

36 INTRODUCTION

37

38 Perhaps due to their mobile and often cryptic natures, research into the ecology of intertidal fish of
39 the U.K. appears to be lacking. However, some studies have found that intertidal fish species such as
40 the common blenny/shanny (*Lipophrys pholis*) and long-spined sea scorpion (*Taurulus bubalis*)
41 contribute to the diets of commercially valuable species, such as cod (*Gadus morhua*) and haddock
42 (*Melanogrammus aeglefinus*), respectively (Pinnegar & Platts, 2011). Additionally, intertidal fishes
43 are important prey items of the near-threatened European otter (*Lutra lutra*). Therefore, baseline
44 information on their ecologies could be of ecological importance.

45

46 Between October 2009 and October 2012, the author conducted what could be considered the first
47 comprehensive research into the ecology of intertidal (specifically, rock pool) fish from the English
48 (Yorkshire) and Welsh (Anglesey) coasts, in order to identify the mechanisms which allow for their
49 coexistence. This was achieved through seven topic areas of research: (i) the spatiotemporal
50 distributions and abundances, (ii) the predictors of presence, (iii) the degrees of co-occurrences, (iv)
51 the diets, (v) the conditions, (vi) the ecomorphologies, and (vii) the diel activities, of intertidal fish.

52

53 To summarise, it was found that *Lipophrys pholis* and *Taurulus bubalis* are 'residents' of all the
54 sampled rocky shore sites, and on the east coast, *L. pholis* appear on-shore before *T. bubalis*. Also,
55 on both a monthly and seasonal scale, *L. pholis* populations persisted on the shores for longer
56 periods of time than other fish species. When *T. bubalis* appear, usually in the lower-shore pools, *L.*
57 *pholis* tend to extend their spatial range, moving up-shore. *T. bubalis* were rarely found on the
58 upper-shore (which may indicate less resilience to environmental stresses), except for at shores of
59 high fish diversity. This resulted in high degrees of co-occurrence at the Thornwick site, although co-
60 occurrence did not occur between *L. pholis* and *T. bubalis* at the Penrhos site, indicating that here,
61 although both species occurred at the same tidal height, they were occupying different pools. This
62 may be because the smaller of the species were competitively excluded from pools of which the two

63 species initially shared, which may be why factors which predict the presence of these two species
64 were dissimilar. Also, it was found that on the east coast that the presences of all fish were predicted
65 by algal abundance, whereas this was less of an important feature on the west coast.

66

67 It was assumed that pools were being used for shelter, rather than for their food availability. In the
68 case of *L. pholis*, at Thornwick Bay, they were found to consume large quantities of the acorn
69 barnacle, *Semibalanus balanoides*, while none were found on the site itself, and so the algae which
70 predicted the presence of the fish, may have been as a means of shelter/protection. However,
71 previous studies (Utne *et al.*, 2003; as described later) have found that primarily, fish will seek food
72 and will only prioritise shelter if a predator is in the vicinity. As the Anglesey fish were not predicted
73 by algal abundance (at least, not to the same degree that the English fish were), this may mean that
74 they were in more favourable (food plentiful) pools, as predation risks were lower. While this was
75 not necessarily demonstrated in the co-occurrence study, predation could also have been in the
76 form of piscivorous fish other than *T. bubalis*, birds or large crab species, which *may* have been in
77 greater numbers on the east coast, although this is uncertain. It *could* however, also mean that fish
78 such as *L. pholis* and *T. bubalis* are quite flexible in their choices of habitat.

79 Additionally, the factors which predicted the presence of *L. pholis* and *T. bubalis* differed between
80 coasts. Where they co-occurred, their total lengths were similar, which would minimise the risk of
81 the piscivorous (as determined by the dietary studies) *T. bubalis* predating on *L. pholis*. Morphology,
82 similar to predictors of fish presence, differed between coasts. This was possibly due to restricted
83 gene flow between populations and local adaptation to different habitats, as also found in Eurasian
84 perch (*Perca fluviatilis*) by Svanbäck & Eklöv (2006). Anglesey specimens of *L. pholis* appeared more
85 efficient at predator detection (more laterodorsally positioned eyes) while the Yorkshire species
86 seemed more efficient escaping a predator (larger pectoral fin sizes, for speed and manoeuvrability)
87 and perhaps swimming in exposed conditions and for 'anchoring' in wave surges. If these
88 assumptions are true, the Anglesey specimens *may* have the more optimal avoidance mechanism, as

89 their conditions were found to be 'good' throughout the year, while Yorkshire specimen condition
90 lowered significantly during the winter. It *may* be that generating high speeds to escape predators
91 are energetically taxing (hence the lower condition), while, like the Anglesey specimens, detecting a
92 predator well in advance may not require the need for fast swimming (hence no change in their
93 condition).

