

1 **Habitat complexity and food item size modify the foraging behaviour of a freshwater**
2 **fish**

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12 **Running headline:** Fish foraging modifications

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25 **Abstract**

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27 The functional response describes the relationship between feeding rate and prey density, and
28 is important ecologically as it describes how the foraging behaviour of an animal changes in
29 response to food availability. The effects of habitat complexity and food item size was
30 experimentally tested here on the foraging parameters and the functional responses of the
31 freshwater fish roach *Rutilus rutilus* (L.). Habitat complexity was varied through the
32 manipulation of substrate and turbidity, and food item size was varied by using fishmeal
33 pellets, in two sizes. As water turbidity and substrate complexity increased, the reaction
34 distance and consumption rate of the fish significantly decreased. Increased food item size
35 significantly decreased consumption rates but had no influence on any other foraging
36 parameter. Analysis of the interactions between substrate complexity, turbidity and food item
37 size revealed food item size had the greatest influence on consumption rate. Turbidity has the
38 least effect on all the foraging parameters tested. Across all experiments, the functional
39 responses were best described by the Type II response, a relatively consistent finding for *R.*
40 *rutilus*. These outputs reveal that fish foraging behaviours and functional responses are highly
41 context dependent, varying with environmental parameters and the availability of prey of
42 different sizes.

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47 **Key words:** Foraging behaviour, Type II functional response, consumption rate, prey size,
48 abiotic, *Rutilus rutilus*

49 **Introduction**

50

51 The functional response is the relationship between the feeding rate of a forager and its prey
52 density, and is used to describe and model foraging behaviour (Solomon 1949; Holling 1959;
53 Holling 1966). It is an ecologically important metric as under conditions of limited resource
54 availability, individuals will attempt to maximise their energy intake whilst minimising the
55 costs associated with prey searching and handling (Galarowicz & Wahl, 2005; Oyugi et al.
56 2012a,b; Murray et al. 2013). Consequently, measuring how animals respond to variations in
57 food availability helps the understanding of how individuals optimise their foraging
58 behaviour (Werner et al. 1983; Galarowicz & Wahl, 2005; Murray et al. 2013). This provides
59 knowledge to assist interpretation of the effect of prey availability on consumer condition,
60 growth and fitness (Werner et al. 1983). Moreover, functional responses provide insights into
61 the mechanics of consumer-prey relationships that can have cascading effects through the
62 food web (Koski & Johnson, 2002). They have considerable ecological applications with, for
63 example, their use as important parameters within individual based models (e.g. Stillman
64 2008) and as explanatory variables in the success of invasive species (e.g. Bollache et al.
65 2008; Dick et al. 2013).

66

67 Due to how consumers can influence the structure and stability of their prey populations
68 (Alexander et al. 2013), it is ecologically important to distinguish the type of functional
69 response being exhibited (Murray et al. 2013). There are three major function response types:
70 I, II and III (Hassell et al. 1977). Type I describes a linear increase in feeding rate with prey
71 density until it reaches a constant value at saturation (Jeschke et al. 2004) whereas the feeding
72 rate of the Type II response increases at a decreasing rate with prey density until it reaches its
73 maximum value (Holling 1959; Murray et al. 2013). Type II is thus inversely density-
74 dependent and so for the prey population, mortality risks decrease with increasing density

75 (Jeschke & Hohberg, 2008). The Type III response describes a sigmoidal, density-dependent
76 relationship, where an initial increasing risk of prey mortality switches to a decreasing risk of
77 mortality as the prey density increases above a threshold level (Real 1979; Morgan & Brown,
78 1996).

79

80 Despite their apparent simplicity, it has been established that functional responses are not
81 fixed within specific predator–prey relationships; conversely, under different contexts,
82 foraging and anti-predator behaviours can shift and significantly alter the form of the
83 response (Holling 1959; Alexander et al. 2013). This may involve subtle changes in, for
84 example, the ability of the consumer to detect and respond to the presence of prey items, or
85 may even involve a shift in the functional response type should there be, for example, a
86 substantial increase in the time spent foraging (Abrams 1982). Environmental variables that
87 have been found to influence functional responses, e.g. temperature and light levels (Lipcius
88 & Hines, 1986; Koski & Johnson, 2002), and also habitat structure (Alexander et al. 2012).
89 Indeed, habitat structure and complexity have been found to both alter the search ability of
90 the consumer (Savino & Stein, 1989; Heck & Crowder, 1991) and the refuge area of their
91 prey (Gotceitas 1990; Warfe & Barmuta, 2004; Alexander et al. 2012). Prey body size might
92 also be important in determining the values of foraging parameters, given trade-offs between
93 the ease of detection of larger items versus their increased handling time and energetic
94 profitability (Wankowski & Thorpe 1979; Bean & Winfield, 1983; Oksanen & Lundberg,
95 1995). Nevertheless, there remains a paucity of information on how foraging behaviours are
96 modified between simple and more complex habitats for specific taxonomic groups, such as
97 many benthic feeding freshwater fishes.

98 Consequently, the aim of this study was to determine how effects of habitat complexity
99 and prey item size, and their interactions, modify the foraging parameters and functional

100 response of a model freshwater fish, whose foraging behaviour is generally reliant on visual
101 cues (Hjelm et al. 2003; Bogacka-kapusta 2007). The model species selected was roach
102 *Rutilus rutilus* (Diehl 1988; Murray et al. 2013), a freshwater fish ubiquitous to many
103 temperate European freshwaters (e.g. Lappalainen et al. 2008) and invasive in others (e.g.
104 Elvira & Almodovar, 2001; Winfield et al. 2011). Their ecological importance includes their
105 potential for invoking cascading effects on freshwater ecosystems through their high
106 zooplankton grazing rates (e.g. Jeppesen et al. 2010) and thus understanding the context-
107 dependency of their foraging behaviours and functional responses can be ecologically
108 significant. Previous studies have indicated *R. rutilus* can exhibit a Type II (e.g. Johanson &
109 Persson 1986; Persson 1987; Murray et al. 2013) and Type III (Winkler & Orellana, 1992)
110 response. These were, however, based on a range of field and experimental approaches,
111 making inter-study comparison of outputs difficult. Thus, here we build on the study of
112 Murray et al. (2013) who used highly controlled experimental conditions to reveal that in a
113 simple environment *R. rutilus* demonstrated a Type II response. We tested the prediction that
114 increases in both habitat complexity and food item size will significantly modify *R. rutilus*
115 foraging behaviour through significantly reduced reaction distance and consumption rate, and
116 increased searching time, handling time and reaction distance, impacting their functional
117 response.

