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1 **A food-web based comparison of the drivers of helminth parasite species richness in**

2 **coastal fish and bird definitive hosts**

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12 Running page head: Drivers of coastal parasite richness

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ABSTRACT

Studies on the factors determining parasite richness in hosts are typically performed using data compiled for various sets of species from disparate habitats. However, parasite transmission is embedded within local trophic networks and proper comparisons among host species of the drivers of parasite richness should ideally be conducted among hosts belonging to the same local network. Here, we used data from six well-resolved coastal food webs which include parasites to investigate patterns and drivers of species richness of trophically transmitted helminths in coastal fish and bird definitive hosts. We first investigated whether previous notions that birds harbour more trophically transmitted parasite species than fish hold true for food-web based comparisons; and then we investigated the role of host prey range, trophic level and body size in driving parasite richness patterns in coastal birds and fish. Our analyses indicated that bird hosts, on average, harboured higher parasite richness than fish hosts. While there was no consistent driver of parasite richness at the level of entire food webs, host prey range and host trophic level were positively correlated with parasite richness in birds within individual food webs. For fish hosts, the effect of host prey range was less consistent and trophic level had no effect on parasite richness. For both host types, host body size did not affect parasite richness. These results suggest that host prey range and trophic level seem to be more consistent drivers of parasite richness for coastal bird than for fish hosts.

INTRODUCTION

Habitat characteristics are the fundamental determinants of local community diversity; for

parasites, these habitat features are those of their hosts. Various host features have been

proposed to explain interspecific differences in parasite richness among host species (Poulin

1995, Poulin & Morand, 2004). For example, host body size emerges as an almost universal

predictor of parasite species richness in meta-analyses of published comparative studies

among host species (Kamiya et al. 2014), although individual comparative studies sometimes

fail to detect an effect of body size (e.g. Poulin et al. 2011, Lima et al. 2012). In addition, the

mean parasite species richness per host may also differ among specific taxa of hosts. For

example, bird hosts have been reported to have a typically greater species richness of

gastrointestinal helminth parasites than fish hosts (Kennedy et al. 1986, Bush et al. 1990).

The reasons for this difference given by Kennedy et al. (1986) include the greater vagility of

birds, their more complex digestive tract providing more niches for helminths, and their

broader diet.

Importantly, previous comparisons of parasite richness among host species or taxa

have been performed using data on parasite richness per host species compiled for various

sets of species from disparate habitats. Hence, the datasets for such analyses have typically

been assembled from the literature, by pooling data points from different geographic areas

and types of habitat (e.g., Kennedy et al. 1986, Poulin 1995, Gregory et al. 1996, Sasal et al.

1997, Luque & Poulin 2008). However, parasite transmission is embedded within local

trophic networks, or food webs (Lafferty et al. 2008). Therefore, proper comparisons among

host species of what makes some of them more prone to accumulate many parasite species

than others should ideally be conducted among hosts belonging to the same local network, to

account for any differences among localities. This has been difficult to achieve to date

because of the limited availability of food web networks in which parasites have been

included; the very rare comparisons of parasite richness among hosts that have been food-web based have revealed interesting new patterns (Chen et al. 2008). The use of local food web data also allows the direct measurement of the trophic properties of each host species in the relevant local community, instead of relying on species-typical values obtained from the literature. These trophic properties include diet breadth, or the range of prey species consumed, as well as trophic level, or the average position of a species in the food chains of which it is part, a factor previously suggested to be associated with parasite species richness (Poulin & Leung 2011, Timi et al. 2011).

Here, we use data on six relatively well-resolved coastal food webs which include parasites to investigate patterns and drivers of species richness of trophically transmitted helminth parasites in coastal fish and bird definitive hosts. Our approach allows contrasts between individual fish and bird host species that are parts of the same communities, and thus accounts for any idiosyncrasies of particular food webs or other local effects. We first investigated whether previous notions that birds harbour more trophically transmitted parasite species than fish also hold true for trophically transmitted helminths in costal fish and bird definitive hosts when using a food-web based comparison. Furthermore, we investigated the role of three host properties in driving parasite richness patterns in bird and in fish hosts. We focussed on two trophic properties (host diet breadth and trophic level) and one general life history trait already assumed to play an important role (host body size) as predictors of parasite community richness. Our main goal was to determine the relative contribution of these three factors in determining trophically transmitted helminth parasite richness in coastal fish and bird definitive hosts.