94

95 It was found that morphology helped to promote coexistence between the more common species.

96 At shores where numbers of, and degrees of co-occurrence with, *T. bubalis* were high, their
97 potential prey, *L. pholis* had developed deeper bodies and larger heads, which may create too long a
98 handling time for a gape-limited predator such as *T. bubalis* to consider them energetically
99 profitable. However, some small specimens of *L. pholis* were found to be prey items of *T. bubalis*,
100 albeit in very small frequencies. This may have been as a result of high numbers of *L. pholis* recruits,
101 which would be easy prey for larger specimens of *T. bubalis*. In general however, *L. pholis* and *T.*
102 *bubalis* were found to have very broad diets (more so of *L. pholis*, though). While some prey item
103 overlap did exist (the extent of which was small) *T. bubalis* and the rock goby (*Gobius paganellus*)
104 shared a prey preference of the shore crab, *Carcinus maenas*. Found to be a specialist, this may be
105 one reason why *G. paganellus* was in relatively low numbers when *T. bubalis* also occurred on the
106 same shore, and in larger numbers, when *T. bubalis* did not.

107

108 Lastly, the diel activity research revealed that *L. pholis* did not differ in numbers or sizes between day
109 and night samples. This may indicate that it was the same specimens being recorded throughout the
110 sample period, which hints that (at least during the time of study), *L. pholis* did not migrate very far,
111 if at all. As no predators (such as *T. bubalis*) were detected during this investigation, their lack of
112 movement may suggest that specimens were in their 'ideal' surroundings and that food availability
113 may have been plentiful (the primary preference of a fish, according to Utne *et al.*, 2003) and should
114 a predator have been present, shelter/protection opportunities may also have been sufficient.

115
116
117
118
119
120
121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140

MECHANISMS OF COEXISTENCE

Armstrong & McGehee, (1980) dictate (following a mathematical model by Volterra (1928) and Gause's (1934) 'Competitive Exclusion Principle') that two species which use the same resources cannot permanently coexist (Hardin, 2005). This implies that interspecific competition cannot allow permanent coexistence. However, Hardin (2005) goes on to state that in stable conditions, "*Complete competitors cannot coexist,*" and does not state whether these competitors are, as Volterra (1928)/Gause (1934) suggested, of different species, or whether the competitors are/could be from the same species. The implication is that intraspecific (as well as interspecific) competition cannot allow permanent coexistence.

The studies directly recognised seven mechanisms of interspecific coexistence, which is promoted when one or more of the following is/are met:

- 1) Fish diversity on a shore is low, thus minimising high degrees of co-occurrence within pools.** This compliments the findings of Wilson (1990), who considers niche diversification as a mechanism of coexistence, where species either inhabit different niches within a habitat, to demote co-occurrence, or utilise the niche at different times, which would also demote co-occurrence. The latter was proven true by Ranta *et al.*, (1981) who found that Scandinavian flora of the same community had significantly different flowering times, which promoted coexistence, lowering competition for pollinators.
- 2) Co-occurrence on shores (at tidal height level) is minimal, and when fishes *do* co-occur, they are of similar sizes, thus reducing size-dominated hierarchies.** Therefore, size variation

141 may promote coexistence if the different sized fishes target different prey taxa. This needs
142 to be further tested. Levin (1974) suggested that if species grow at a similar rate,
143 coexistence can be promoted, presumably because size dominance would not occur. This
144 was named 'initial patch composition' by Wilson (1990) and Wilson (2011), although it is
145 only theory based and has not been applied to actual species before.