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123 **Methods**

124

125 *Ethical note*

126 All animal work was conducted in accordance to national and international guidelines to
127 minimize discomfort to animals. All regulated procedures completed under the Animals
128 (Scientific Procedures) Act 1986 were licensed by the UK Home Office under project licence
129 number PPL 30/2626. The Ethics Review Panel of the School of Applied Sciences of
130 Bournemouth University approved this project licence.

131

132 *Experimental design overview*

133 The experimental design used replicated groups of three *R. rutilus* individuals in
134 experimental arenas, exposed them to different numbers of prey items (10, 25, 50, 100 or
135 150) and captured their foraging behaviours using a two-camera videography system. One
136 camera was positioned horizontally, facing the side of the tank, with the second camera
137 positioned vertically, above the surface of the water. The actual positions and distances
138 moved by the fish were calculated using trigonometry based on footage from both cameras
139 (Murray et al. 2013). The specific details of the experimental arena, video capture, validation
140 of fish movement data, and the use of the Hollings Disc equation for the Type II functional
141 response are detailed in Murray et al. (2013). In summary, there were 12 behavioural arenas
142 (fish aquaria of $0.46 \times 0.31 \times 0.39$ m) in the experiments that were maintained at 18°C on a
143 12:12 hour light/ dark regime. Three randomly selected roach from a batch of 78 fish
144 (average length = 129 mm \pm 2.5 mm; age 1+ years) were introduced into each arena and
145 allowed to acclimatize to the tanks for 14 days prior to the start of the experiments.

146 Throughout the acclimatization and experimental period, the food items used were
147 pelletized fish-meal ('pellets'). This was due to: (i) the experimental fish were originally

148 farmed fish that had been reared on pellets and so were used to consuming them; (ii) cyprinid
149 fish (such as *R. rutilus*) tend to respond well to such pellets in foraging experiments in tanks
150 (e.g. Britton et al. 2012; Oyugi et al. 2012a,b); (iii) as a non-motile 'prey' item that can
151 neither actively select a refuge area, nor display evasive behaviour, measuring the effect of
152 habitat complexity on the consumer would not be confounded by changes in the behaviour of
153 their prey; and (iv) pellets are available in different sizes so food item size could be easily
154 and accurately manipulated. Note that when compared to live prey, the use of pellets
155 precludes the display of more complex foraging behaviours under certain conditions, as prey
156 mobility has been shown to influence feeding rates both negatively, through the confusion
157 effect (whereby large numbers of evasive prey can reduce attack rates and/or capture
158 efficiencies) (Ioannou et al. 2007; Tosh et al. 2009), or positively, with the movement of prey
159 items increasing predator reaction distance, especially in turbid environments (Utne-Palm
160 1999).

161

162 During the experimental period, a single feeding trial, across all the tanks was conducted
163 every other day, with feeding on the day in between comprised of a maintenance ration of
164 approximately 1.5 % body weight. A maintenance ration was used rather than *ad libitum* to
165 ensure feeding motivation on the experimental days, given that functional responses relate to
166 optimal foraging and therefore behaviour seeking to maximise net energy gain should be
167 promoted. Thus, feeding on experimental days occurred 24 hours after the last exposure to
168 the maintenance ration. Each feeding trial consisted of exposing each tank of fish, in turn, to
169 one randomly selected food density of 10, 25, 50, 100 or 150 pellets per tank (equivalent to
170 75, 187, 375, 750 and 1125 items m⁻² respectively). By discounting a food density previously
171 used in a tank, eventually each of these food item densities was used across all 12 arenas,
172 with the process then being repeated once more (i.e. each food item density was used twice in

173 each tank). During the trials, the pellets were introduced to the tank across the entire surface
174 of the water with all pellets sinking through the water column and settling on the base of the
175 tank, with pellets being taken by the fish both as they fell through the water and once they
176 had settled on the bottom of the tank. On the release of the food, the filming of the foraging
177 behaviour commenced for 10 minutes (Oyugi et al. 2012a,b). At the end of this period, all
178 uneaten food was removed immediately using a siphon.

179

180 *Experimental treatments*

181 To test the effect of habitat complexity and food item size on the foraging parameters and the
182 functional response, the manipulated parameters were substrate complexity, water turbidity
183 and food item size. The effect of substrate complexity was tested first and then turbidity and
184 food item size.

185

186 To test the effect of substrate complexity, the treatments were (1) arenas with no substrate
187 (i.e. simply the glass bottom of the arena) (n=6) and (2) arenas with a layer of dark aquarium
188 gravel (2 to 5 mm) of approximately 10 mm depth on the arena bottom to represent the
189 complex substrate (n=6). Other than the change in substrate, the arenas were identical
190 regarding water turbidity (clear) and food item size (1 mm pellets). These trials were
191 completed separately from the trials of water turbidity and food item size, and used different
192 fish. A table listing the experimental treatments is included in Online Resource 1.

193

194 To test the effect of water turbidity and food item size, a two-factor experimental design
195 was used as it enabled testing of the influence on foraging of both factors and their
196 interactions. These two factors were used together as their interactions will be important in
197 more natural systems where habitats are already complex and their interactions are likely to

198 have synergistic effects on a visual forager. Across the 12 arenas, 6 were used with clear
199 water and 6 with water turbidity being increased through addition of a fine powder of
200 bentonite clay to the arena ($1\text{g} \pm 0.1\text{g}$) 5 minutes prior to the experiments commencing. This
201 was as per Vollset & Bailey, (2011) who demonstrated the method had no harmful effects to
202 the fish. At the end of each feeding trial, the water turbidity of each arena was quantified
203 through measurement with a turbidity meter (Hanna Instruments, HI 93703 Micro processor,
204 www.hannainst.co.uk), average turbidity in the increased turbidity areas being recorded as
205 equal to 3.41 ± 0.5 FTU, compared to the clear treatments (average = 0.01 ± 0.0 FTU), with
206 this difference being significant (ANOVA: $F_{1,528} = 110.43$, $P < 0.01$). As the clay settled out
207 of solution in approximately six hours, it was then able to be removed by siphoning. The
208 arenas used as clear and turbid water treatments remained constant throughout the
209 experiments.