MATERIALS AND METHODS

Food webs and host data

91   We used six highly-resolved coastal food webs, all in the public domain, that include data on

92   metazoan parasites (Table 1). The first three webs (see Hechinger et al. 2011) are from

93   estuarine salt marshes along the North American Pacific coast: Carpinteria Salt Marsh,

94   California, USA; Estero de Punta Banda, Baja California, Mexico; and Bahia Falsa in Bahia

95   San Quintín, Baja California, Mexico. The three other food webs are from Flensburg Fjord, a

96   brackish shallow water inlet on the Baltic Sea between Germany and Denmark (Zander et al.

97   2011), Sylt Tidal Basin, an intertidal bight ecosystem on the North Sea between Germany and

98   Denmark (Thieltges et al. 2011a), and Otago Harbour, an intertidal mudflat ecosystem in

99   New Zealand (Mouritsen et al. 2011). Information on how parasite inclusion affects various

100   properties of these food webs is available elsewhere (Thompson et al. 2005, Lafferty et al.

101   2006, Dunne et al. 2013).

102   We focused on trophically-transmitted helminths (trematodes, cestodes, nematodes

103   and acanthocephalans) in their definitive hosts. For each host species in each food web, we

104   recorded the following variables: (i) its parasite species richness; (ii) whether it was a fish or

105   a bird; (iii) its prey range, measured as the number of prey species consumed; (iv) its body

106   size, measured as maximum body length for fish (from www.fishbase.org) and average body

107   mass for birds (from Dunning 2007); and (v) its short-weighted trophic level (TL), an index

108   suitable for topological networks which has been used in previous analyses of parasite-

109   inclusive food webs (Williams & Martinez 2004, Dunne et al. 2013) and that we found to

110   correlate with other measures of trophic level (preliminary analyses, data not shown). Short-

111   weighted TL is measured as the average of the shortest TL and prey-averaged TL, with

112   shortest TL calculated as one plus the shortest chain length from a consumer to a basal

113   species and prey-averaged TL calculated as one plus the mean TL of all the consumer's

114   trophic resources (for more details see Williams & Martinez 2004). Calculations of short-

115   weighted TL were done using the Network3D Software (Yoon et al. 2004, Williams 2010). If

116   the same host species occurred in more than one web, each occurrence was treated as a

117   separate entry (or as a separate 'species') in our dataset, since our analyses are web-based and

118   not species-based. Overall, our analyses included 7-21 species of fish hosts and 17-45 species

119   of bird hosts per web, across all webs (Table 1).

120

121   **Analysis**

122   In a first step, we investigated whether parasite species richness differed both between bird

123   and fish hosts and among the different food webs. In a second step, we studied whether

124   trophic level and prey range differed between bird and fish hosts and among the food webs.

125   Because bird species in the Flensburg food web were lumped into higher taxonomic

126   categories in the original food web, and not treated as separate species, they were excluded

127   from these analyses. However, we included calculations of mean parasite richness, trophic

128   level and prey range in Flensburg fish hosts in the respective figures for comparison with

129   other webs. We fitted general linear models (GLM) to either parasite species richness (log+1-

130   transformed), prey range (log-transformed) or trophic level, with food web identity and host

131   type (bird vs. fish) as fixed factors. Model assumptions were checked using residual plots.