146

147 **3) The significant variables which predict fish presences differ.** Where mechanism (2) is not
148 maintained, i.e. fishes are of different sizes, a size-dominance hierarchy often occurs
149 (Costello, 1992 and Wiederholm, 1987), but coexistence may still be maintained if the
150 smaller species shift to different microhabitats. Costello (1992) observed that the painted
151 goby (*Pomatoschistus pictus*), a small species, were found in open water, whilst the red-
152 mouthed goby (*Gobius cruentatus*), were found in areas of greater protection (holes, under
153 rocks). Widerholm (1987) made similar observations; the black goby, the largest of three
154 observed gobioids (*Gobius niger*) occupied well vegetated habitats, while the smallest
155 species, the common goby (*Pomatoschistus microps*) occupied open water and the middle
156 sized gobioid, the sand goby (*Pomatoschistus minutus*) occurred between the two habitat
157 types. As the variables which predict fish presence does not necessarily mean habitat
158 'preference,' such variables may change, depending on factors such as availability of shelter,
159 presence of predators, prey availability and presence of competitors. This may be why the
160 variables which predicted the presence of species such as *L. pholis* and *T. bubalis* on the east
161 shore were different to those variables which predicted the presence of the same species on
162 the west shore.

163

164 **4) There is an abundance of shelter/protection readily available, which reduces the**
165 **competition to access such features.** This supports the 'pool load capability' hypothesis of

166 Monteiro *et al.*, (2005). This hypothesis assumes that a pool contains only a limited amount
167 of shelter/protection, to a limited size and number of fish. Monteiro *et al.*, (2005) believed
168 that where these limits are not reached, intraspecific coexistence of *L. pholis* is promoted, as
169 is interspecific coexistence of *L. pholis* and *Coryphoblennius galerita*, Montagu's blenny. If
170 these limitations *are* exceeded, in a pool which is low of, or lacks such characteristics, these
171 fishes would then be more prone to predation or may become competitively excluded.

172

173 **5) Morphology is such that for the majority of the year (excluding breeding times, when**
174 **recruits will be targeted), it is more profitable for the piscivorous fishes (such as *Taurulus***
175 ***bubalis*) to predate on food items other than fish.** This finding was very similar to the study
176 of Webster *et al.*, (2011) who found that in areas of high predator presence, the three-
177 spined stickleback (*Gasterosteus aculeatus*) had deeper bodies, which would increase their
178 handling time and also their time to escape, should they be targeted as prey. In the
179 morphology study, *L. pholis* were found to have deeper bodies and larger heads where *T.*
180 *bubalis* numbers were high (and also possibly other predators such as large crab species and
181 sea birds, although this was not confirmed). Here, it would be less energy taxing for *T.*
182 *bubalis* to consume a larger number of smaller, less mobile prey items, than a smaller
183 number of larger, mobile prey items.

184

185 **6) Competition for prey items is reduced, when variability of resources is high,** as resources
186 were found to be high on all shores. Coexistence may further be strengthened if the fish
187 species consume different sizes of the same prey species, if a size range is available. Such a
188 mechanism has also been found to promote the coexistence of two sympatric bat species,
189 *Rhinolophus affinis* and *Rhinolophus pearsoni* (Jiang *et al.*, 2008). Here, as prey resources
190 were high and varied, Jiang *et al.*, (2008) found that the coexistence of these Chinese bats
191 were promoted, as interspecific competition was greatly reduced. Similarly, Scognamillo *et*

192 *al.*, (2003) found that an abundance of medium-sized prey items also allowed the jaguar
193 (*Panthera onca*) and puma (*Puma concolor*) to coexist, in Venezuela.

194

195 **7) There is a difference in the most targeted prey items between fish species, despite some**
196 **overlap in targeted prey items.** When Zaret & Rand (1971) looked at the diet of nine,
197 sympatric, Panama stream fishes, overlap was found to be reduced in the dry season by
198 fishes shifting to different microhabitats, reportedly due to increased competition, meaning
199 fishes had to target different prey items. However, the taxonomic resolution of prey items
200 applied in their (Zaret & Rand, 1971) study may be one reason why their study appeared to
201 (perhaps erroneously) validate competitive exclusion. The prey items within the fish
202 specimens were recorded at a relatively low taxonomic resolution (to order level), which
203 would provide a less accurate representation of dietary preference than species-level data,
204 as recorded where possible in the current study. For example, in the current study, *Lipophrys*
205 *pholis* and *T. bubalis* were found to consume *Littorina littorea*, *Littorina obtusata* and
206 *Littorina saxatilis* at Filey, during summer. However, *L.pholis* also consumed high frequencies
207 of *Littorina neglecta*, while *T. bubalis* did not consume any. A lower taxonomic resolution
208 (even to genus level) would therefore have shown a higher degree of dietary overlap
209 between the two fishes than the more accurate, higher (species level) taxonomic resolution.
210 Had Zaret & Rand (1971) conducted their dietary studies at such a resolution as the current
211 study, perhaps their findings may have differed.