210

211 Across these 12 tanks of varying turbidity, two different sizes of sinking pellets were used:
212 1 mm and 2 mm; the numbers released across the trials were as per the substrate experiment
213 (*cf.* Experimental design). Whilst this meant at a given food density, the biomass of food
214 being introduced would differ between the sizes of pellet, this was justified through
215 functional response analyses generally being based on the consumption rate according to food
216 item density. During each experimental food exposure, the density of food items used was
217 selected randomly for each tank. Once each density had been tested, the trials were later
218 repeated, i.e. each food item density was tested twice in each tank for both pellet sizes. The
219 actual size of pellet used alternated from one experimental food exposure to the next. A table
220 listing the experimental treatments is included in Online Resource 1.

221

222

223 *Data capture*

224 The recorded footage of each feeding trial in both sets of experiments was analysed using a
225 purpose-built event-logger program (Event; Bournemouth University 2012). This allowed
226 frame-by-frame viewing and estimation of the position of objects in three dimensions,
227 enabling parameter estimates of fish foraging behaviour to be measured that formed the basis
228 of the functional response equations (Holling 1959; Murray et al. 2013). These parameters
229 were: (i) swimming speed (s) whilst searching for food, characterised by relatively slow
230 swimming, with frequent changes in body orientation and leading to food item capture; (ii)
231 reaction distance (d), determined as the distance a fish would travel in a straight line directly
232 towards a food item, quickly followed by capture of the food item, often following a change
233 in body orientation towards the food item; and (iii) handling time (h), determined as the time
234 taken to move towards and consume a food item, and then be ready to consume a further food
235 item. Handling time was determined on occasions when food items were captured in rapid
236 succession and when no other behaviour was observed between food item capture. Other
237 parameters recorded, but not used in the functional response equations were: (i) Consumption
238 rate, which was estimated directly, taken as the time between a fish taking its first and fifth
239 food item, and expressed as the number of items consumed per second (Murray et al. 2013).
240 By repeating across the range of food densities, the shape of functional response was able to
241 be described; and (ii) Searching time, recorded as a percentage proportion of the total
242 foraging time that was spent actively searching. This was used to gain insight into the level of
243 risk-taking behaviour displayed by the fish. When perceived risk is reduced, it has been
244 shown that fish will spend a greater proportion of their time searching for food as a
245 compromise between energy intake and potential risks (Milinski & Heller, 1978; Oksanen &
246 Lundberg, 1995).

247

248 *Data analysis*

249 Across the feeding trials in both experiments, there were insufficient data points related to
250 forager parameters collected for each individual fish to enable analyses of their foraging
251 behaviour at that level. Consequently, for the parameters of swimming speed, reaction
252 distance and handling time, separate average parameter values were calculated, based on the
253 arithmetic mean, for each food density and treatment, whilst limiting the number of data
254 points collected for each parameter from any one fish to four, limiting the potential impact of
255 pseudo-replication (Hurlbert 1984). Any further potential impact on the experimental
256 outcomes through familiarisation and learning of optimum feeding behaviour at the
257 experimental food item densities was limited by the use of maintenance rations and time
258 between trials of the same density. Given that the effect of substrate was tested separately
259 with respect to turbidity and food item size, with substrate trials using the same fish
260 population, its effect on the foraging parameters used repeated measures ANOVA. When two
261 factors were being tested (turbidity and food item size experiment) then linear mixed effects
262 models were used, with either food item size or turbidity as a random effect (depending on
263 the test). When comparing the proportion of time spent searching (as a percentage of total
264 experimental time) binomial generalised linear models (GLM) were used.

265

266 The foraging behaviour parameters were used to parameterise both a Type I (Jeschke et al.
267 2002; Jeschke et al. 2004; Murray et al. 2013) and Type II (Holling 1959; Murray et al. 2013)
268 functional response equation, after being tested for density independence (Murray et al 2013).
269 These used the same variables of attack rate (derived from swimming speed and reaction
270 distance) and handling time, together with food item density, differing only in how these
271 parameters were treated. Note that the selection and parameterisation of the functional

272 response models, and the estimation of the foraging parameters, are described in more detail
273 in Murray et al. (2013). The Type I model was:

$$274 \quad F = \begin{cases} aD & \text{if } D \leq \frac{1}{ah} \\ \frac{1}{h} & \text{if } D > \frac{1}{ah} \end{cases} \quad (\text{Eqn 1})$$

275 The Type II model was Holling's Disc Equation (Holling 1959):

$$276 \quad F = \frac{aD}{1 + aDh} \quad (\text{Eqn 2})$$

277 Where F = feeding rate (items s^{-1}), a = searching rate (i.e. search area per unit time) ($m^2 s^{-1}$),
278 D = food density (items m^{-2}) and h = handling time (s) (Holling 1959). In both cases a was
279 defined as:

$$280 \quad a = 2ds \quad (\text{Eqn 3})$$

281 Where s = swimming speed (ms^{-1}) and d = reaction distance (m).

282

283 Thus, the outputs provided the predicted functional response of the fish according to Type
284 I and II equations. These were then compared to the observed functional response i.e. the
285 observed consumption rate data, taken directly from the recorded footage. The best fit
286 between predicted models and observed functional response was then determined by its lower
287 value of the akaike information criterion (AIC) using linear regression models, with each
288 factor (substrate, turbidity and food item size) being tested separately.

289

290 Finally, to assess the relative influence of all three factors on the consumption rate and the
291 foraging parameters, as the experimental conditions were the same across both sets of
292 experiments, the data were combined for further testing using linear mixed effects models. To
293 test the relative effects of the factors on each foraging parameter, food density and body
294 length of individual fish were the covariates and experimental arena number was set as a

295 random effect (to account for the fact that different experimental arenas were used across the
296 two experiments). Depending on the model, consumption rate and foraging parameters were
297 the dependent variables and were fitted through stepwise removal of non-significant terms
298 according to non-significant P values. All statistics and testing were completed in R (R version
299 2.15.1) (R Development Core Team 2012), where reported below, average values include
300 standard deviation (\pm).

301

302 **Results**

303

304 *Substrate complexity*

305 The effect of increasing the complexity of the substrate on the foraging behaviours was a
306 significantly decreased reaction distance between the no-substrate (average = 13.2 ± 5.5 cm)
307 and substrate treatment (average = 7.3 ± 3.9 cm) (ANOVA: $F_{1,18} = 6.75$, $P < 0.05$). There was
308 also a significant difference in searching time, with fish in the substrate treatment searching
309 longer (average = 91.0 ± 3.7 %) than the no-substrate treatment (average = 28.5 ± 3.1 %;
310 GLM: $F_{1,67} = 99.04$, $P < 0.01$). By contrast, there were no significant differences between the
311 treatments for swimming speed and handling time (ANOVA: $F_{1,28} = 0.91$, $P > 0.05$ and $F_{1,10} =$
312 0.28 , $P > 0.05$ respectively). See Online Resource 2 for a summary of the behavioural
313 parameter values.