132   Following these initial analyses, we investigated the relative contributions of host

133   prey range, host trophic level and host body size to variation in parasite species richness

134   among host species. As the initial analyses revealed significant interaction terms (host type x

135   food web), indicating the effect of host type to be conditional on food web identity, we

136   analysed all food webs separately. In addition, we treated fish and bird hosts separately for

137   three reasons. First, our goal was to evaluate the respective effects of different predictors of

138   helminth species richness independently in the two types of hosts, necessitating that they be

139   treated separately. Second, helminth species richness values were generally higher in birds

140   (see results), therefore pooling them for a combined analysis would have resulted in a

141   bimodal distribution of the response variable. Finally, because of data availability, we had to

142   use different metrics of body size for birds (mass) and fish (length), forcing these to be

143   analysed separately. For these analyses, we considered data from fish hosts from the

144   Flensburg food web but omitted data from bird hosts due to the species lumping mentioned

145   above. We could not include taxonomic or phylogenetic information to the analyses as there

146   was insufficient replication of taxa for the two host types within individual webs. General

147   linear models (GLM) were fitted to log+1-transformed helminth species richness values, with

148   host prey range (log-transformed), host trophic level and host body size (log-transformed) as

149   fixed factors. Model assumptions were verified using residual plots. In addition, we checked

150   for collinearity among these variables, and found relatively weak correlations (based on R^2

151   values) between variables in 6 out of the 33 comparisons (see Table S1). For all GLMs we

152   calculated the proportion of variance (V) explained by the different factors as

153      $V = SS_{factor}/SS_{total} \times 100$.

154

155   **RESULTS**

156   Mean parasite species richness of trophically transmitted helminths was significantly lower in

157   fish hosts compared to bird hosts in all five food webs investigated (Figure 1, Table 2).

158   However, the effect of host type depended on the identity of the food web as indicated by the

159   significant interaction term, resulting from varying magnitudes of the difference between

160   values in fish and bird hosts among the webs (Figure 1, Table 2). Finally, mean parasite

161   species richness in bird and fish hosts also significantly differed among the five food webs

162   (Figure 1, Table 2).

163   Further analyses revealed that the mean prey ranges as well as the mean trophic levels

164   of fish and bird hosts differed among webs. However, the effect of host type was not

165   consistent among webs as indicated by the significant interaction terms (Table 2). In some

166 food webs, fish and bird hosts showed similar values of prey ranges and trophic level while in

167 others fish or bird hosts had higher values than their respective counterpart (Figure 2).

168 Although not integrated in the statistical analyses, mean parasite richness as well as mean

169 trophic level and mean prey range of fish hosts in the Flensburg web were within the range of

170 values observed in the other webs (Figures 1 & 2).

171   The separate analyses of the factors driving parasite richness in bird and fish hosts

172 within each food web revealed different patterns for the two host types. In fish hosts, prey

173 range was the only factor that had a significant positive effect on parasite species richness in

174 hosts in two of the six food webs (Sylt & Flensburg) while in another one the effect was

175 marginally significant (Carpinteria; p= 0.089; Figure 3; Table 3). This effect was particularly

176 strong in the Flensburg web where it explained 80% of the variance (Table 3). In contrast,

177 neither trophic level nor host body size showed a significant effect on parasite richness (Table

178 3). Additional analyses indicated mild collinearity (based on R^2 values) only in 2 out of the

179 18 comparisons (electronic appendix Table S1), thus considered not to affect the analyses.

180   In bird hosts, prey range had a significant (positive) effect on parasite richness in all

181 webs apart from Otago, where it was marginally significant (0.059; Figure 4; Table 4). In one

182 web (Sylt), this relationship was mainly driven by a lumping of many data points at around a

183 log prey range of 3 (Fig. 3). In addition, trophic levels had a significant positive effect on

184 parasite richness in all webs apart from Otago (Figure 5; Table 4). However, in most webs the

185 effect of prey range was stronger (explaining 8.2 to 44.4 % of the variance) than the one of

186 trophic level (8.5-20.0%; Table 4). Only in the Bahia food web, trophic level was a stronger

187 predictor of parasite richness than prey range (20.9 vs. 8.2%; Table 4). In contrast, host body

188 size had no effect in any of the five food webs (Table 4). Additional analyses indicated weak

189 collinearity (based on R^2 values) in only four out of the 15 comparisons (electronic appendix