212

213

214

215

216

217 **OBSERVATIONS**

218 Other mechanisms may also have been inadvertently recognised from findings of the research
219 chapters. For example, species diversity and degrees of co-occurrence were noticeably less between
220 the monthly sampling in 2010 and seasonal sampling in 2011, at Thornwick Bay. This *may* be
221 evidence of the ‘intermediate timescale-disturbance’ coexistence mechanism, as described by
222 Wilson (1990 & 2011), as it is likely that disturbances such as anthropogenic and environmental
223 stresses occurred ‘intermediately’ between these years. At Abberfraw for example, weather may
224 have influenced fish diversity, as at this shore in the winter of 2009, pools were frequently ice-
225 covered, which was again observed at the Penrhos shore, in the winter of 2012. This was not
226 observed, during the current study, for shores on the Yorkshire coast during winter sampling, which
227 may be due to the more saline conditions on this coast (Dooley, 1974) than the west coast. Crisp
228 (1964) described similar adverse conditions around Anglesey, during the winter of 1962-1963, calling
229 it ‘severe.’ This implies that such conditions may not occur frequently (*every year*), but such
230 conditions (Bayliss, 1958 and Wardle & Allen, 1983) may mean that fish diversity becomes high
231 again, if the ‘intermediate-timescale disturbance’ concept is true here. This however, would need to
232 be determined during further work.

