

1 **Parasites as prey in aquatic food webs: implications for predator infection and parasite**
2 **transmission**

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4 David W. Thieltges*^a, Per-Arne Amundsen^b, Ryan F Hechinger^c, Pieter T.J. Johnson^d,
5 Kevin D. Lafferty^e, Kim N. Mouritsen^f, Daniel L. Preston^d, Karsten Reise^g, C. Dieter
6 Zander^h, Robert Poulinⁱ

7

8 ^a Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research; P.O. Box 59; 1790 AB
9 Den Burg Texel; The Netherlands

10 ^b Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of
11 Tromsø, N-9037 Tromsø, Norway

12 ^c Marine Science Institute and Department of Ecology, Evolution & Marine Biology, University of California,
13 Santa Barbara, CA 93106 USA

14 ^d Ecology and Evolutionary Biology, University of Colorado, Ramaley N122, Campus Box 334, Boulder, CO
15 80309, USA

16 ^e Western Ecological Research Center, U.S. Geological Survey. c/o Marine Science Institute, UC, Santa
17 Barbara, CA 93106, USA

18 ^f Department of Biological Sciences, Marine Ecology, Aarhus University, Ole Worms Allé 1, DK-8000 Aarhus
19 C, Denmark

20 ^g Alfred Wegener Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstrasse 43, 21 25992
21 List/Sylt, Germany

22 ^h Biozentrum Grindel & Zoologisches Museum, Martin-Luther-King-Platz 3, D-20146 Hamburg-Rotherbaum,
23 Germany

24 ⁱ Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand

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26 *Corresponding author: David.Thieltges@nioz.nl

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31

32 **Abstract**

33 While the recent inclusion of parasites into food-web studies has highlighted the role of
34 parasites as consumers, there is accumulating evidence that parasites can also serve as prey
35 for predators. Here we investigated empirical patterns of predation on parasites and their
36 relationships with parasite transmission in eight topological food webs representing marine
37 and freshwater ecosystems. Within each food web, we examined links in the typical predator-
38 prey sub web as well as the predator-parasite sub web, i.e., the quadrant of the food web
39 indicating which predators eat parasites. Most predator-parasite links represented
40 “concomitant predation” (consumption and death of a parasite along with the prey/host; 58-
41 72%), followed by “trophic transmission” (predator feeds on infected prey and becomes
42 infected; 8-32%) and predation on free-living parasite life-cycle stages (4-30%). Parasite life-
43 cycle stages had, on average, between 4.2 and 14.2 predators and were involved in up to 40%
44 of the total prey links of predators. Among the food webs, as predator richness increased, the
45 number of links exploited by trophically transmitted parasites increased at about the same rate
46 as did the number of links where these stages serve as prey. On the whole, our analyses
47 suggest that predation on parasites has important consequences for both predators and
48 parasites, and food web structure. Because our analysis is solely based on topological webs,
49 determining the strength of these interactions is a rich avenue for future research.

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51

52

53 **Introduction**

54 Food webs depict the network of feeding relationships within ecological communities. During
55 the last few decades, a large body of food-web theory has sought to generalize food-web
56 patterns and processes (Cohen 1978, Pimm et al. 1991, Williams and Martinez 2000, Dunne
57 2006, Allesina et al. 2008). Simple summary parameters used to characterize food webs
58 include species richness (S), the number of realised links (L), vulnerability (the number of
59 consumer links per resource), generality (the number of resource links per consumer), and
60 connectance, which is the proportion of realised links out of the total number of possible links
61 (often expressed as L/S). The relationship among these measures and their role in the stability
62 of ecosystems has long been of interest to ecologists (e.g. May 1973, Dunne et al. 2005).
63 However, most previous food-web studies have neglected what is perhaps the most frequent
64 trophic interaction – parasitism (Marcogliese and Cone 1997). Recent efforts to include the
65 missing parasite links in food-web studies have shown that adding parasite-host links to
66 conventional predator-prey food webs increases food chain length, and may increase
67 connectance and nestedness (Huxham et al. 1995, Thompson et al. 2005, Lafferty et al.
68 2006a,b, Hernandez and Sukhdeo 2008, Amundsen et al. 2009, Preston et al. in revision).
69 Given that diversity, connectance, and food chain length have all been hypothesized to
70 influence stability, these observations raise the intriguing possibility that parasites play a
71 ‘hidden’ role in mediating ecosystem stability (Dobson et al. 2006, Wood 2007, Lafferty et al.
72 2008).

73

74 While parasites as consumers can markedly affect food-web topologies, there is accumulating
75 evidence that parasites can also serve as prey for predators (Johnson et al. 2010). Predation on
76 parasites can take various forms and is probably much more significant in food webs than is

77 indicated by its typical neglect (Johnson et al. 2010). There are two main routes by which
78 parasites become prey. First, parasites become prey when their current host is consumed by a
79 predator that is not a suitable downstream host (i.e. the next host in the parasite's life cycle).
80 In this case, predation leads to the consumption and most likely digestion of the parasite along
81 with the prey (*concomitant predation*; see Johnson et al. 2010). Second, parasites can become
82 prey when their free-living stages are eaten by predators (Thieltges et al. 2008a, Johnson et al.
83 2010, Johnson and Thieltges 2010). While there exist a few other routes by which parasites
84 become prey, these are relatively rare (see below). It is important to note that predation is not
85 always fatal for parasites. Trophically transmitted parasites depend on the predation of their
86 current hosts to infect down-stream hosts and thus exploit predator-prey links (Marcogliese
87 and Cone 1997, Lafferty 1999). Hence, for trophically transmitted parasites, predation and
88 transmission are inextricably linked.

89
90 The interplay of predation on parasites and parasite transmission should have important
91 implications for both predators and parasites in food webs (Johnson et al. 2010). For
92 predators, the greater a predator's generality (i.e. its diet breadth), the greater the probability it
93 will consume a variety of parasites via concomitant predation (Chen et al. 2008, Rossiter and
94 Sukhdeo 2011). At the same time, generalist predators could become infected by more
95 trophically transmitted parasite species compared with more specialized predators. For
96 parasites, concomitant predation or predation on free-living life-cycle stages might be an
97 important source of mortality and regulate parasite population size, which, in turn, might
98 result in reduced disease risk for hosts (Anderson et al. 1978). For parasites in food webs,
99 predation (in terms of vulnerability and not absolute predation levels) might be positively
100 linked to predator richness as the chances that a given parasite will fall within the prey
101 spectrum of at least one predator likely increases with the number of predator species.