190 Table S1), thus considered not to affect the analyses.

DISCUSSION

In all food webs, mean parasite richness was higher in birds than in fish, corroborating

a proposed general pattern of a fish versus bird difference in trophically transmitted helminth

community diversity based on comparative analyses using data compiled from the literature

(Kennedy et al. 1986, Bush et al. 1990). In our analyses, both bird and fish hosts are

embedded in the same trophic networks, thus allowing for a more direct comparison than in

comparative studies that have to rely on data from different localities. The significant

interaction term (food web vs. host type) in our food-web based comparison indicated that the

magnitude of the difference in parasite richness between birds and fish depended on the

specific context of the food web. Parasite transmission is intricately embedded in local

trophic networks (Lafferty et al. 2008) so that any difference in network composition and

structure among food webs is likely to lead to differences in parasite richness among these

webs. Such differences in structure cannot only be related to varying roles of hosts among

food webs, but also to varying degrees of non-host interference with parasite transmission,

e.g. in the form of predation on infective stages (Johnson & Thieltges 2010, Thieltges et al.

2013). Similarly, birds and fish may be differently integrated into trophic and transmission

networks among food webs, leading to the observed variation in the magnitude of the bird

versus fish difference in parasite species richness among the food webs. That the integration

of birds and fish into trophic networks is indeed different among the food webs studied here

is indicated by the fact that birds and fish did not show a consistent pattern in their mean

trophic level or prey range among the food webs: while in some webs, birds showed higher

values than fish, it was the opposite in others or there was no difference between the two host

types. Hence, at the level of entire food webs none of the factors considered here (host

215   trophic level and prey range) seems to be a universal driver of the difference in parasite

216   richness between bird and fish hosts.

217   That fish nevertheless showed consistently lower levels of parasite richness than birds

218   may be caused by other factors not studied here. For example, the larger body mass and

219   longer intestinal tract of birds have been suggested to underlie the bird-fish difference in

220   parasite richness (Kennedy et al. 1986, Gregory et al. 1996). In our study, we could not test

221   for an effect of body mass due to the lack of available data for fish, but it may be relevant

222   because many fish species in the food webs used for our analyses are small benthic fish (e.g.

223   Gobiidae). In addition, the observed pattern may be related to the fact that coastal food webs

224   like the ones used for our analyses are dominated by trematodes (Mouritsen & Poulin 2002).

225   In these ecosystems, trematodes predominantly use birds as definitive hosts while fish act

226   mainly as intermediate hosts (e.g. Thieltges et al. 2006). Hence, the observed pattern may, at

227   least in part, be related to the respective biology of the parasites involved. Alternatively, it

228   could be an artefact resulting from the way parasite inclusive food webs are usually

229   assembled. While parasite data for fish are often based on extensive sampling of hosts in the

230   respective food webs, data for birds are more difficult to obtain due to the generally high

231   legal protection status of birds; thus, data assembly must rely on lower host sample sizes

232   accompanied by additional inference from observations of larval parasite life cycle stages in

233   intermediate hosts and general knowledge of parasite life cycles in the respective systems.

234   This may introduce a bias in the accuracy of parasite species richness values, but given the

235   well-known dominance of trematodes using birds as definitive hosts in coastal ecosystems

236   (Mouritsen & Poulin 2002) it is highly likely that the observed pattern reflects more a

237   biological reality than a methodological artefact. However, the potential extent of

238   methodological artefacts and the exact mechanisms driving the observed pattern at the level

239   of entire food webs remain to be investigated. In particular, it would be valuable to explore

240   innovative non-invasive methods of investigating parasite infections in birds to be able to

241   obtain more empirical data on actual parasite richness in birds.