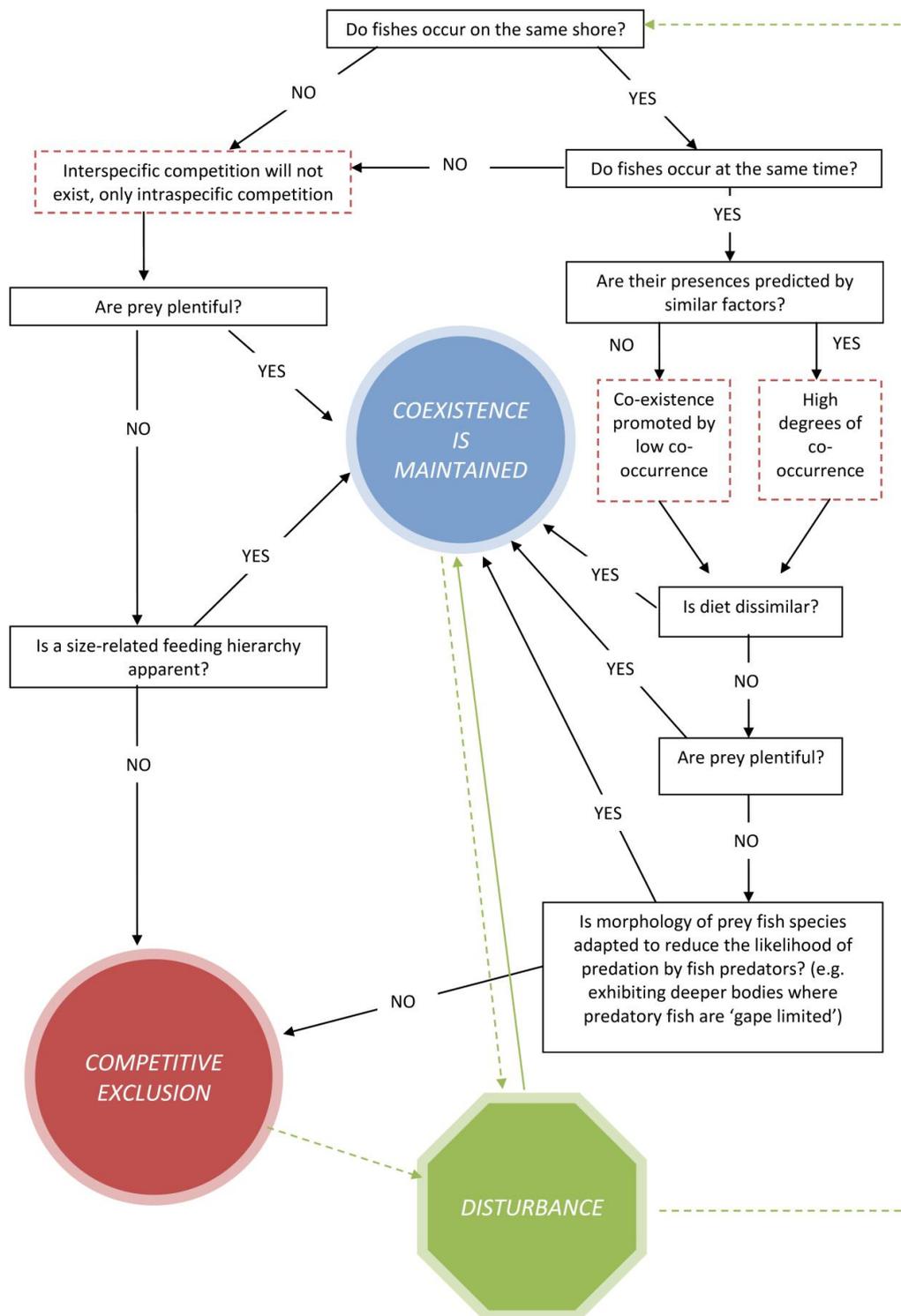
233

234 When trapping the fish during the diel activity study, it was observed that *L. pholis* surrounded the
235 bait at a set distance. It was then the larger specimens who sampled the bait first and the smaller
236 specimens, last. It was observed that if a smaller specimen tried to sample the bait first, the larger
237 specimens showed aggression, trying to attack them. This may imply that intraspecific coexistence is
238 maintained via a size-related hierarchy, but was not possible to directly test during the field work.

239

240 *If* these observations are found to be valid, during further studies, in conjunction with the seven
241 mechanisms of coexistence mentioned earlier, the model in *Fig 1* may provide an example of how
242 intertidal fishes are able to coexist. The model (*Fig 1*) includes ‘disturbance’ as a factor which will

243 alter the coexistence or exclusion of fishes, whether the disturbance be anthropogenic or
244 environmental. If disturbance(s) is/are 'intermediate,' coexistence should be promoted, as fish
245 numbers will be reduced and therefore, so will the levels of competition (Wilson, 1990 and Wilson,
246 2011). Disturbances are inevitable on a rocky shore, although their severities and periods may vary
247 greatly. It would be particularly difficult to determine whether a disturbance can be classified as
248 'intermediate' and because of this complication, if disturbance(s) is/are identified *following* such
249 studies as those conducted in this thesis, the research should be carried out again, as mechanisms
250 which allowed for coexistence of fishes before may no longer apply, or may have changed.



251

252 *Fig 1: A conceptual model of the ways in which coexistence can be achieved for intertidal fish. Green*
 253 *lines indicate environmental factors. Assuming the 'intermediate-timescale disturbance' concept is*
 254 *valid, broken lines denote that coexistence (or competitive exclusion) is never permanent, as when*
 255 *disturbance occurs, the mechanisms which allow for coexistence may change. However, if*
 256 *disturbance is intermediate, coexistence can be promoted if numbers of competitors are reduced, but*
 257 *if the level of disturbance is too great, all fish may be removed from the shore. Where 'NO,'*
 258 *competition is increased. (Model created by author).*
 259

260 **THE COSTS OF COEXISTENCE (TRADE-OFFS)**

261 It has been documented (Kneitel & Chase, 2004; Chase & Leibold, 2003; Turnbull *et al.*, 1999 and
262 Levine & Rees, 2002) that in order for maintained coexistence, trade-offs must occur, and of the
263 mechanisms identified in the current study, trade-offs have surely featured in maintaining such
264 synchronicity.

265

266 If it is not due to intermediate disturbance, the mechanism of a low degree of species co-occurrence
267 may be due to a trade-off between interspecific competition and availability of resources and/or
268 shelter, similar to the findings of Utne *et al.*, (1993) and Wiederholm (1987). Utne *et al.*, (1993)
269 describe a trade-off between food availability and predation risk in the two-spotted gobies
270 (*Gobiusculus flavescens*), whereby (*ex-situ*) specimens tended to favour shelter availability over food
271 availability in the presence of a predator (a cod, *Gadus morhua*). Before the presence of this
272 predator, *G. flavescens* preferred locations where food availability was high, regardless of the level
273 of shelter in these areas.