314

315 The effect of substrate complexity on the consumption rate of the fish was significant,
316 with reduced rates in the substrate treatment (ANOVA: $F_{1,16} = 6.21$, $P < 0.05$; Fig. 1).
317 Comparison between observed functional response and that predicted by the foraging
318 parameters fitted to equations 1, 2 and 3 revealed that a predicted Type II response was the
319 better fit in both substrate and non-substrate treatments (adjusted $R^2 = 0.94$ $F_{1,3} = 48.84$, $P <$

320 0.01 and adjusted $R^2 = 0.96$, $F_{1,3} = 64.86$, $P < 0.01$ respectively) compared to a Type I
321 functional response (adjusted $R^2 = 0.92$, $F_{1,3} = 53.55$, $P < 0.01$; adjusted $R^2 = 0.94$, $F_{1,3} =$
322 72.52 , $P < 0.01$). Similarly, the Type II functional response was a better fit when compared to
323 a simple linear increase (adjusted $R^2 = 0.91$, $F_{1,3} = 68.65$, $P < 0.01$; adjusted $R^2 = 0.92$, $F_{1,3} =$
324 77.87 , $P < 0.01$). Lastly, the predicted Type II functional response was a better fit than Type I
325 for both the substrate and non-substrate treatment according to AIC (predicted Type II:
326 substrate AIC = -51.15; non-substrate AIC = -44.96; predicted Type I: substrate AIC = -
327 31.42; non-substrate AIC = -14.97).

328

329 **(Figure 1)**

330

331 *Water turbidity and food item size*

332 When controlling for the effect of food item size, the effect of increased water turbidity was a
333 significant increase in searching time, with fish searching significantly longer (average = 85.0
334 ± 3.2 %) than in the clear treatments (average = 25.0 ± 2.9 %) (GLM: $F_{1,69} = 58.21$, $P < 0.01$).
335 Its effect on consumption rate was also significant, with reduced rates in turbid conditions
336 (LMEM: $t_{74} = -4.37$, $P < 0.01$; Fig. 2). There were, however, no significant differences for
337 swimming speed, reaction distance or handling time between the turbid and clear conditions
338 (LMEM: $t_{48} = 1.43$, $P = 0.13$; $t_{89} = -2.92$, $P = 0.06$; $t_{87} = 0.149$, $P = 0.88$ respectively). See
339 Online Resource B for a summary of the behavioural parameter values.

340

341 When controlling for the effects of turbidity, increasing food item size resulted in a
342 significant reduction in consumption rate (LMEM: $t_{74} = 2.51$, $P = 0.02$; Fig. 3). There was,
343 however, no significant effect on searching time, swimming speed, reaction distance or

344 handling time (GLM: $F_{1,69} = 2.53$, $P = 0.05$; LMEM: $t_{48} = 1.22$, $P = 0.18$; $t_{89} = 2.90$, $P = 0.06$
345 and $t_{87} = -1.57$, $P = 0.11$ respectively).

346

347 **(Figures 2 and 3)**

348

349 **(Table 1)**

350

351 The effect of turbidity on functional response was analysed separately for both food item
352 sizes. Under turbid conditions, the functional response closely matched a Type II response
353 using both 1 mm and 2 mm pellets (Table 1). Furthermore, the Type II functional response
354 was a better fit compared to a Type I functional response for both food item sizes in the
355 turbidity treatment (Table 1). Similarly, the Type II functional response provided a better fit
356 when compared to a simple linear increase (Table 1). Lastly, the predicted Type II functional
357 response was seen to be a better fit than Type I through lower values using Akaike's
358 Information Criterion (Table 1).

359

360 Under clear water conditions, the functional response for both food item sizes closely
361 matched a Type II response in both food item size treatments (Table 1). Furthermore, the
362 functional response was a better fit when compared to a Type I functional response and a
363 simple linear increase (Table 1). When the models were compared, the lower AIC values
364 were always for the predicted Type II response rather than predicted Type I (Table 1).

365

366 *Factors influencing observed behaviour*

367 The linear mixed effects model (LME) output for all experimental factors combined, revealed
368 that substrate and food item size tended to have the greatest consequences for the foraging

369 parameters (Table 2, Online Resource B). The most significant effect on consumption rate
370 was food item size ($t_{223} = 8.36$, $P < 0.01$), and for reaction distance and handling time it was
371 substrate complexity ($F_{1,50} = 12.3$, $P < 0.01$) and handling time by substrate complexity ($t_{526} =$
372 5.19 , $P < 0.05$). Within the model, the effects of turbidity on the foraging parameters were
373 not significant.

374

375 **(Table 2)**

376

377 **Discussion**

378

379 The experiments demonstrated that changes in habitat complexity and food item size had
380 significant consequences for the foraging parameters and functional responses of *R. rutilus*.
381 Thus, aspects of their foraging behaviour were influenced by both their environment and food
382 resources, and this requires consideration in studies that relate to either foraging behaviours
383 and or functional responses. These responses to changing conditions are likely to relate to
384 their foraging being strongly reliant on visual cues (e.g. Aksnes & Utne, 1997; Diehl 1988;
385 Podolsrky, Uiblein & Winkler, 1995; Wanzenbock et al. 1996). Regarding the type of
386 functional responses elicited by *R. rutilus*, the best fitting functional response model in each
387 experiment was always Type II. This is a similar outcome to most other studies on *R. rutilus*
388 (e.g. Johanson & Persson 1986; Persson 1987; Murray et al. 2013). The only exception is
389 Winkler & Orellana, (1992) where Type III functional response was measured, with this
390 likely to relate to the role of capture probability as a result of evasive behaviour displayed by
391 the live prey.