242   A clearer pattern emerged from the analyses of the drivers of parasite richness within

243   individual food webs, which were run separately for fish and bird hosts. For both fish and

244   birds, host prey range had a significant effect on parasite richness, although its relevance was

245   more consistent among the food webs in birds than in fish. In general, the broader the range

246   of prey consumed by a host species, the higher the numbers of parasites associated with this

247   species was. Since the parasite species considered here are all trophically transmitted, this

248   pattern was expected. With an increase in prey range, predators should face a higher risk of

249   consuming a prey species that serves as an intermediate host for a trophically transmitted

250   parasite. Indeed, this relationship has been found in previous analyses and seems to be a

251   universal pattern of parasite transmission in food webs (Chen et al. 2008, Thieltges et al.

252   2013). However, the strength of this relationship differed among the food webs in our study.

253   For example, prey range explained 80% of the variance in fish parasite richness in the

254   Flensburg web while it was not or only marginally significant as a predictor in four out of the

255   six food webs. In contrast, for bird parasites prey range was a significant or marginally

256   significant driver of parasite richness in all five food webs. This may point to a stronger

257   importance of prey range for parasite transmission in bird than in fish hosts, though the

258   relatively low numbers of fish species may have compromised our power to detect this

259   relationship in fish. Hence, more well-resolved food webs including fish and bird parasites

260   will be needed to verify that prey range is indeed a stronger driver for bird than for fish

261   parasites.

262   In contrast to prey range, trophic level only had a significant effect on parasite

263   richness in birds but not in fish hosts. In four of the five webs, bird parasite richness was

264   positively correlated with trophic level, the latter explaining 8-21% of the variance in parasite

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265   richness. This difference in the importance of trophic level between bird and fish hosts may

266   be due to their different role in the biology of the main parasite taxa in the food webs

267   analysed. As discussed above, trematodes are the dominant parasites in intertidal ecosystems

268   and mainly use birds as their definitive hosts, with fish more often serving as intermediate

269   hosts (Mouritsen & Poulin 2002). Birds feeding at a higher trophic level will thus face a

270   greater likelihood of feeding on fish (and other taxa) that serve as intermediate hosts for

271   parasites, leading to the observed pattern. This reflects the observation from a previous study

272   that the proportion of larval taxa in fish hosts is highest in small fish hosts with low trophic

273   levels, i.e. parasites utilise mainly those hosts as intermediate hosts because they offer the

274   highest chance to be consumed by a larger definitive hosts at a higher trophic level (Poulin &

275   Leung 2011). That parasite infection risk for a predator indeed increases with its trophic level

276   has previously been shown for hosts in the Carpinteria web (Lafferty et al. 2006). Similarly, a

277   comparative study of fish parasite communities using trophic levels from Fishbase

278   (www.fishbase.org) has found a positive correlation between trophic level and average

279   taxonomic distinctness of the parasite assemblage in a fish (Luque & Poulin 2008). However,

280   our study is now the first to (i) corroborate this pattern for several food webs by using food-

281   web generated measures of trophic level (instead of literature data), and to (ii) investigate

282   differences in its relevance for bird and fish hosts. Although trophic level was a significant

283   factor determining bird parasite richness in most food webs, it was a weaker driver of parasite

284   richness compared to prey range in all webs apart from the Bahia food web. This suggests

285   that parasite richness in a host is more strongly determined by the number of prey species it

286   consumes than by its position in the food chain. It would be informative to investigate in the

287   future whether the different influence of trophic level for bird and fish hosts also holds true

288   for other food webs from terrestrial and freshwater ecosystems.

289   Finally, an unusual finding of our study is that for both fish and bird species, parasite

290   species richness did not correlate with host body size. This goes against the general trend

291   uncovered in previous comparative studies (e.g. Poulin 1995, Gregory et al. 1996, Luque &

292   Poulin 2008) and confirmed recently by meta-analysis (Kamiya et al. 2014). The main

293   difference between the present study and earlier comparative analyses is that ours is food-

294   web based, and that it simultaneously accounts for diet breadth (prey range) and trophic level,

295   factors notoriously difficult to quantify for any host species in studies that do not have a local

296   focus. Our results indicate that the diversity of the host's diet (fish & birds) and its trophic

297   level (birds) outweigh its body size as a determinant of helminth species richness. Such

298   overriding effects of other factors may also explain the fact that individual comparative

299   studies sometimes fail to detect an effect of body size (e.g. Poulin et al. 2011, Lima et al.