102 However, some parasites require their host to be preyed upon to complete their life cycle (i.e.
103 trophic transmission). In fact, Lafferty et al. (2006a) found that one third of predator-parasite
104 links in the Carpinteria Salt Marsh food web led to transmission to a down-stream host.

105 Although these processes have important implications for predators and parasites, only few
106 food-web studies have examined single predator-parasite sub webs in more detail (Lafferty et
107 al. 2006, Amundsen et al. 2009) or looked at the specific aspect of host network position and
108 parasite richness without detailed analyses of predator-parasite sub webs (Chen et al. 2008,
109 Rossiter and Sukhdeo 2011). Hence, empirical generalisations of how predation and
110 transmission of parasites are coupled in food webs are missing, a void we attempt to fill here.

111

112 In this study, we quantify predation on parasites and its relationship with parasite transmission
113 using a comparative approach for eight different topological food webs from marine and
114 freshwater ecosystems systems with high parasite diversity. We focus on measures of
115 vulnerability (the number of predator species that feed on a parasite species or life cycle
116 stage) and generality (the number of resource items used by a consumer, 'diet breadth'), both
117 common measures in food-web studies. Using the predator-prey and predator-parasite sub
118 webs of the eight food webs, we aim to investigate some general patterns of predation on
119 parasites and its relationship with parasite transmission from the perspective of 1) the
120 predators, 2) the parasites, and 3) the whole food web. First, we investigate how common
121 predation on parasites is for individual predators by determining what proportion of the total
122 number of links represents predation on parasites. We also ask how predation on parasites and
123 parasite transmission are linked from a predator's perspective by investigating whether the
124 frequency of parasite consumption via concomitant predation increases with a predator's
125 generality and whether generalist predators face a higher vulnerability to infection by
126 trophically transmitted parasites than specialist predators. Second, we look at the importance

127 of predation on parasites from the perspective of parasites by determining the overall
128 vulnerability of parasites in the food webs. And third, we analyse the interplay of predation on
129 parasites and parasite transmission on the level of entire food webs by investigating whether
130 the vulnerability of parasites and trophic transmission are linked to predator richness of the
131 entire food web. Our study is among the first empirical quantifications of general patterns of
132 predation on parasites and transmission in real food webs and is based on all existing food
133 webs with the necessary sub webs. The results of this study will foster a better understanding
134 of the functioning of ecological networks and can subsequently be used for the development
135 of better food-web models.

136

137 **Methods**

138 For all analyses, we used eight topological food webs that included both a predator-prey and a
139 predator-parasite sub web. A predator-prey sub-web encompasses all feeding links of
140 predators to their prey, the type of web commonly used in food-web studies that do not
141 include parasites. A predator-parasite sub web denotes all feeding links of predators on
142 parasites (e.g. by feeding on infected prey; see below for details). Two other sub-webs of
143 parasite-inclusive food webs (for details see Lafferty et al. 2008) were not used in our
144 analysis: parasite-host (denoting the feeding links of parasites to their hosts) and parasite-
145 parasite (denoting feeding links between parasites, e.g. hyperparasitism).

146

147 Two of the food webs are from marine intertidal systems (Otago Harbour, New Zealand
148 (Mouritsen et al. 2011); List Tidal Basin, Germany/Denmark (Thieltges et al. 2011)), one
149 food web is from a shallow brackish water system 150 (Flensburg Fjord, Germany/Denmark
150 (Zander et al. 2011)), three food webs are from North American Pacific coast estuaries
151 (Carpinteria Salt Marsh, USA; Estero de Punta Banda, Mexico; Bahía Falsa in Bahía San

152 Quintín, Mexico (Lafferty et al. 2006a,b, Hechinger et al. 2011)), and two others are from
153 freshwater lake or pond systems (Lake Takvatn, Norway (Amundsen et al. 2009); Quick
154 Pond, USA (Preston et al. 2012)). All webs were assembled using data from field sampling
155 and literature surveys (see the original publications for details) and consist of interaction
156 matrices denoting species interactions (predator-prey and parasite-host sub-webs) but not
157 including interaction strength (topological webs). Information on predator-parasite links was
158 available directly from the webs or could be logically inferred by using the other two sub-
159 webs (predator-prey and parasite-host sub-webs): a predator is assumed to eat all the parasites
160 that infect its prey and the parasite-host sub-web can be used to categorise the links into the
161 respective transmission and predation links.

162

163 While interactions in the predator-prey sub-webs noted only the presence or absence of
164 predation links, entries in the predator-parasite sub webs distinguished between six types of
165 links: 1) *trophic transmission*: a predator preys on infected prey and becomes infected with a
166 parasite, thus leading to the parasite transmitting to the next host in its life cycle (down-stream
167 host), 2) *concomitant predation*: a predator preys on infected prey but kills the parasite and
168 does not become infected because it is not a suitable host, 3) *predation on free-living stages*: a
169 predator preys on free-living non-feeding stages of a parasite, e.g. on trematode cercariae, and
170 this does not lead to transmission, 4) *predation on commensal stages*: a predator preys on
171 commensal non-feeding stages of a parasite, e.g. trematode metacercariae attached to sea
172 grass blades, 5) *trophic transmission via free-living parasite stage*: a predator becomes
173 infected by preying on a free-living parasite life-cycle stage, e.g. trematode cercariae infecting
174 a fish predator when it preys on them; and 6) *direct predation on parasitic plants*: a predator
175 directly preys on a parasitic plant, i.e. not on its free-living stages or indirectly via
176 concomitant predation.

177

178 We initially used these six link types to quantify the various ways that parasites interact with
179 predation. For subsequent analyses, either all types of predation on parasites were subsumed
180 under *predation on parasites* (concomitant predation, predation on free-living stages,
181 predation on commensal stages, direct predation on parasitic plants) to distinguish them from
182 *trophic transmission* links, or analyses were conducted with specific link types of interest
183 (concomitant predation, predation on free-living stages or trophic transmission). For all eight
184 food webs, this link type information was available for each parasite life-cycle stage as
185 parasite species were split into life-cycle stages in all predator-parasite sub webs. In contrast,
186 predator species were split into life-cycle stages for a few species in the predator-prey sub
187 webs for only the three North American Pacific coast estuaries webs; for the other 5 webs this
188 information was not available. This imbalance in resolution between predator-prey and
189 predator-parasite sub webs needs to be considered when directly comparing food-web
190 measures of the two sub webs. However, for our main purpose, i.e. to analyse the
191 relationships of predation on parasites and parasite transmission, a high resolution of the life-
192 cycle stages of the parasites is necessary to be able to disentangle the various types of
193 predation. In contrast, the level of life-cycle stage resolution of predators is not relevant for
194 our analyses as a predator simply acts as a predator of parasites no matter what life-cycle
195 stage it is.