274

275 As previously mentioned, *in-situ*, on the Swedish coast, Wiederholm (1987) found a trade-off
276 between predation risk and competition for prey and shelter, with the largest species being in the
277 prime location and the smallest being in the least desirable location. This meant that *P. microps* (the
278 smallest species) had prey and refuge less readily available, but was able to avoid competition with
279 the larger fishes. Accepting the thesis research, if the same applies, it may mean that the factors
280 which predicted fish presence did not necessarily reflect their 'preferred' habitat type, as the
281 variables identified may have been as a compensation, to avoid competition or predation. For
282 example, in Wiederholm's (1987) study, *P. microps* was found in a micro-habitat of mud, with no
283 vegetation present (used for shelter and prey availability). This however, was not the *preferred*
284 habitat type of this species, but instead, was exhibiting a trade-off, as its existence in the lesser

285 preferred habitat type meant a much lower (perhaps even non-existent) degree of competition with
286 the larger gobioid species.

287

288 The morphological mechanism of coexistence, as found in the thesis, appears similar to the
289 threespine stickleback (*Gasterosteus aculeatus*) study of Webster *et al.* (2011). They found that
290 where coexistence was occurring between the sticklebacks and piscivorous, gape-limited fish, the
291 sticklebacks had developed deeper bodies, to reduce the likelihood of being eaten. If attack *did*
292 occur, such morphology would also allow a higher chance of escape, as their handling time would be
293 increased. However, a trade-off occurred (likely to also be the case in the current study) between
294 morphology and energy loss, as the deeper body meant that predation was decreased, but
295 hydrodynamic drag and associated energy expenditure increased. A deeper body may also mean
296 that availability of hiding places is reduced. It could be expected that a similar trade-off would exist
297 for the *L. pholis* in the thesis research. Where their bodies were deeper and heads were larger, in the
298 presence of high numbers of potential predators, they would surely be subjected to the same
299 increased drag and energy expenditure as the sticklebacks.

300

301 Similar to Velasco *et al.* (2009), diet was also found to be a mechanism of interspecific coexistence,
302 although they (Velasco *et al.*, 2009) did report any considered trade-offs which allow for this
303 mechanism. This finding *could* have been due to a difference in feeding-related morphology
304 between species, although it was found in the current study that *Lipophrys pholis* and *Taurulus*
305 *bubalis* were generalists and *could* eat the same prey items. If both then targeted the more easily
306 accessible, less energetically taxing and more profitable (in terms of energy gain) prey items,
307 competitive exclusion would eventually occur. However, this does not seem to be the case. Instead,
308 a trade-off may be occurring between competition and prey selection. In the presence of other
309 species with similar dietary preference, fish are targeting a wide range of abundant prey items (with
310 a wide range being exhibited in the diet research), rather than a small range of more accessible,

311 profitable prey, thus reducing competition, but requiring greater energy expenditure to get the same
312 energy gains.

313

314

315 **REFERENCES**

316 1.

317 Armstrong, R.A. and McGehee, R. (1980). Competitive Exclusion, *The American Naturalist*, 115, 151-
318 170.

319 2.

320 Baylis, G.T.S. (1958). An example of winter injury to silver beech at moderate altitude, *Proceedings of*
321 *the New Zealand Ecological Society*, 6, 21-22.

322 3.

323 Chase, J.M. & Leibold, M.A. (2003). *Ecological niches*, In: Kneitel, J.M. and Chase, J.M. (2004). Trade-
324 offs in community ecology: linking spatial scales and species coexistence, *Ecology Letters*, 7, 69-80.

325 4.

326 Costello, M.J. (1992). Abundance and spatial overlap of gobies (Gobiidae) in Lough Hyue, Ireland,
327 *Environmental Biology of Fishes*, 33, 239-248.

328 5.

329 Crisp, D.J. (1964). The effects of the Severe Winter of 1962-1963 on Marine Life in Britain, *The*
330 *Journal of Animal Ecology*, 33, 165-210.

331 6.

332 Dooley, H.D. (1974). Hypotheses concerning the circulation of the northern North Sea, *Journal du*
333 *conseil / Conseil international pour l'exploration de la mer*, 36, 54-61.

334 7.

335 Gause, (G.F). (1934). The struggle for existence, in: Hardin, G. (1960). The competitive exclusion
336 principle, *Science, New Series*, 131, 1292-1297.