392

393 Testing of how water turbidity impacted the foraging parameters whilst controlling for the
394 effect of food item size revealed that consumption rate and reaction distance were reduced as
395 turbidity increased, with this likely to be a result of visual foraging behaviour in roach. It was
396 not considered likely that it was related to changes in olfactory cues as bentonite clay is
397 considered odourless (Vollset & Bailey, 2011; Zamor & Grossman, 2007), plus the role of
398 olfaction (compared to visual cues) is limited in roach foraging (Wanzenbock et al. 1996).
399 This outcome is in contrast to findings in three-spined sticklebacks *Gasterosteus aculeatus*
400 whose reaction distance and attack rate actually increased as turbidity increased (Vollset &
401 Bailey, 2011). This outcome was related to the altered conditions; both reducing the
402 perceived conspicuousness of the stickleback to potential predators and increasing prey item
403 contrast in the water column, increasing their visibility (Vollset & Bailey, 2011).
404 Notwithstanding, as the attack rate of *G. aculeatus* increased their capture success actually
405 decreased, resulting in the consumption rate actually remaining the same and the energetic
406 costs of foraging increasing (Vollset & Bailey, 2011). The use of pelletized fish meal in our
407 study meant that there was a much more limited role for capture success in shaping the
408 outcome of the foraging, as evasion behaviour was negligible in this experiment and prey
409 refuge was not available, when the gravel substrate was not used. Similarly, Wanzenböck
410 (1995) described the role of prey size selection in altering handling times during foraging by
411 0+ roach and bleak (*Alburnus alburnus*); whereby, fish and prey size affected handling time
412 as well as feeding rate, and ultimately, prey profitability (Wankowski & Thorpe 1979; Buckel
413 & Stoner 2000). Furthermore, Wanzenböck (1995) showed handling time and prey
414 profitability were seen to vary over the feeding period, as feeding motivation changed. This
415 effect will be limited in our study due to the homogeneity of food item size used within each
416 trial, limiting the potential for prey item selection, altered handling times and profitability.

417 The presence of a gravel substrate within the experimental arenas inhibited the majority of
418 the foraging parameters. Within this, and similar, previous experiments (Murray et al. 2013),
419 food pellets were used due to their being a non-motile food item. This was to eliminate the
420 potential confounding effect of the food items actively seeking refuge in more cryptic
421 environments that could result in any shifts in the foraging parameters being due to prey
422 rather than fish behaviour. Indeed, other studies have revealed that functional responses are
423 significantly affected when the refuge area for live prey is increased, as this provides greater
424 opportunities for prey avoidance (e.g. Gotceitas 1990; Warfe & Barmuta, 2004; Alexander et
425 al. 2012). Nevertheless, in our study, observations on the reduced foraging performance of
426 the *R. rutilus* in the substrate treatment indicated that the reduced consumption rate was
427 largely due to the increased difficulty of the fish being able to detect the pellets once they had
428 settled on the gravel, as the size of pellets allowed a proportion to settle into relatively
429 inaccessible areas (i.e. they provided a 'prey' refuge).

430

431 The outcomes of our study highlighted the respective roles of prey item visibility and
432 environmental conditions in determining the foraging behaviours and parameters of a visually
433 foraging fish (Utne-Palm 1999; Sweka & Hartman, 2003). In natural environments, these
434 dynamic relations are important considerations in habitat selection and optimal foraging,
435 given that foragers will always seek to maximise their energy intake whilst minimising
436 energetic costs and risk of predation (Chick & McIvor, 1997). As such, the potential role of
437 factors other than prey item density that can influence feeding rate under more complex,
438 natural conditions should be understood within the context of the relationships described in
439 our study. For example, predation risk, competition and satiation may all affect the rate of
440 feeding (Mills 1982; Persson 1983; Werner et al. 1983; Brabrand & Faafeng, 1993; Henson
441 & Hallam, 1995; Elliot 2003; Vahl et al. 2005; Priyadarshana et al. 2006) and, potentially,

442 exert a greater influence on feeding rate than that of prey density. Furthermore, given the
443 need to observe feeding behaviour within this study, the 24 hour starvation period used to
444 ensure a high feeding motivation may then be higher than that of fish in the wild, that are less
445 likely to undergo starvation in the same manner (Simpson et al. 1996; Priyadarshana et al.
446 2006). As such, it can be assumed that it is the short-term functional response of roach that
447 we describe here, rather than the longer term, daily functional response when time is also
448 allocated by individuals to non-feeding activities, and where foraging behaviours must also
449 consider trade-offs with predation risk and competition as described above. In order to more
450 accurately account for the role of feeding motivation in forager behaviours, some roach
451 foraging models have included state-dependent variables that explicitly include the hunger-
452 state of the foragers (Holker et al. 2002; Holker & Breckling 2005), where hunger-state can
453 dictate behaviours such as habitat selection in association with both resting and feeding
454 activities. Nevertheless, despite these confounding factors, the basic relationships we reveal
455 here between environmental conditions and foraging rate remain valid, even when influenced
456 by further, complex, factors and trade-offs. The results described here will be especially
457 useful in more simple systems, for example in individual-based models (Holker et al. 2002;
458 Railsback & Harvey 2002).

459

460 Frequent changes in the environmental conditions of lowland riverine habitats (where the
461 presence of *R. rutilus* tends to be ubiquitous across their range) are common, in response to
462 prevailing weather conditions or more general shifts in lowland river management. This latter
463 aspect is important given that many lowland river management techniques that are aligned to
464 flood management works substantially modify fish habitats through, for example, removal of
465 instream vegetation that tends to increase turbidity, decrease refugia and increase flow rates
466 (e.g. Allouche & Gaudin, 2001; Copp 1997; Gregg & Rose, 1985; Grenouillet & Pont, 2001).

467 This suggests that works such as these are likely to affect *R. rutilus* foraging performance,
468 with adult roach switching to less productive filter feeding behaviour in response to
469 environmental challenges. Such changes include increased flow rates and water turbidity
470 (Van Den Berg et al. 2004; Bogacka-kapusta & Kapusta, 2007; Nurimen et al. 2010) in
471 association with habitat refugia (Garner 1996), and so, the impact of river management on
472 habitat conditions may potentially have substantial implications for fishery and fish
473 population management.

474

475 In conclusion, the investigation revealed that foraging parameters and functional responses
476 of *R. rutilus* are modified by changing conditions, with increased complexity tending to
477 decrease aspects of their foraging performance. Increased turbidity, substrate presence and
478 larger food items significantly reduced their consumption rate. In combination, these
479 outcomes suggest that the foraging performance of this species is context-specific; being
480 subject to prevailing conditions and food item availability, and this requires consideration in
481 all relevant applications of their foraging behaviour.

482

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484

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487

488 **References**

- 489 Abrams, P. A., 1982. Functional Responses of Optimal Foragers. *The American Naturalist*
490 120: 382–390.
- 491 Aksnes, D. L. & C. W. Utne, 1997. A revised model of visual range in fish. *Sarsia* 82: 137-
492 147.
- 493 Alexander, M. E., J. T. A. Dick & N. E. O'Connor, 2013. Trait-mediated indirect interactions
494 in a marine intertidal system as quantified by functional responses. *Oikos* 122: 1521–1531.
- 495 Alexander, M. E., J. T. A. Dick, N. E., O'Connor, N. R. Haddaway & K. Farnsworth, 2012.
496 Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey
497 supply, model selection and habitat complexity. *Marine Ecology Progress Series* 468: 191-
498 202.
- 499 Allouche, S. & P. Gaudin, 2001. Effects of avian predation threat, water flow and cover on
500 growth and habitat use by chub, *Leuciscus cephalus*, in an experimental stream. *Oikos* 94:
501 481–492.
- 502 Bean, C. W. & I. J. Winfield, 1983. Habitat use and activity patterns of roach (*Rutilus rutilus*
503 (L.)), rudd (*Scardinius erythrophthalmus* (L.)), perch (*Perca fluviatilis* (L.)) and pike
504 (*Esox lucius* (L.)) in the laboratory: the role of predation threat and structural complexity.
505 *Ecology of Freshwater Fish* 4: 37-46.
- 506 Bogacka-kapusta, E. & A. Kapusta, 2007. The diet of roach, *Rutilus rutilus* (L.), and bleak
507 *Alburnus alburnus* (L.) larvae and fry in the shallow littoral zone of a heated lake.
508 *Archives of Polish Fisheries* 15: 401-413.

509 Bollache, L., J. T. A. Dick, K. D. Farnsworth & W. I. Montgomery, 2008. Comparison of the
510 functional responses of invasive and native amphipods. *Biology Letters* 4: 166–9.

511 Bond, N., D. McMaster, P. Reich, J. R. Thomson & P. S. Lake, 2010. Modelling the impacts
512 of flow regulation on fish distributions in naturally intermittent lowland streams: an
513 approach for predicting restoration responses. *Freshwater Biology* 55: 1997-2010.

514 Britton, J. R., J. Pegg, D. Baker & C. Williams, 2012. Do lower feeding rates result in
515 reduced growth of a cyprinid fish infected with the Asian tapeworm? *Ecology of*
516 *Freshwater Fish* 21: 172-175.

517 Brabrand, A. & B. Faafeng, 1993. Habitat shift in roach (*Rutilus rutilus*) induced by
518 pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour.
519 *Oecologia* 95: 38–46.

520 Buckel, J. A. & A. W. Stoner, 2000. Functional response and switching behavior of young-
521 of-the-year piscivorous bluefish. *Journal of Experimental Marine Biology and Ecology*
522 245: 25-41.

523 Chick, J. H. & C. C. McIvor, 1997. Habitat selection by three littoral zone fishes: effects of
524 predation pressure, plant density and macrophyte type. *Ecology of Freshwater Fish* 6: 27-
525 35.

526 Copp, G. H.s 1997. Microhabitat use of fish larvae and 0+ juveniles in a highly regulated
527 section of the River Great Ouse. *Regulated Rivers: Research & Management* 13: 267-276.

528 Dick, J. T. A., K. Gallagher, S. Avlijas, H.C. Clarke, S.E. Lewis, S. Leung & A. Ricciardi,
529 2012. Ecological impacts of an invasive predator explained and predicted by comparative
530 functional responses. *Biological Invasions* 15: 837–846.

- 531 Diehl, S., 1988. Foraging Efficiency of Three Freshwater Fishes: Effects of Structural
532 Complexity and Light. *Oikos* 53: 207.
- 533 Elliott, J. M., 2003. Interspecific interference and the functional response of four species of
534 carnivorous stoneflies. *Freshwater Biology* 48: 1527-1539.
- 535 Elvira, B. & A. Almodovar, 2001. Freshwater fish introductions in Spain: facts and figures at
536 the beginning of the 21st century. *Journal of Fish Biology* 59: 323–331.
- 537 Event; Bournemouth University (Version 1.0 Software). Available from:
538 <http://individualecology.bournemouth.ac.uk/software.html>. Last accessed 24 September
539 2013.
- 540 Galarowicz, T. L. & D. H. Wahl, 2005. Foraging by a young-of-the-year piscivore: the role of
541 predator size, prey type, and density. *Canadian Journal of Fisheries and Aquatic Sciences*
542 62: 2330-2342.
- 543 Gotceitas, V, 1990. Variation in plant stem density and its effects on foraging success of
544 juvenile bluegill sunfish. *Environmental Biology of Fishes* 27: 63–70.
- 545 Gregg, W. & F. Rose, 1985. Influences of aquatic macrophytes on invertebrate community
546 structure, guild structure, and microdistribution in streams. *Hydrobiologia* 128: 45-56.
- 547 Grenouillet, G. & D. Pont, 2001. Juvenile fishes in macrophyte beds: influence of food
548 resources, habitat structure and body size. *Journal of Fish Biology* 59: 939–959.
- 549 Hassell, M. P., J. H. Lawton & J. R. Beddington, 1977. Sigmoid functional responses by
550 invertebrate predators and parasitoids. *Journal of Animal Ecology* 46: 249–262.

- 551 Heck, K. L. Jr. & L. B. Crowder, 1991. Habitat structure and predator—prey interactions in
552 vegetated aquatic systems. In Bell, S. S., E. D. McCoy & H. Muchinsky, ed. Habitat
553 Structure: the physical arrangement of objects in space. New York: 281 -299.
- 554 Henson, S. M. & T. G. Hallam, 1995. Optimal feeding via constrained processes. Journal of
555 Theoretical Biology 176: 170-177.
- 556 Hjelm, J., G. H. van de Weerd & F.A. Sibbing, 2003. Functional link between foraging
557 performance, functional morphology, and diet shift in roach (*Rutilus rutilus*). Canadian
558 Journal of Fisheries and Aquatic Sciences 60: 700–709.
- 559 Hölker, F. & B. Breckling, 2005. A spatiotemporal individual-based fish model to investigate
560 emergent properties at the organismal and the population level. Ecological Modelling 186;
561 406–426.
- 562 Hölker, F., S.S. Haertel, S. Steiner & T. Mehner, 2002. Effects of piscivore-mediated habitat
563 use on growth, diet and zooplankton consumption of roach: an individual-based modelling
564 approach. Freshwater biology 47: 2345–2358.
- 565 Holling, C. S, 1959. Some Characteristics of Simple Types of Predation and Parasitism. The
566 Canadian Entomologist 91: 385-398.

- 567 Holling, C. S, 1966. The functional response of predators to prey density and its role in
568 mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 48:
569 5–60.
- 570 Hurlbert, S. H, 1984. Pseudoreplication and the Design of Ecological Field Experiments.
571 *Ecological Monographs* 54: 187.
- 572 Ioannou, C. C., C. R. Tosh, L. Neville & J. Krause, 2007. The confusion effect from neural
573 networks to reduced predation risk. *Behavioral Ecology* 19: 126–130.
- 574 Jeppesen, E., M. Meerhoff, K. Holmgren, I. González-Bergonzoni, F. Teixeira-de Mello, S.
575 A. J. Declerck, L. Meester, M. Søndergaard, T. L. Lauridsen, R. Bjerring, J. M. Conde-
576 Porcuna, N. Mazzeo, C. Iglesias, M. Reizenstein, H. J. Malmquist, Z. Liu, D. Balayla & X.
577 Lazzaro, 2010. Impacts of climate warming on lake fish community structure and potential
578 effects on ecosystem function. *Hydrobiologia* 646: 73–90.
- 579 Jeschke, J. M. & K. Hohberg, 2008. Predicting and testing functional responses: An example
580 from a tardigrade–nematode system. *Basic and Applied Ecology* 9: 145–151.
- 581 Jeschke, J. M., M. Kopp & R. Tollrian, 2002. Predator functional Responses: Discriminating
582 between handling and digesting prey. *Ecological Monographs* 72: 95-112.
- 583 Jeschke, J. M., M. Kopp & R. Tollrian, 2004. Consumer-food systems: why Type I functional
584 responses are exclusive to filter feeders. *Biological Reviews* 79: 337–349.
- 585 Johansson, L. & L. Persson, 1986. The fish community of temperate eutrophic lakes. In:
586 Riemann, B. & M. Søndergaard, (eds), *Carbon dynamics in eutrophic, temper-ate lakes*.
587 Elsevier, Amsterdam: 237-266.

588 Kasumyan, A. O, 2004. The olfactory system in fish: Structure, function and role in
589 behaviour. *Journal of Ichthyology* 44: 100-108.

590 Koski, M. L. & B. M. Johnson, 2002. Functional response of kokanee salmon (*Oncorhynchus*
591 *nerka*) to *Daphnia* at different light levels. *Canadian Journal of Fisheries and Aquatic*
592 *Sciences* 716: 707-716.

593 Lappalainen, J., A. S. Tarkan & C. Harrod, 2008. A meta-analysis of latitudinal variations in
594 life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non- linear
595 relationships? *Freshwater Biology* 53: 1491–1501.

596 Lipcius, R. N. & A. H. Hines, 1986. Variable functional responses of a marine predator in
597 dissimilar homogeneous microhabitats. *Ecology* 67: 1361–1371.1

598 Milinski, M. & R. Heller, 1978. Influence of a predator on the optimal foraging behaviour of
599 sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275: 642-644.

600 Mills, N. J., 1982. Satiation and the functional response: a test of a new model. *Ecological*
601 *Entomology* 7: 305-315.

602 Morgan, R. A. & J. S. Brown, 1996. Using giving-up densities to detect search images.
603 *American Naturalist* 148: 1059-1074.

604 Murray, G. P. D., R. A. Stillman, R. E. Gozlan & J. R. Britton, 2013. Experimental
605 predictions of the functional response of a freshwater fish. *Ethology* 119: 751-761.

606 Nurminen, L., Z. Pekcan-Hekim & J. Horppila, 2010. Feeding efficiency of planktivorous
607 perch *Perca fluviatilis* and roach *Rutilus rutilus* in varying turbidity: an individual-based
608 approach. *Journal of Fish Biology* 76: 1848–55.

609 Oksanen, L. & P. Lundberg, 1995. Optimization of reproductive effort and foraging time in
610 mammals: the influence of resource level and predation risk. *Evolutionary Ecology* 9: 45-
611 46.

612 Oyugi, D. O., J. Cucherousset, D. J. Baker & J. R. Britton, 2012a. Effects of temperature on
613 the foraging and growth rate of juvenile common carp, *Cyprinus carpio*. *Journal of*
614 *Thermal Biology* 37: 89-94.

615 Oyugi, D. O., J. Cucherousset, J. & J. R. Britton, 2012b. Temperature-dependent feeding
616 interactions between two invasive fishes competing through interference and exploitation.
617 *Reviews in Fish Biology & Fisheries* 22: 499-508.

618 Persson, L, 1983. Food consumption and the significance of detritus and algae to intraspecific
619 competition in roach *Rutilus rutilus* in a shallow eutrophic lake. *Oikos* 41: 118-125.

620 Persson, L, 1987. Effects of habitat and season on competitive interactions between roach
621 (*Rutilus rutilus*) and perch (*Perca fluviatilis*). *Oecologia* 73: 170-177.

622 Podolsky, D., F. Uiblein & H. Winkler, 1995. Visual habitat choice in cyprinid fishes: an
623 experimental approach. *Ecology of Freshwater Fish* 4: 160-167.

624 Priyadarshana, T., T. Asaeda & J. Manatunge, 2006. Hunger-induced foraging behavior of
625 two cyprinid fish: *Pseudorasbora parva* and *Rasbora daniconius*. *Hydrobiologia* 568:
626 341-352.

627 R Development Core Team 2012. R: A language and environment for statistical computing.
628 R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL
629 <http://www.R-project.org/>.

630 Real, L. A, 1977. The Kinetics of Functional Response. The American Naturalist
631 111: 289-300.

632 Railsback, S. F. & B. C. Harvey, 2002. Analysis of habitat-selection rules using an
633 individual-based model. Ecology 83: 1817–1830.

634 Savino, J. F. & R. A. Stein, 1989. Behavior of fish predators and their prey: habitat choice
635 between open water and dense vegetation. Environmental Biology of Fishes 24: 287–293.

636 Simpson, A. L., N. B. Metcalfe, F. A. Huntingford & J. E. Thorpe, 1996. Pronounced
637 seasonal differences in appetite of atlantic salmon parr, *Salmo salar*: effects of nutritional
638 state and life-history strategy. Functional Ecology 10: 760-767

639 Solomon, M. E, 1949. The Natural Control of Animal Populations. Journal of Animal
640 Ecology 18: 1-35.

641 Stillman, R. A, 2008. MORPH—An individual-based model to predict the effect of
642 environmental change on foraging animal populations. Ecological Modelling 216: 265–
643 276.

644 Sweka, J. A. & K. J. Hartman, 2003. Reduction of reactive distance and foraging success in
645 smallmouth bass, *Micropterus dolomieu*, exposed to elevated turbidity levels.
646 Environmental Biology of Fishes 67: 341-347.

647 Tosh, C. R., J. Krause & G. D. Ruxton, 2009. Basic features, conjunctive searches, and the
648 confusion effect in predator – prey interactions. Behavioral Ecology and Sociobiology 63:
649 473–475.

650 Utne-Palm, A. C, 1999. The effect of prey mobility, prey contrast, turbidity and spectral
651 composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey.
652 Journal of Fish Biology 54: 1244-1258.

653 Vahl, W. K., Van Der Meer, F. J. Weissing, D. V. Van Dullenmen & T. Piersma, 2005. The
654 mechanisms of interference competition: two experiments on foraging waders. Behavioral
655 Ecology 16: 845-855.

656 Van Den Berg, C., J. G. M. Van Den Boogaart, F. A. Sibbing & J. W. M. Osse, 1994.
657 Zooplankton feeding in common Bream (*Abramis brama*), White Bream (*Blicca*
658 *Bjoerkna*) and Roach (*Rutilus rutilus*): Experiments, models and energy intake.
659 Netherlands Journal of Zoology 44: 15–42.

660 Vollset, K. W. & K. M. Bailey, 2011. Interplay of individual interactions and turbidity affects
661 the functional response of three-spined sticklebacks *Gasterosteus aculeatus*. Journal of
662 Fish Biology 78: 1954-64.

663 Wankowski J. W. J. & J. E. Thorpe, 1979. The role of food particle size in the growth of
664 juvenile Atlantic salmon (*Salmo salar L.*) Journal of Fish Biology 14: 351-370.

665 Wanzenböck, J., M. Zaunreiter, C. M. Wahl & D. L. G. Noakes, 1996. Comparison of
666 behavioural and morphological measures of visual resolution during ontogeny of roach
667 (*Rutilus rutilus*) and yellow perch (*Perca flavescens*). Canadian journal of Fisheries and
668 Aquatic Sciences 53: 1506-1512.

669 Wanzenböck J. 1995. Changing handling times during feeding and consequences for prey
670 size selection of 0+ zooplanktivorous fish. Oecologia 104: 372-378.

671 Warfe, D. M. & L. A. Barmuta, 2004. Habitat structural complexity mediates the foraging
672 success of multiple predator species. *Oecologia*: 141, 171–178.

673 Werner, E. E., 1974. The Fish Size, Prey Size, Handling Time Relation in Several Sunfishes
674 and Some Implications. *Journal of the Fisheries Research Board of Canada* 31: 1531-1536.

675 Werner, E. E., J. F. Gilliam, D. J. Hall & G. G. Mittelbach, 1983. An Experimental Test of
676 the Effects of Predation Risk on Habitat Use in Fish. *Ecology* 64: 1540-1548.

677 Winkler, H. & C. P. Orellana, 1992. Functional responses of five cyprinid species to
678 planktonic prey. *Environmental Biology of Fishes* 33: 53-62.

679 Zamor, R. G. & Grossman, 2007. Turbidity Affects Foraging Success of Drift-Feeding
680 Rosyside Dace. *Transactions of the American Fisheries Society* 136: 167-176.

681

682

683 **Table 1** Outputs of the linear regression and AIC values, testing the fit of each predicted
 684 model against the observed functional response. Model selection was based on the AIC
 685 scores with tests performed separately for each factor.

Turbidity	Food Item Size	Model	df	R²	F	P	AIC
Turbid	1mm	Type II	66	0.93	60.76	<0.01	-30.26
Turbid	2mm	Type II	62	0.95	43.65	<0.01	-18.68
Turbid	1mm	Type I	66	0.91	65.94	<0.01	-20.65
Turbid	2mm	Type I	62	0.91	46.59	<0.01	-13.89
Turbid	1mm	Linear	66	0.92	38.3	<0.01	-5.65
Turbid	2mm	Linear	62	0.91	26.1	<0.01	-4.45
Clear	1mm	Type II	59	0.93	34.71	<0.01	-8.23
Clear	2mm	Type II	69	0.97	66.01	<0.01	-3.17
Clear	1mm	Type I	59	0.90	38.36	<0.01	11.47
Clear	2mm	Type I	69	0.92	72.6	<0.01	13.84
Clear	1mm	Linear	59	0.91	49.2	<0.01	15.29
Clear	2mm	Linear	69	0.95	26.1	<0.01	16.38

686

687

688 **Table 2** Outputs of the linear mixed effects models testing the effect of food item size,
689 substrate presence and increased turbidity on consumption rate and foraging parameters.
690 Fixed effects listed by the significance of their effect on each dependent variable. F =
691 consumption rate; d = Reaction Distance; h = Handling Time and s = Swimming Speed.

Dependent:	df	1st Factor:	F	P	2nd Factor:	F	P	3rd Factor:	F	P
F	223	Food Item Size	8.36	<0.01	Substrate	0.13	0.73	Turbidity	2.75	0.87
d	50	Substrate	12.32	0.01	Food Item Size	0.53	0.81	Turbidity	-	-
h	526	Substrate	5.20	0.02	Food Item Size	2.16	0.11	Turbidity	0.01	0.97
s	1976	Food Item Size	2.55	0.07	Substrate	0.28	0.86	Turbidity	1.73	0.18

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Figure Captions

698 **Fig.1** Comparison of observed functional responses for the no-substrate (filled squares)
699 versus substrate treatments (clear circles), where the lines represent the modelled Type II
700 functional response from Holling's Disc Equation parameterised using observed foraging
701 parameters under the no-substrate (solid line), and the substrate treatments (dashed line)

702

703 **Fig.2** Comparison of observed functional responses for clear water (filled squares) and
704 turbidity treatments (clear circles) using (a) 1mm pellets and (b) 2mm pellets. The lines
705 represents the modelled Type II functional response from Holling's Disc Equation
706 parameterised using observed foraging parameters, under clear (solid line) and turbid
707 treatments (dashed line)

708

709 **Fig.3** Comparison of observed functional responses for differences in food item size, where
710 filled squares represent 1 mm pellets and clear circles 2 mm pellets and under (a) clear
711 conditions and (b) turbid conditions. The lines represents the modelled Type II functional
712 response from Holling's Disc Equation parameterised using observed foraging parameters,
713 under 1mm food item size (solid line) and 2mm food item size treatments (dashed line)