196

197 As a first step, we calculated food-web summary statistics for the eight webs. We determined
198 the total number of free-living species (basal taxa plus predators, S) as well as parasite species
199 or life-cycle stages (P) in each food web and calculated the number of realised or observed
200 (L_o) and potential (L_p) links for each of the predator-prey ($L_p=S*S$) and predator-parasite ($L_p=$
201 $S*P$) sub webs. Using the link data, we calculated connectance as $C= L_o/L_p$ for each of the

202 predator-prey and predator-parasite sub webs. In addition, we determined the proportion of
203 the six previously mentioned link types in the predator-parasite sub webs.

204

205 To determine the mean frequency of predation on parasites for individual predator species, we
206 calculated the number of links leading to predation on parasites relative to the total number of
207 predation links of an individual predator. To determine whether the chance of consuming
208 parasites via concomitant predation increases for predators as a function of their prey range
209 (predator generality), we regressed the number of concomitant predation links per predator in
210 the predator-parasite sub web against the number of prey species consumed by each predator
211 in the predator-prey sub web. To investigate whether generalist predators (broad prey range)
212 had more predator-parasite links that led to infection with trophically transmitted parasites, we
213 regressed the number of transmission links in the predator-parasite sub web against the
214 number of prey species consumed by each predator in the predator-prey sub web. This
215 analysis only included predators that served as down-stream hosts for at least one trophically
216 transmitted parasite species. These species are, in principle, suitable hosts for which there is a
217 risk of becoming infected during predation events while predators that are unsuitable hosts do
218 not face this risk and were thus excluded from the analysis. For both analyses (concomitant
219 predation and parasite transmission), in addition to separate linear regressions for each web,
220 we also tested for an overall effect of predator generality on concomitant predation or parasite
221 transmission by running two General Linear Models (GLM) on the combined datasets with
222 predator generality and food web identity as factors (after using residual plots to check for
223 normality and homoscedasticity of the data).

224

225 To estimate the vulnerability of individual parasite life-cycle stages, we calculated the mean
226 number of predators per parasite life-cycle stage for each food web (including life-cycle

227 stages with no predators). In addition, we calculated the proportion of links in the predator-
228 parasite sub web leading to transmission for all trophically transmitted parasites (trophic
229 transmission vs. concomitant predation links).

230

231 Finally, we tested whether the mean vulnerability of parasite life-cycle stages (predation on
232 free-living stages and concomitant predation) in a food web was related to total predator
233 richness of the web. This analysis evaluated the number of likely predators of a given parasite
234 stage, which relates to food web connectance, rather than the likelihood or intensity of
235 predation on that stage (actual interaction strength). In addition, we investigated whether the
236 mean number of trophic transmission links per trophically transmitted stages was related to
237 total predator richness of the web. We did this using linear regression and mean values for
238 each web as data points, correcting for the actual number of parasite life-cycle stages or
239 trophically transmitted stages of each web in an effort to control for the scale-dependence of
240 these measures with food web size. As other types of predation on parasites were very rare or
241 absent in the eight webs, we did not investigate their relationship with predator richness.

242

243 **Results**

244 The eight food webs included 37 to 163 free-living species or life-cycle stages, with 29 to 144
245 of them acting as predators, the remaining being basal taxa like plants. In addition, the webs
246 included 30-190 parasite life-cycle stages (Table 1). Connectance varied widely in both the
247 predator-prey (0.064-0.270) and the predator-parasite (0.075-0.231) sub webs (Table 1). In all
248 eight food webs, most links in the predator-parasite sub webs were concomitant predation
249 links (58-72%), followed by links leading to transmission (8-32%), predation on free-living
250 parasite 250 stages (4-30%) and very low proportions of the remaining link types (Table 1).

251

252 On average, the feeding links in the predator-parasite sub webs accounted for 18 to 40% of
253 the total number of predation links (predator-prey and predator-parasite sub webs) per
254 individual predator species (Fig. 1). The number of concomitant predation links increased
255 with a predator's generality, as indicated by the GLM including food web as a co-factor, i.e.
256 predators with broad prey ranges showed higher numbers of concomitant predation links than
257 predators with narrow prey ranges (Fig. 2, Table 2). However, the significance of food-web
258 identity indicated that levels of concomitant predation differed among webs. Overall,
259 predators ingested 0.3-1.2 parasite species for each prey type, given the slopes from the seven
260 significant separate linear regressions (Fig. 2; Table 3).

261

262 Predators with wide diet breadths (high predator generality) served as hosts for more
263 trophically transmitted parasites than predators with narrow diet breadths, as indicated by the
264 GLM (Fig. 3; Table 2). The significance of food-web identity indicated differences in the
265 levels of parasite transmission among the webs. Overall, predators acquired 0.2-0.7
266 trophically transmitted parasites for each additional new prey type added to their prey range,
267 as indicated by the slopes of the six significant separate linear regressions (Fig. 3; Table 3). In
268 the Quick Pond food-web this relationship was marginally non-significant, whereas it was
269 non-significant in the Otago web (Fig. 3; Table 3).

270

271 The mean number of predators per parasite life-cycle stage (including 274 stages with no
272 predators) ranged from 4.2 to 14.2 among the different food webs (Fig. 4). Overall,
273 trophically transmitted parasite stages used 44-79% of the links in the predator parasite sub
274 webs for transmission to their down-stream hosts (Table 1). These figures are higher than the
275 percentages of trophic transmission in Table 1 because only parasite life-cycle stages which

276 are trophically transmitted (e.g. trematode metacercariae) to a down-stream host were
277 considered in this analysis.

