	2242	161	Enclosure net	46	10.4 $\pm$ 13.2	Ronnback et al. (1999)
Gazi Bay, Kenya	661	1074	9	Enclosure net	49	0.9 $\pm$ 1.5	Crona and Ronnback (2007)
Qeshm Island, Iran	6750	200	6837	Block net	26	0.0085 $\pm$ 0.02	Shahraki and Fry (2016)
Al Khor & Al Dhakira, Qatar	234.5	75	5400	Block net	20	1.4 $\pm$ 0.8	This study

589 <sup>1</sup> Wolff et al. (2000); <sup>2</sup> Simard et al. (2006); <sup>3</sup> UNEP (2006); <sup>4</sup> SOPAC (2007); <sup>5</sup> Accad et al. (2016)

590

591 Conclusions

592 This study presents a first estimate of the proportion of the primary productivity that may be  
593 outwelled by mobile aquatic species through the phenomenon known as trophic relay. The study  
594 indicates that only small amounts (1.4%) of mangrove leaf litter produced is consumed and only 0.8%  
595 outwelled by fauna via two modes: through the excretion and respiration of the ingested mangrove  
596 matter by migratory fauna during low water periods when the mangroves are dry; and through the  
597 mortality of migratory fauna. Our trapping studies produced biomass estimates with lower statistical  
598 variation than other studies, and our isotopic evidence supports the dietary reliance of migratory  
599 fauna on mangrove production. Our sites were flooded just 40% of the time, meaning that these  
600 water-dependent fauna were spending at least 60% of the time in habitats subtidal to the mangrove.  
601 We suggest arid mangroves are ideal sites for studying the faunal movement of carbon due to the lack  
602 of rainfall driven outwash of mangrove carbon that increases the certainty that the mangrove carbon  
603 in the tissues of mobile fauna originated from feeding within the mangrove forest. We suggest that  
604 the biomass of migratory fauna moving between mangrove and subtidal habitats and the amount of  
605 faunally outwelled mangrove carbon is likely to be highly correlated. However the proportion of NPP  
606 that is faunally outwelled may vary according to the difference in mangrove leaf litter processing and  
607 retention in old and new world mangrove. The differences in biomass estimates from mangrove  
608 forests in some other regions of the world suggest that migratory faunal biomass has the potential to  
609 contribute correspondingly more to the outwelling of carbon. Finally, although the proportion of  
610 faunal outwelled carbon is small, that carbon is more readily bioavailable to coastal foodwebs than  
611 other forms of outwelled carbon (DIC, DOC & POC), given the value of fauna to higher consumers in  
612 the coastal foodweb. Thus, faunal-mediated carbon export may be of much greater significance, for  
613 example in support of commercial fish biomass, than its relatively small proportion of the total  
614 mangrove carbon budget suggests. The small proportion of carbon outwelled by migratory fauna  
615 supports the current mass-balance models that suggest 40-50% of mangrove production is indeed  
616 outwelled as DIC.

617



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626

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CRediT author statement

**M. Walton:** Conceptualization, Methodology, Writing- Original draft preparation; **I. Al-Maslamani:** Investigation, Writing - Review & Editing; **M. Chatting:** Investigation, Writing - Review & Editing; **D. Smyth:** Investigation, Writing - Review & Editing; **A. Castillo:** Investigation, Writing - Review & Editing; **M.W. Skov:** Methodology, Investigation, Writing - Review & Editing; **L. Le Vay:** Methodology, Investigation, Writing - Review & Editing, Supervision.

**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: