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1 Does a bigger mouth make you fatter? Linking intraspecific gape
2 variability to body condition of a tropical predatory fish

3
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19
20 **Declaration of authorship.** A.J.K., D.A.C., J.D.O., M.J.K., M.M.D and T.M.S. conceived
21 the study. A.J.K., D.W. and O.J.L collected the data. O.J.L. analyzed the data and wrote the
22 first draft of the manuscript and all authors contributed to revisions.

23

24

25 **Abstract**

26 In gape-limited predators, gape size restricts the maximum prey size a predator is capable to
27 ingest. However, studies investigating the energetic consequences of this relationship remain
28 scarce. In this study we tested the hypothesis that gape-size variability influences individual
29 body condition (a common proxy for fitness) in one of the largest freshwater teleost
30 predators, the barramundi. We found that individual barramundi with larger gapes relative to
31 body size had higher body condition values compared to conspecifics with smaller gapes.
32 Body condition was highest soon after the wet-season, a period of high feeding activity on
33 productive inundated floodplains, and body condition decreased as the dry-season progressed
34 when fish were restricted to dry season remnant habitats. The increased condition obtained
35 during the wet season apparently offsets weight loss through the dry season, as individuals
36 with large gapes were still in better condition than fish with small gapes in the late dry
37 season. Elucidation of the links between intraspecific variability in traits and performance is a
38 critical challenge in functional ecology. This study emphasizes that even small intraspecific
39 variability in morphological trait values can potentially affect individual fitness within a
40 species' distribution.

41

42 **Key-words:** barramundi, gape limitation, *Lates calcarifer*, morphological trait, wet-dry
43 tropics

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45

46

47 **Introduction**

48 Mouth size, or oral gape, is perhaps the most important factor influencing the feeding
49 behaviour of predatory animals (Maret and Collins 1996; Urban 2007; Detmer et al. 2018).
50 Predation opportunities are gape-limited when a predator's diet is constrained to items they
51 can only swallow whole (Hambright 1991). Recent decades have witnessed a renewed
52 interest in the study of animal gape morphology because of its apparent role in species
53 invasions. For example, larger gapes favor the dispersal of nonnative loquat plant seeds by
54 crows (Voshikawa and Higuchi 2018) and gape-limitation in predators facilitates
55 establishment of fast-growing nonnative freshwater fishes (Vatland and Budy 2007), whereas
56 selective pressures have favored smaller gapes in native snakes to limit the ingestion of
57 poisonous invasive cane toads (Phillips and Shine 2004).

58 Gape limitation is particularly prominent in limbless animals such snakes and fish,
59 which generally swallow their food whole (Forsman 1996). Studies evaluating predator-prey
60 size relationships among fishes report that average body size of prey consumed increases
61 with predator gape size (Schmitt and Holbrook 1984; Persson et al. 1996; Scharf et al. 2000;
62 Magnhagen and Heibo 2001). The importance of gape limitation in fish predator-prey
63 relationships is also demonstrated by the prevalence of prey defense mechanisms designed to
64 constrain passage through a predators' oral gape; for example, long dorsal and pectoral
65 spines, body inflation and extreme lateral compression of body shape (Hobson 1979; Nilsson
66 and Brönmark 2000). Conversely, prey exposed to nongape-limited predators are often small,
67 lack defenses, or exhibit reduced morphological defense (e.g., Kristjánsson et al. 2002). This
68 has led to evidence for directional selection on prey traits based on gape limitation of
69 predators (e.g., Miehl et al. 2014).

70 Inter-specific variability in gape- to body-size ratio is a commonly used trait in studies
71 of fish functional ecology (Villéger et al. 2017). Species with larger size-specific gape sizes

72 are assumed to be able to forage on a wider range of prey sizes than species with relatively
73 smaller mouths (Gatz 1979). Comparative trait analyses have found that variability in gape
74 size among species influence feeding mode, trophic guild position and diet overlap (Gerking
75 1994; Karpouzi and Stergiou 2003; Albouy et al. 2011). For example, ambush fish piscivores
76 tend to have large gape sizes, allowing them to better engulf large individual prey (Juanes et
77 al. 2002). By contrast, fish that feed on zooplankton or small benthic invertebrates tend to
78 have small gapes relative to body size, as small gapes help increase suction power when
79 associated with long snouts (Gerking 1994; Norton 1995; Cooper et al. 2017).

80 Within species, maximum swallowing capacity often defines the amount of food
81 available to an individual to consume (Forsman 1996). Gape size and swallowing capacity
82 increase with body length, but there is often natural residual variation in gape size among
83 individuals of the same body size (Forsman 1996; Forsman and Shine 1997). The extent to
84 which intraspecific variability in relative gape size (i.e. gape size adjusted for the individual
85 body length) influences foraging success and fitness of individuals has not been widely
86 tested. A theoretical model, which is supported by data from snake feeding experiments,
87 predicts a positive relationship between net energy gain and relative gape size (Forsman
88 1996). However, the relationship between relative gape size and individual fitness in fishes
89 remains unexplored.

90 Body condition is generically described as the well-being or robustness of an
91 individual (Pope and Kruse 2007), and is an indicator of foraging success and, ultimately,
92 fitness (Jakob et al. 1996). Body condition has typically been estimated by 1) comparing an
93 individual weight to a standard weight for a given length and assuming that larger ratios
94 (condition index) reflect a better physiological state or 2) by directly measuring physiological
95 parameters related to energy stores, such as tissue lipid content (Bolger and Connolly 1989;
96 Peig and Green 2009). Measures of condition are commonly used as an indicator of tissue

97 energy reserves, with the expectation that individuals in good condition should demonstrate
98 relatively high growth rates, reproductive potential, and survival (Sutton et al. 2000).
99 Furthermore, at a population level, body condition is used to measure the overall health or
100 fitness of a population, particularly reflecting the abundance and quality of food resources
101 available.

102 In the wet–dry tropics of northern Australia, rivers are characterized by strong
103 seasonality in their flow regimes (Warfe et al. 2011), which is thought to drive significant
104 fluctuations in food resources and individual fish condition (Bishop et al. 2001). In the wet
105 season, floodplains and associated riparian zones become inundated, allowing the lateral
106 movement of fish for feeding (Jardine et al. 2012). In the dry season, flows either cease or
107 low flows are maintained by sub-surface and local groundwater flow (Kennard et al. 2010).
108 The reduction or loss of aquatic connectivity during the dry season potentially imposes
109 limitations on food availability, consequently inducing seasonal variability in fish body
110 condition and growth rate (Balcombe et al. 2012; 2014; Xiao 2000).

111 Here, we use a large predatory riverine fish as a model organism to test the widely
112 held though poorly validated hypothesis that gape size variability influences individual
113 fitness. Furthermore, while we expect antecedent conditions (particularly flow) to influence
114 body condition (Hoeinghaus et al. 2006), we also hypothesize that fish with larger relative
115 gapes will be better able to capitalize on wet season periods of high food availability when
116 compared to fish with smaller gapes. It was demonstrated that it is energetically
117 advantageous for individuals to select large prey (Norin and Clark 2017). Therefore, our
118 expectation is that large-gaped individuals will have better body condition (a common proxy
119 for fitness), at the end of the wet season and offset condition decay over the dry season, thus
120 resulting in a positive relationship between relative gape size and body condition.

121

122 **Material and Methods**

123 The barramundi, or Asian sea bass, *Lates calcarifer* (family Latidae), is a large (~180 cm
124 maximum total length) iconic teleost predator inhabiting tropical and semi-tropical coastal
125 seas, estuaries, and river waters of the Indo-West Pacific Region (Pusey et al. 2004). It is
126 highly regarded as a trophy and food fish in recreational and commercial fisheries, resulting
127 in significant economic importance in some parts of Australia (Ebner et al. 2016; Saunders et
128 al. 2018). Barramundi are sequential, protandrous hermaphrodites with complex biology and
129 life-history characteristics showing much variability at individual and population levels
130 (Crook et al. 2017). It exhibits an ontogenetic shift in diet, preying predominantly on macro-
131 crustaceans as juveniles and becoming increasingly piscivorous as adults (Pusey et al. 2004).
132 Prey are swallowed whole, drawn into the mouth by an extremely powerful sucking action
133 effected by the rapid expansion of the buccal cavity (Davis 1985). Gape size in barramundi,
134 therefore, imposes physical limitations on the potential maximum size of prey that can be
135 consumed (Davis 1985; Mihalitsis and Bellwood 2017) and, consequently, affects fish energy
136 budgets by constraining feeding opportunities.

137 Field collection of wild barramundi was performed on four sampling occasions across
138 one year, encompassing a range of river flow conditions (Fig. 1) from the 2016 late-dry
139 season (October-November 2016), to the next early dry season (May-June 2017), mid-dry
140 (August 2017) and the late-dry season (late September-November 2017). Using boat
141 electrofishing and gill net fishing, 197 barramundi individuals with sizes ranging from 310 to
142 872 mm (standard length, SL) were collected from 11 sites in seven rivers in the Australia's
143 Northern Territory (Fig. 1b, Table 1). Barramundi of similar sizes were collected on each
144 sampling season (Fig. 2; ANOVA d.f. = 193, $F = 1.743$, $P = 0.16$). Fish were euthanized
145 using an overdose of Aqui-S, placed on ice and transported to the laboratory and stored in a
146 freezer at -20°C prior to measurement. All fish caught was measured (SL) to the nearest mm

147 and weighed on an electronic scale to the nearest mg. In addition, the mouth depth (Md) and
148 mouth width (Mw) were measured to the nearest mm using Vernier calipers. Relative gape
149 (RG) was calculated by the product of Md and Mw standardized by SL (Karpouzi & Stergiou
150 2003):

151

$$152 \quad RG = \frac{Md * Mw}{SL^2}$$

153

154 The relative condition factor index (K_n) was calculated for individual samples using the
155 following equation:

$$156 \quad K_n = \frac{W}{W'}$$

157 Where W is individual fish weight and W' is the predicted length-specific weight based on ln
158 transformed pooled data of all individuals collected for this study (Pope and Kruse 2007).

159 We tested the effect of RG and season on K_n using a linear mixed-effect (lme) model.
160 Because variation in fish condition may reflect multiple environmental and ecological factors
161 (e.g. habitat, prey availability, parasites and competition), we included the sampling site as a
162 random factor to account for these potential spatially varying effects. The lme model was
163 fitted using the packages 'lme4' (Bates et al. 2018) and 'lmerTest' (Kuznetsova et al. 2018)
164 in the statistical programming language R 3.6.0 (R Development Core Team 2019).

165

166 **Results**

167 Relative mouth gape of barramundi varied substantially among individuals, showing a 2.74-
168 fold increase from the lower to the higher range endpoints. The condition factor also varied
169 considerably among barramundi individuals and across seasons, increasing 2.12-fold across
170 its range and peaking in the early dry season and reaching its lower values in the late-dry

171 season (Fig. 3a). The lme model indicated both relative gape size and season as significant
172 factors predicting barramundi condition factor (Table 2). Gape size was positively related to
173 condition factor (Fig. 3b) and the slope of this relationship in the early dry season was
174 significantly higher than in all other seasons (Table 1). No statistically significant interaction
175 detected between RG and Season was detected. The relationship between gape size and
176 condition factor is robust regardless of whether condition factor is estimated from all
177 individuals pooled across all seasons (present analysis; Fig. 3b; Table 1) or estimated
178 separately for each season only from individuals captured in that season (Fig. S1, Table S2).

179

180 **Discussion**

181 Association between variability of relative mouth gape size and individual fitness remain
182 relatively unexplored. We found that barramundi, a high-order aquatic predator of rivers in
183 tropical Australia, with larger gape relative to body length exhibited higher body condition
184 values than conspecifics with smaller gapes. In gape-limited predators, gape size is widely
185 correlated with the maximum prey size a predator is capable of ingesting (Schmitt and
186 Holbrook 1984; Hambrigh 1991; Scharf et al. 2000). However, studies investigating the
187 energetic consequences of this relationship are very scarce. Forsman (1996) has shown that
188 snakes with similar body sizes but higher relative gape size benefit from a higher rate of net
189 energy gain and therefore, fitness. Our finding broadens the taxonomic coverage of this
190 relationship, filling an important gap in understanding the potential outcomes of intraspecific
191 morphological variability on the fitness of gape-limited fish predators.

192 We found that barramundi body condition peaked soon after the wet-season and that
193 body condition decreased as the dry-season progressed. The effect of seasonality on body
194 condition has been previously reported for some species inhabiting Australian rivers
195 (Balcombe et al. 2012; 2014), including barramundi (Bishop et al. 2001). In northern

196 Australia, peak feeding activity by barramundi occurs during the wet season when fish often
197 move onto temporarily inundated and highly productive floodplains (Crook et al. 2017; Pettit
198 et al. 2017) and declines during the dry season when fish are restricted to river channels and
199 off-channel waterholes (Davis 1985; Bishop et al. 2001). Consequently, the relatively high
200 body condition of barramundi observed during the early dry season is likely the result of
201 elevated food availability and high feeding activity during the wet season. It is perhaps not
202 unexpected, therefore, that the relationship between gape size and body condition was
203 stronger in the early-dry than in the mid- and late-dry seasons (Table 1, Fig. 3a), because that
204 is the time of year when feeding opportunities are at the greatest and barramundi can reap the
205 predatory benefits of having a large gape. Migration of fish onto floodplain habitats to access
206 rich food resources during the tropical wet season has been widely reported (Arrington et al.
207 2005; Anderson et al. 2009), with the pulsed input of energy and nutrients during such
208 periods considered a key driver of ecosystem productivity (Winemiller and Jepsen 1998).
209 Further research on the relationships between food resource availability, gape size and body
210 condition in other systems, and across functional feeding groups, would shed light on the
211 generality of our findings for fishes and other taxa.