278

279 When looking at the entire food web, parasite vulnerability (i.e., number of predator types
280 consuming a parasite and not actual predation rates) tended to increase in predator-rich
281 systems (Fig. 5), but this relationship was only significant for the vulnerability to concomitant
282 predation of all life-cycle stage ($r^2 = 0.60$; $p=0.025$; Fig. 5b) and of trophically transmitted
283 stages only ($r^2 = 0.89$; $p<0.001$; Fig. 5c) but only marginally significant for vulnerability of
284 free-living stages ($p=0.097$; Fig. 5a). The number of trophic transmission links per trophically
285 transmitted stage also significantly increased with predator richness of a web ($r^2 = 0.59$;
286 $p=0.026$; Fig. 5d). Overall, the number of trophic transmission links of trophically transmitted
287 parasite life-cycle stages increased at approximately the same rate as their vulnerability.

288

289 **Discussion**

290 Our analyses facilitated a numerical investigation of the interplay between predation on
291 parasites and parasite transmission in eight topological food webs. The observed patterns had
292 previously not been verified nor quantified in multiple food webs. We showed that all webs
293 have predator-parasite sub webs of considerable size. The separation of parasite species into
294 life stages increased the number of potential predator-parasite links such that a direct
295 comparison of their connectance with predator-prey links is not appropriate, but this is beyond
296 the scope of the questions addressed here. Partitioning parasites into life-cycle stages
297 contributes valuable additional information because the type of link in the predator-parasite
298 sub web often differs among the life-cycle stages of a given parasite species. For example, for
299 a trophically-transmitted stage of a parasite species, many links might be transmission links,
300 whereas for its free-living stages these are almost entirely predation links. In addition, the

301 different life-cycle stages of a parasite may represent very different kinds of prey. For
302 example, predation on free-living larval stages will offer a different quality of food for a
303 predator compared to concomitant predation on the adult stages of the same parasite species.
304

305 Overall, most links in the predator-parasite sub webs involved concomitant predation (Table
306 1). It is remarkable that this pattern was similar in all eight food webs despite the considerable
307 differences among the systems, which ranged from marine to freshwater and from mainly
308 benthic to mainly pelagic webs, and also vary in the number and types of parasites included.
309 This suggests that concomitant predation on parasites is a defining feature of food-web
310 structure. How this affects energy flow in food webs remains to be seen. With some important
311 exceptions (e.g., high biomass trematode infections in snails or certain tapeworms in fishes),
312 the fraction of energy gained from parasites inside a prey item will often be negligible. More
313 important is the potential for parasites to increase predation rates on infected prey. For
314 instance, in the Carpinteria web, killifish infected with trematode metacercariae are 10-30
315 times more likely to be eaten by birds than are uninfected killifish (Lafferty and Morris 1996).
316 It is also possible that parasite infections alter the energetic value of infected prey (Mouritsen
317 and Jensen 2006, Sánchez et al. 2009). Parasites can also contribute energy to food webs via
318 the production of free-living stages, many of which were eaten in the food webs analysed.
319 Here, the parasite comprises the entire meal. Many free-living species are known to prey on
320 free-living stages of parasites with high consumption rates (Thieltges et al. 2008a; Johnson
321 and Thieltges 2010) and the production of some free-living stages of parasites like trematode
322 cercariae has been shown to be high in marine and estuarine benthic ecosystems (Thieltges et
323 al. 2008b, Kuris et al. 2008, Preston et al. in revision). However, it is unclear how much free-
324 living stages actually contribute to the diet of predators (but see Kaplan et al. 2009). Overall,

325 predation on parasites in its various forms might represent a substantial unrecognised path of
326 energy flow through food webs that deserves further attention.

327

328 The high proportion of concomitant predation links in the eight food webs is also reflected at
329 the level of individual predators. The various forms of predation on parasites added a
330 significant number of prey nodes to predators' diets, with parasite life-cycle stages
331 constituting, on average, up to 40% of the total prey links of predators (Figure 1). For many
332 predator species, this value is much higher. The observed differences among the food webs
333 can probably largely be ascribed to differences in their size (number of species) as discussed
334 below. Within a particular food web, a large part of the differences in the numbers of parasite
335 predation links among predators can be ascribed to the generality of a predator. The positive
336 relationship between the number of concomitant predation links and predator generality
337 (Figure 2) suggests that generalist predators have a higher chance of consuming parasites.
338 However, being a generalist may also expose predators to higher numbers of parasite species
339 because the number of trophically transmitted parasite links also increased with predator
340 generality in most webs (Figure 3). This is consistent with results of several comparative
341 studies that show a link between predator generality (diet breadth) and parasite species
342 richness (Bell and Burt 1991, Guegan and Kennedy 1993, Morand et al. 2000). However, the
343 lack of such a relationship in other comparative studies (e.g. Gregory et al. 1991, Poulin 1995,
344 Watve and Sukumar 1995) suggests that a predator's diet may not be an important driver of
345 its parasite richness in all parasite-host systems. This might also be the case of the Otago and
346 Quick Pond food-webs where the relationship between a predator's generality and the number
347 of transmission links was absent. However, both webs show the same general trends but low
348 numbers of replicates and some outliers may confound the general pattern (this also applies to
349 the Takvatn web in Fig. 2). Overall, there is considerable scatter in most relationships and

350 some of the separate linear regressions gave relatively low r^2 values (Table 3), indicating that
351 there are also other factors driving these relationships. More studies are needed to further test
352 the generality of the relationship between parasite species richness and predator
353 specialisation.

354

355 The high proportion of links leading to predation in the predator- parasite sub webs suggests
356 that predation may constitute a significant source of mortality for parasites. For individual
357 parasite species, this predation pressure might be substantial, given that the average number of
358 predator species ranges from about 4 to 14 predators per parasite life-cycle stage (Figure 4).

359 The notable differences in predation levels among the food webs are clearly linked to the size
360 of the respective food webs (see below). However, there is little information on the actual
361 magnitude of predation on parasites and on its consequences for parasite population
362 dynamics. Predators can consume a large fraction of free-living stages, leading to reduced
363 infection levels in down-stream hosts (Thieltges et al. 2008a; Orlofske et al. 2012), but we
364 know far less about the effects of concomitant predation on parasite transmission and
365 population dynamics. However, the various kinds of predation on parasites can all be
366 expected to affect parasite population dynamics and models of parasite population dynamics
367 would gain from incorporating predator-parasite interactions to explore their actual relevance
368 for specific parasite-host systems (Johnson et al. 2010). In addition to predation, parasite
369 population dynamics are also strongly affected by successful transmission, e.g. of trophically-
370 transmitted parasite life-cycle stages to their down-stream hosts. Overall, trophically
371 transmitted life-cycle stages used, on average, a substantial proportion of predation links in
372 the eight food-webs (44-79%; Table 1) suggesting that they are well embedded in the host
373 matrix of the respective ecosystems. For established parasites with an evolutionary history of
374 host adaptations, this is probably not surprising. However, the situation will be different for

375 recent invasions of parasites or potential hosts, with likely effects on food web structure.
376 However, only a few studies have tried to quantify actual transmission rates to down-stream
377 hosts (e.g. Zander et al. 1994, Amundsen et al. 2003) or investigated the potential effects of
378 invasive species on food web structure (Lafferty and Kuris 2009). Further studies are needed
379 to quantify the actual loss and gain in transmission through predator-parasite interactions in
380 food webs.