- 337 8.
- 338 Hardin, G. (1960). The Competitive Exclusion Principal, *Science*, 131, 1292-1297.
- 339 9.
- 340 Jiang, T., Feng, J., Sun, K. and Wang, J. (2008). Coexistence of two sympatric and morphologically
341 similar bat species *Rhinolophus affinis* and *Rhinolophus pearsoni*, *Progress in Natural Science*, 18,
342 523-532.
- 343 10.
- 344 Kneitel, J.M. and Chase, J.M. (2004). Trade-offs in community ecology: linking spatial scales and
345 species coexistence, *Ecology Letters*, 7, 69-80.
- 346 11.
- 347 Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion
348 principle, *The American Naturalist*, 104, 413-423.
- 349 12.
- 350 Levine, J.M. and Rees, M. (2002). Coexistence and relative abundance in annual plant assemblages:
351 the roles of competition and colonization, *American Naturalist*, 160, 452–467.
- 352 13.
- 353 Monteiro, N.M., Quinteira, S.M., Silva, K., Vieira, M.N. and Almada, V.C. (2005). Diet preference
354 reflects the ontogenetic shift in microhabitat use in *Lipophrys pholis*, *Journal of Fish Biology*, 67, 102-
355 113.
- 356 14.
- 357 Pinnegar, J.K. and Platts, M. (2011). DAPSTOM – An Integrated Database & Portal for Fish Stomach
358 Records. Version 3.6. Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, U.K.
359 Phase 3, Final Report, July 2011, 35pp.
- 360 15.
- 361 Ranta, E., Teras, I. and Lundberg, H. (1981). Phenological spread in flowering of bumblebee-
362 pollinated plants, *Annales Botanici Fennici*, 18, 229-236.

- 363 16.
364 Scognamillo, D., Maxit, I.E., Sunquist, M. and Polisar, J. (2003). Coexistence of jaguar (*Panthera onca*)
365 and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos, *Journal of Zoology*
366 (*London*), 259, 269-279.
- 367 17.
368 Svanbäck, R. and Eklöv, P. (2006). Genetic variation and phenotypic plasticity: causes of
369 morphological and dietary variation in Eurasian perch, *Evolutionary Ecology Research*, 8, 37-49.
- 370 18.
371 Turnbull, L.A., Rees, M. and Crawley, M.J. (1999). Seed mass and the competition/colonization trade-
372 off: a sowing experiment, *Journal of Ecology*, 87, 899–912.
- 373 19.
374 Utne, A.C.W., Aksnes, D.L. and Giske, J. (1993). Food, predation risk and shelter: an experimental
375 study on the distribution of adult two-spotted goby *Gobiusculus flavescens* (Fabricius), *Journal of*
376 *Experimental Marine Biology and Ecology*, 166, 203-216.
- 377 20.
378 Velasco, E.M., Gómez-Cama, M.C., Hermandó, J.A and Soriguer, M.C. (2010). Trophic relationships in
379 an intertidal rockpool fish assemblage in the gulf of Cádiz (NE Atlantic), *Journal of Marine Systems*,
380 80, 248-252.
- 381 21.
382 Volterra, V. (1928). Variations and fluctuations of the number of individuals in animal species living
383 together, in: Armstrong, R.A. and McGehee, R. (1980). Competitive Exclusion, *The American*
384 *Naturalist*, 115, 151-170.
- 385 22.
386 Wardle, J.A. and Allen, R.B. (1983). Dieback in New Zealand *Nothofagus* forests, *Pacific Science*, 37,
387 397-404.
- 388 23.

389 Webster, M.W., Atton, N., Hart, P.J.B. and Ward, A.J.W. (2011). Habitat-Specific Morphological
390 Variation among Threespine Sticklebacks (*Gasterosteus aculeatus*) within a Drainage Basin, *Public*
391 *Library of Science ONE*, 6, e21060

392 24.

393 Wiederholm, A.M. (1987). Habitat Selection and Interactions between Three Marine Fish Species
394 (Gobiidae), *Oikos*, 48, 28-32.

395 25.

396 Wilson, J.B. (1990). Mechanisms of species coexistence: twelve explanations for Hutchinson's
397 'paradox of the plankton': evidence from New Zealand plant communities, *New Zealand Journal of*
398 *Ecology*, 13, 17-42.

399 26.

400 Wilson, J.B. (2011). The twelve theories of co-existence in plant communities: the doubtful, the
401 important and the unexplored, *Journal of Vegetation Science*, 22, 184-195.

402 27.

403 Zaret, T.M. and Rand, A.S. (1971). Competition in Tropical Stream Fishes: Support for the
404 Competitive Exclusion Principle, *Ecology*, 52, 336-342.

405

406

407

408

409

410

411