212 Gape size also plays a role in mediating the effects of resource fluctuations on fish
213 condition. For example, individuals with large relative gape size in the late dry season have
214 equal or better body condition than small gaped individuals in the early-dry season. To cope
215 with variable food resource levels, fish store energy as fat during productivity booms,
216 enabling them to survive through extended periods of limited food resources and allocate
217 energy for reproduction (Balcombe et al. 2014). Our results suggest that individuals with
218 large gapes may be able to capitalize on the many feeding opportunities provided by rivers
219 and their wetlands during floods, gaining more weight than conspecifics with similar length
220 but smaller gapes. The good condition obtained in the late-wet/early-dry period apparently

221 offsets weight loss through the dry season, as individuals with large gapes were still in better
222 condition than fish with relatively small gapes in the late-dry season.

223 Given the intimate associations between food intake and nutritional gain, we suggest a
224 likely causal relationship between relative gape size and body condition. Nonetheless, other
225 factors can potentially influence variability in relative gape size and body condition. First,
226 piscivores may frequently consume prey much smaller than their maximum gape limitation
227 (Juanes 1994). Second, rapid changes in prey availability like invasion of a novel prey
228 (Cattau et al. 2018), different prey densities and types (Magnhagen & Heibo 2001) and
229 foraging in multiple habitats (Ehlinger & Wilson 1988) are thought to produce intra-specific
230 morphological variability through phenotypic plasticity. Further studies on gape size
231 plasticity under different conditions should generate fruitful insights into the role of
232 individual variation in driving ecomorphological responses to a rapidly changing
233 environment.

234 Species traits, rather than taxonomic species, are increasingly acknowledged as
235 providing new opportunities to enhance our understanding of ecological patterns and
236 processes operating in nature (McGill et al. 2006). Traits have now become the central
237 component of the growing area of functional or trait-based ecology, where ‘functional traits’
238 relate to the performance (growth rate, survival, reproduction) of an organism and/or its
239 contribution to ecological processes (Violle et al. 2007). However, trait-based studies in fish
240 ecology typically use phenotypic traits as proxies for functions and most of these
241 relationships have been tested only for a few fish families. This study provides empirical
242 support for a mechanistic link between gape size and individual performance in a gape-
243 limited predatory fish. We caution, however, that this result may not apply to fishes that feed
244 at other trophic levels. Species that do not swallow their food whole, like browsing
245 herbivores or detritivores, for example, are not gape limited and therefore gape size may not

246 influence their rate of energy acquisition and condition. Further tests investigating
247 correlations between gape size and body condition across a range of species with distinct diet
248 strategies are needed to assess the generality of our findings.

249 Elucidating the links between intraspecific variability in traits and performance is a
250 key challenge for fish ecologists and in functional ecology more generally (Violle et al. 2012;
251 Villéger et al. 2017). Recent meta-analysis points to comparable ecological importance of
252 variation within species versus variation among species (Des Roches et al. 2018). Plasticity in
253 species' functional traits can occur at a range of spatial scales in response to varying biotic
254 and abiotic conditions (e.g. Blanck and Lamouroux 2007; Messier et al. 2010; Hall et al.
255 2018). In practice, however, values for most traits are recorded for a set of individuals and
256 these values are averaged at the species level assuming that intraspecific variability is weak
257 compared to interspecific variability (known as the "mean field approach"). This study
258 emphasizes that even small intraspecific variability in trait values can result in marked
259 differences in individual performance over a portion of species' distribution.

260

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268

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443 **Table captions**

444 Table 1. Number of individual barramundi collected per site and season.

445

446 **Table 2.** Parameters of the linear mixed-effect model predicting variation in barramundi
447 condition factor (K_n) as a function of relative gape size and season of sampling (fixed
448 effects), with site as a random effect. Presented are parameter estimates (\pm standard error),
449 degrees of freedom (d.f.), test statistic (t-value) and probability (p -value). Reference levels
450 for the 'season' category were set as 'Early dry'17'.

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453 **Figures Captions**

454

455 Figure 1. (a) Mean daily discharge in the Adelaide River during the study period. The timing
456 of fish sampling periods is indicated with black bars. (b) Location of fish sampling sites
457 (green circles) in the four study rivers. Inset map shows the location of the study region in
458 northern Australia. Discharge data shown in (a) was sourced from stream gauge located at the
459 Adelaide River fish sampling site indicated in (b) with crossed green circle.

460

461 Figure 2. Scatter plot of the length-weight relationship of the fish collected for each sampling
462 season.

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464 Figure 3. (a) Seasonal variation in barramundi condition factors (K_n). Vertical lines, grey
465 bars, black horizontal lines and black dots represent, respectively, data upper and lower
466 extremes, interquartile range, median and outliers. (b) Relationship among barramundi

467 condition factor (K_n) and relative gape for each sampling season. Lines are the predicted
468 values of the lme model for each season plus the 95% CI.
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