381

382 Finally, on the level of the entire food web, we found evidence for the prediction that the
383 mean vulnerability of parasites increases with the free-living predator diversity of the food
384 web. This relationship was statistically significant in the case of the vulnerability of parasites
385 to concomitant predation (both for all life-cycle stages and for trophically transmitted stage
386 only) and suggestive for the vulnerability of free-living stages. If there is an increase in
387 vulnerability of free-living infective stages with free-living diversity, this would support the
388 hypothesis that the transmission of free-living stages of a parasite could decline in high-
389 diversity communities. However, because vulnerability does not directly correspond to
390 predation rates, the impact of predation on parasites will ultimately be determined more by the
391 total abundance of these predators and their rates of predation on infective stages. Although
392 overall levels of predation on parasites might increase with predator richness of food webs,
393 opportunities for transmission also increase as suggested by the significant positive
394 relationship between predator diversity and the mean number of trophic transmission links per
395 trophically transmitted stage. In fact, the number of trophic transmission links increased with
396 predator diversity at approximately the same rate as did parasite vulnerability when
397 considering only trophically transmitted life-cycle stages. This may reflect selection for
398 increased down-stream host generality by parasites in food webs with diverse predator
399 communities. These potentially contrasting effects emphasize the complexity and scale-

400 dependence of the diversity-disease relationship. While increases in host diversity have the
401 potential to limit parasite transmission at a local scale (Keesing et al. 2010), higher host
402 diversity can also facilitate increases in parasite colonization and diversity by adding new
403 trophic pathways (Hechinger and Lafferty 2005; Hudson et al. 2006; Johnson and Thielges
404 2010).

405

406 **CONCLUSION**

407 Our analyses show that food-web studies can inform us about the interplay between predation
408 and transmission of parasites in natural systems. Our data suggest that predation on parasites
409 has important implications for both predators and prey. For predators, parasites often
410 constitute an additional food source that has largely been omitted in previous food-web
411 studies. And for parasites, predation on hosts or free-living stages is possibly a strong
412 regulating factor. Our analyses also suggest that network analyses neglecting parasites present
413 a rather distorted numerical picture, potentially misleading our conclusions about the
414 functioning of ecosystems. However, these inferences are based on topological webs, which
415 do not include information on the actual strength of interactions among nodes. What is needed
416 next is more detailed information on energy flows through predator-parasite sub webs. The
417 present data suggest that this will be a worthwhile effort on the way to a more complete and
418 general understanding of ecosystem properties and functioning.

419

420

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- 543

544

545 **Figure captions**

546

547 **Figure 1:** Mean proportion (+SE) of predator-parasite links out of the total number of
548 predation links (sum of predator-prey and predator-parasite links) per predator. Note that
549 predator-parasite links include all links in predator-parasite sub webs, i.e., concomitant
550 predation and trophic transmission. For numbers of predators per web, see Table 1.

551

552 **Figure 2:** Relationship between predator generality (no. prey species per predator in predator-
553 prey sub web) and the number of concomitant predation links a predator incurs by consuming
554 parasites while preying on free-living prey. Data based on all predators in the respective webs.
555 Note the different scales on axes. Lines indicate the best fit of significant regressions (Otago:
556 $y = 0.020 + 0.270 * x$; Sylt: $y = -1.483 + 1.094 * x$; Flensburg: $y = -2.838 + 1.177 * x$; Carpinteria:
557 $y = 2.546 + 0.921 * x$; Bahia Falsa: $y = 3.364 + 0.654 * x$; Punta Banda: $y = 4.191 + 0.841 * x$;
558 Quick Pond: $y = -1.654 + 0.529 * x$). For regression statistics and sample sizes, see Table 3.

559

560 **Figure 3:** Relationship between predator generality (no. of prey species preyed on per
561 predator in predator-prey sub web) and the vulnerability of predators to becoming infected
562 during predation events (no. links in predator-parasite sub web leading to transmission). Data
563 based on predators that serve as hosts for at least one trophically transmitted parasite. Note the
564 different scales on axes. Lines indicate the best fit of significant regressions (Sylt: $y = -0.425 +$
565 $0.656 * x$; Flensburg $y = 1.306 + 0.268 * x$; Carpinteria : $y = 5.051 + 0.370 * x$; Bahia Falsa : $y =$
566 $7.682 + 0.238 * x$; Punta Banda : $y = 5.072 + 0.207 * x$; Takvatn: $y = 1.520 + 0.285 * x$). For
567 regression statistics and sample sizes, see Table 3.

568

569 **Figure 4:** Mean vulnerability (no. of predators) (+SE) per individual parasite life-cycle stage
570 in the eight predator-parasite sub webs. For no. of parasite life-cycle stages, see Table 1.

571

572 **Figure 5:** Relationship between total predator richness per food web and a) vulnerability of
573 free-living stages per parasite life-cycle stage considering free-living stages only; b)
574 vulnerability to concomitant predation per parasite life-cycle stage (total no. links/no. of
575 parasite life-cycle stages) considering all parasite life-cycle stages; c) vulnerability to
576 concomitant predation per parasite life-cycle stage considering only trophically transmitted
577 (tt) life-cycle stages (total no. links/no. of trophically transmitted parasite life-cycle stages);
578 and d) number of trophic transmission links per trophically transmitted life-cycle stage (total
579 no. of links/no. of trophically transmitted stages). Lines indicate the best fit of significant
580 regressions (b: $y = 2.946 + 0.049 * x$; c: $y = -0.746 + 0.089 * x$; d: $y = 0,4116 + 0,0786 * x$).

581

582

583 **Tables**

584

585 **Table 1:** Summary web metrics for the eight food webs, showing the number of free-living
 586 species (basal taxa and predators) and the number of predators as well as the number of
 587 parasite life-cycle stages per web, the number of realised and potential links and the resulting
 588 connectance for the predator-prey and predator-parasite sub webs, the proportion (%) of six
 589 types of predation links in the predator-parasite sub web and the mean proportion (%) of links
 590 (\pm SE) leading to transmission per trophically transmitted parasite life-cycle stage.

591

Web metrics	Otago Harbour	Sylt Tidal Basin	Flensburg Fjord	Carpinteria Salt Marsh	Bahia Falsa	Estero de Punta Banda	Takvatn Lake	Quick Pond
No. free-living species	123	126	77	124	137	163	37	48
No. of predators	119	120	71	110	114	144	29	42
No. of parasite life cycle stages	57	104	103	147	151	190	30	34
<i>Predator-prey sub-web</i>								
Realised no. of links	1206	1052	579	1006	1104	1694	198	576
Potential no. of links	15129	15876	5929	15376	18769	26569	1369	2304
Connectance	0.080	0.066	0.098	0.065	0.059	0.064	0.145	0.250
<i>Predator-parasite sub-web</i>								
Realised no. of links	525	1655	669	2027	1903	3280	180	377
Potential no. of links	7011	13104	7931	18228	20687	30970	1110	1632
Connectance	0.075	0.126	0.084	0.111	0.092	0.106	0.162	0.231
<i>Proportion link types</i>								
% Concomitant predation	62.5	58.8	71.8	59.5	58.1	61.8	65.6	62.3
% Trophic transmission	19.9	23.5	16.6	25.8	32	17.6	30	8
% Predation on free-living stages	16.8	16.7	11.6	14.5	9.7	20.5	4.4	29.7
% Predation on commensal stages	0.8	1						
% Direct predation no transmission				0.1				
% Direct predation transmission				0.1	0.2	0.1		
% links leading to transmission in trophically transmitted stages	44.3 \pm 5.6	60.9 \pm 4	70.2 \pm 6.5	64.8 \pm 4.2	62.5 \pm 4.0	53.9 \pm 3.9	79.3 \pm 6.8	59.1 \pm 13

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595

596 **Table 2:** Results of GLMs with predator generality and food-web identity as factors and
597 levels of concomitant predation or parasite transmission as response variable. The tests are
598 based on data presented in Figures 2 & 3. dF: degrees of freedom, MS: mean squares, F: f-
599 statics and p: significance level.

	dF	MS	F	p
<i>Concomitant predation (Fig. 2)</i>				
Predator generality	1	45834.78	407.66	<0.001
Food-web	7	1352.17	12.03	<0.001
Error	740	112.43		
<i>Parasite transmission (Fig. 3)</i>				
Predator generality	1	1953.31	46.97	<0.001
Food-web	7	284.77	6.85	<0.001
Error	272	41.59		

600

601

602

603 **Table 3:** Results of simple linear regressions of the relationship between predator generality

604 (no. of prey species preyed upon per predator species in predator-prey sub web) and i)

605 concomitant predation of parasites by a predator (no. of links in predator-parasite sub web;

606 see Fig. 2) and ii) parasite transmission to a predator (no. links in predator-parasite sub web;

607 see Fig. 3). For each regression, the no. of nodes is given in a separate column (n).

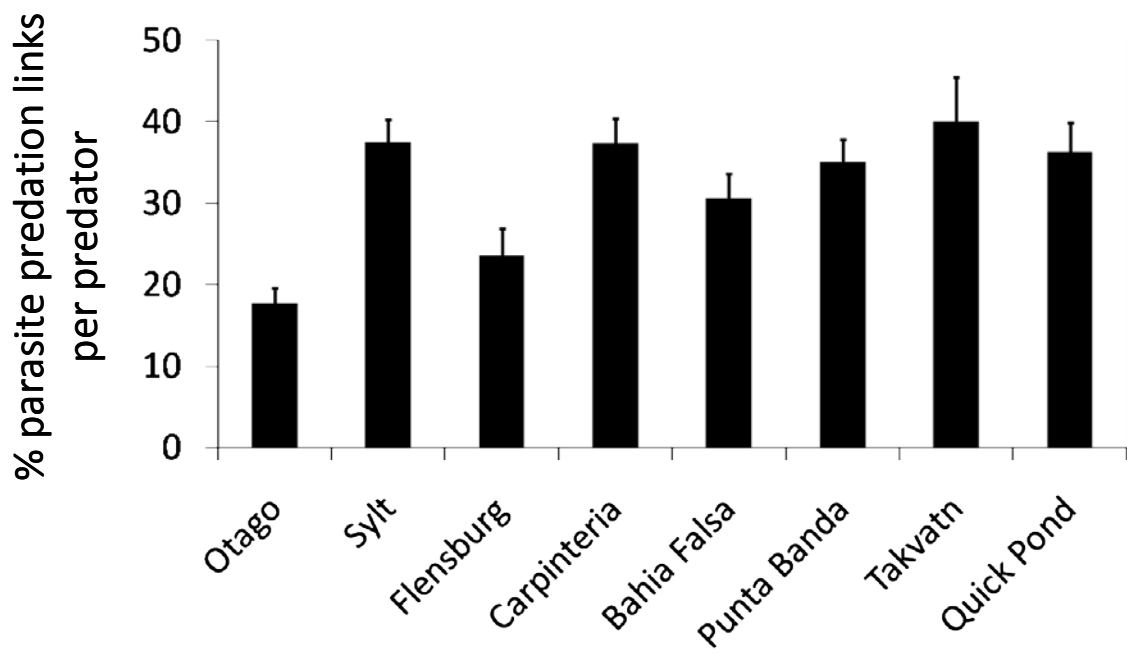
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Food web	Concomitant predation			Parasite transmission		
	r ²	p	n	r ²	p	n
Otago Harbour	0.409	<0.001	119	0.129	0.110	21
List Tidal Basin	0.720	<0.001	120	0.552	<0.001	43
Flensburg Fjord	0.749	<0.001	71	0.437	0.004	17
Carpinteria Salt Marsh	0.345	<0.001	110	0.129	0.008	53
Bahia Falsa	0.367	<0.001	114	0.116	0.012	53
Punta Banda	0.296	<0.001	144	0.088	0.017	64
Takvatn Lake	0.116	0.071	29	0.647	<0.001	16
Quick Pond	0.613	<0.001	42	0.281	0.051	14

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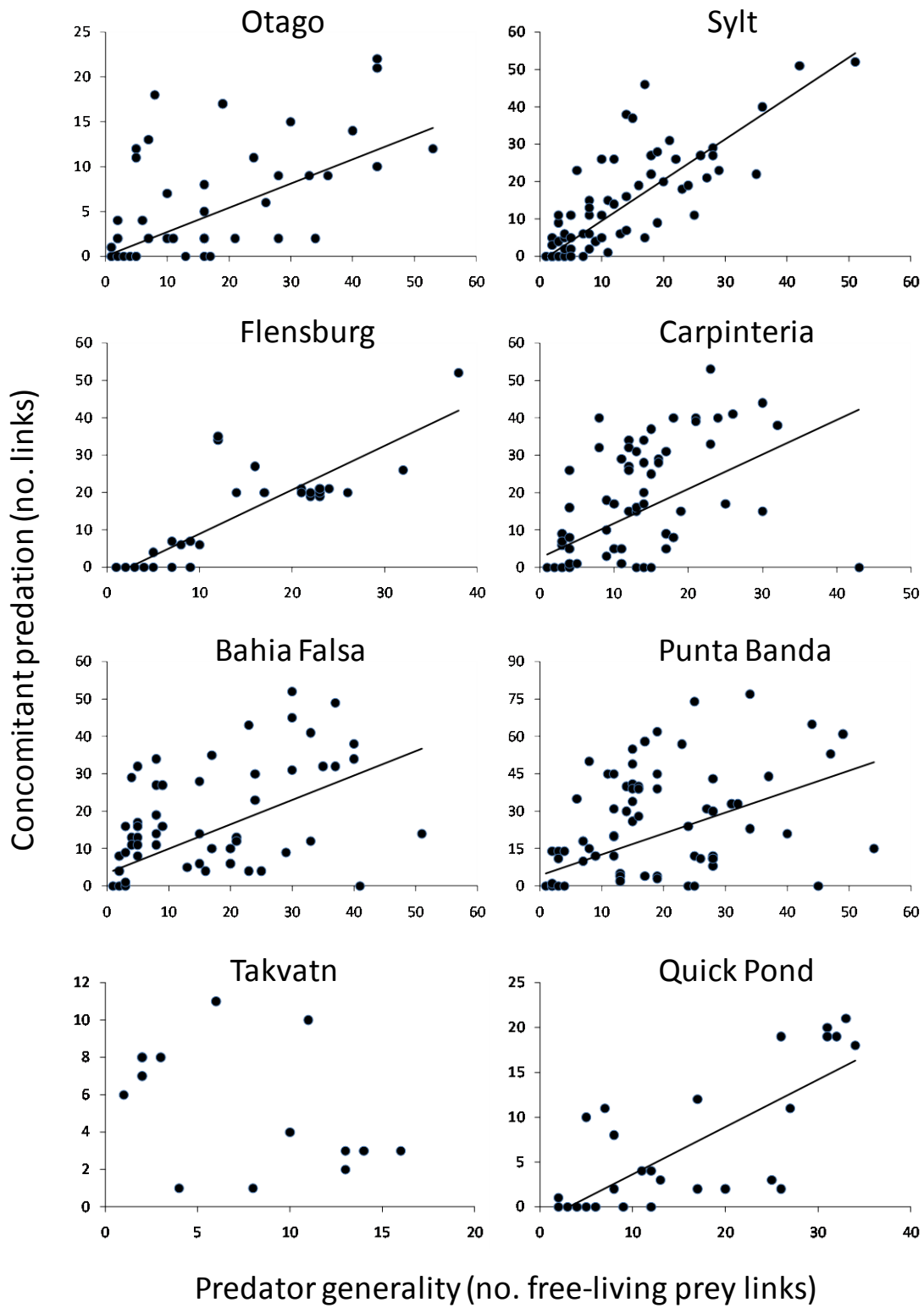


612

613 Figure 1

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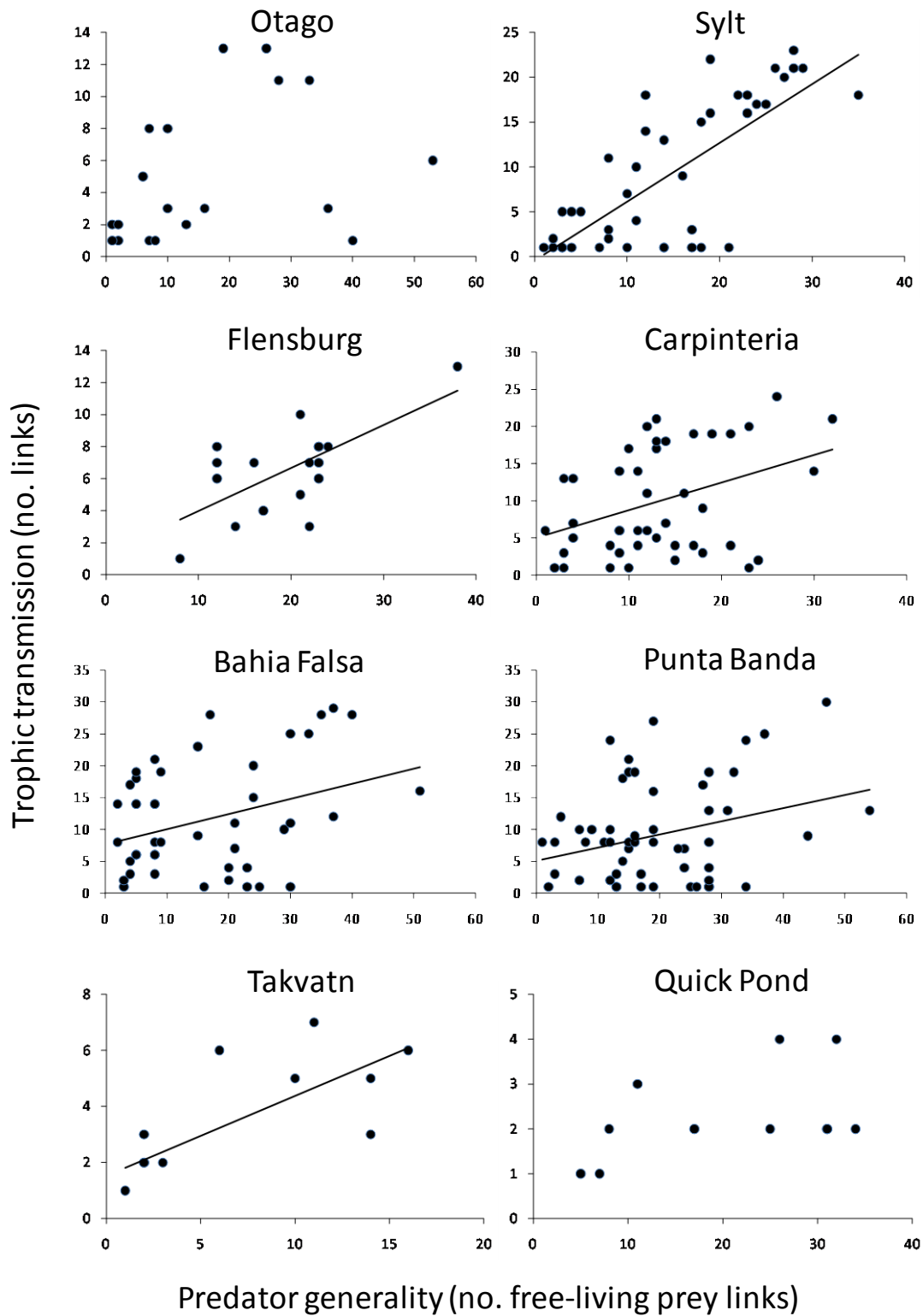
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617 Figure 2

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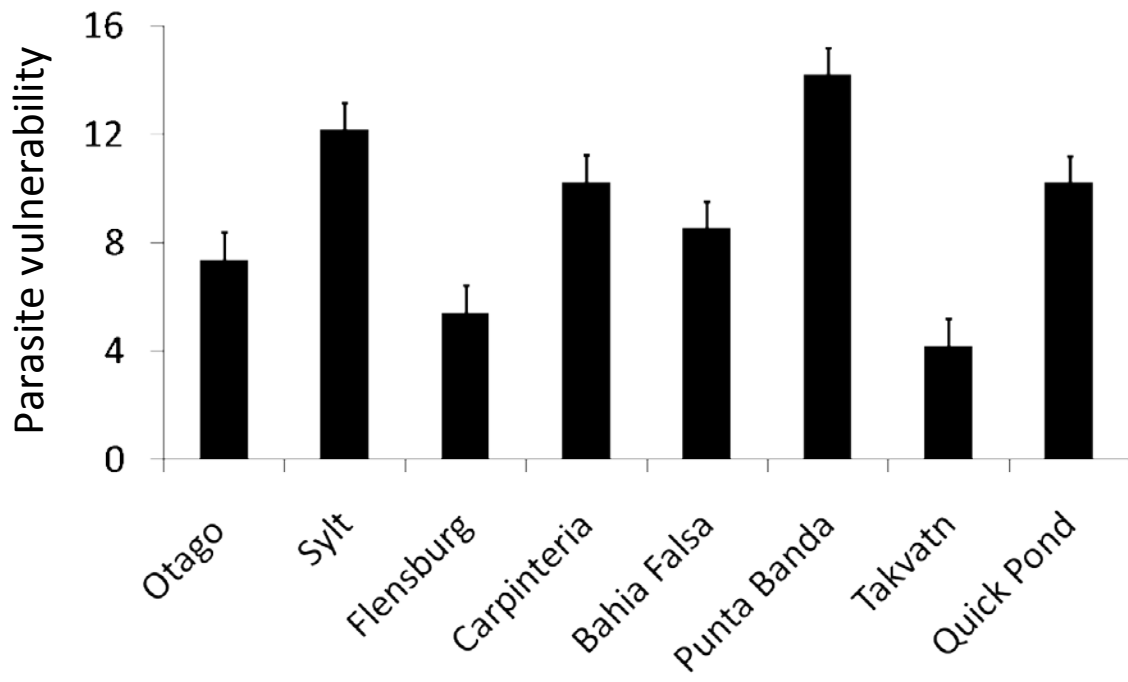
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621 Figure 3

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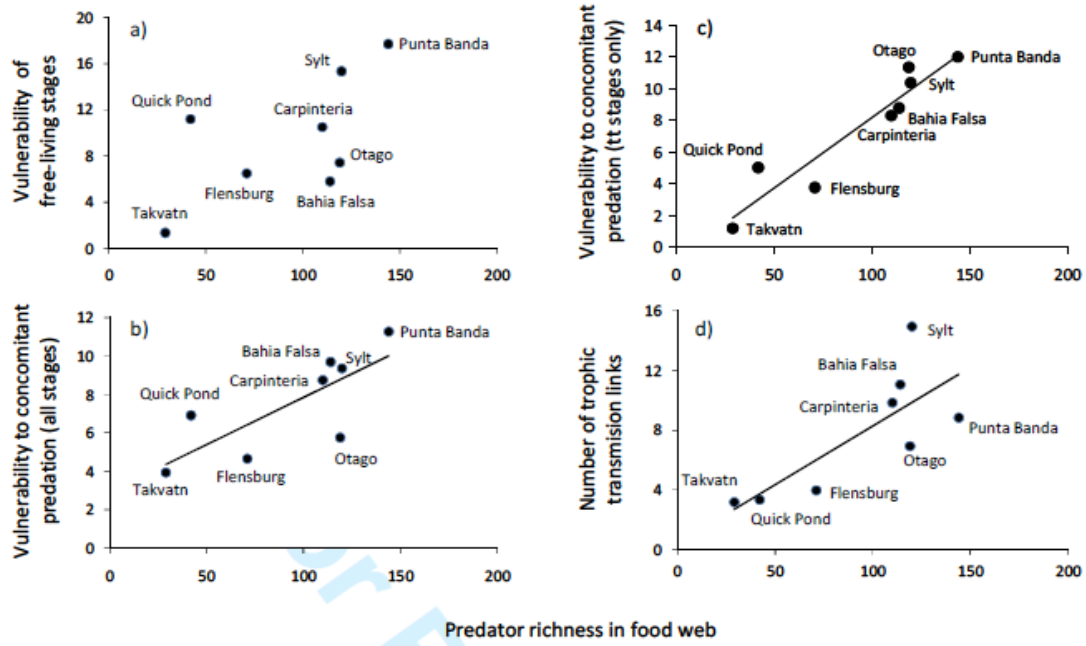


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625 Figure 4

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631 Figure 5