300   2012). However, by using maximum body sizes for fish in our study, we may have

301   overestimated average body masses for fish species which may also occur as juveniles in

302   coastal waters, which are known to often serve as nursery grounds for fish (Horn et al. 1998).

303   Unfortunately, actual body size data of all fish included in the webs are not available, and it

304   remains to be investigated whether using actual body size data would change the outcome of

305   the analyses.

306   In conclusion, our food-web based comparisons showed that parasite richness differed

307   between bird and fish hosts, with higher mean parasite richness in birds than in fish. While

308   there was no consistent driver of parasite richness at the level of entire food webs, parasite

309   richness significantly increased with host prey range in bird and to a lesser extent in fish hosts

310   within individual food webs. For birds but not fish, parasite richness also significantly

311   increased with the trophic level of a host. These results suggest that host prey range and

312   trophic level seem to be more consistent drivers of trophically transmitted helminth parasite

313   richness in coastal bird than in fish definitive hosts, and it will be informative in the future to

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314 assess whether this pattern also holds true for food webs from other ecosystems. Future

315 research may also include the effects of other potential drivers (e.g. host population size) on

316 parasite richness. In addition, one could further investigate whether the observed patterns also

317 hold true for parasite infection levels (e.g. prevalence or intensity). However, a prerequisite

318 for such analyses will be well-resolved parasite-inclusive food webs for which all these data

319 are available. This will be a challenging task but such analyses would significantly advance

320 our current understanding of the drivers of parasite infections in food webs.

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402 **Table 1:**

403 Fish and bird species richness (no. of species) and references for data sources of the six

404 coastal food webs used for the analyses. Due to lumping of bird species into higher taxa in

405 the Flensburg web, we only used the data on fish for this food web.

406

Food web	Fish richness	Bird richness	Reference
Otago Harbour	7	17	Mouritsen et a. 2011
Sylt Tidal Basin	21	29	Thieltges et al. 2011
Carpinteria Salt Marsh	11	42	Hechinger et al. 2011
Bahia Falsa	13	41	Hechinger et al. 2011
Estero de Punta Banda	19	45	Hechinger et al. 2011
Flensburg	12	-	Zander et al. 2011

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409   **Table 2:** Results of general linear models (GLM) testing for the effects of food web identity

410   (5 different webs), host type (fish or bird) and an interaction term between the two fixed

411   factors for three different response variables: log parasite richness, short-weighted trophic

412   level and log prey range of each predator.

413

Response variable	Factor	df	MS	F	p
Log parasite richness	Web	4	2.356	3.136	0.015
	Host type	1	64.067	85.291	<0.001
	Web*Host type	4	2.151	2.864	0.024
	Residual	235	0.751		
Trophic level	Web	4	0.719	3.720	0.006
	Host type	1	0.232	1.198	0.275
	Web*Host type	4	0.510	2.640	0.035
	Residual	235	0.193		
Log prey range	Web	4	2.689	3.570	0.007
	Host type	1	2.299	3.053	0.081
	Web*Host type	4	2.963	3.935	0.004
	Residual	235	0.753		

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Table 3: Results of GLMs testing for the effects of short-weighted trophic level, log prey

417 range and log body size on parasite richness (log-transformed) of fish species in six different

418 food webs.

419

| Food web	Factor	df	MS	F	p	Variance explained
Bahia	Trophic level	1	0.115	0.281	0.609	2.2%
	Log prey range	1	0.800	2.198	0.172	17.5%
	Log body size	1	0.442	1.079	0.326	8.6%
	Residual	9	0.409			
Carp	Trophic level	1	0.349	0.733	0.420	5.3%
	Log prey range	1	1.854	3.891	0.089	28.4%
	Log body size	1	1.005	2.1010	0.190	15.4%
	Residual	7	0.476			
Otago	Trophic level	1	0.335	3.447	0.160	44.5%
	Log prey range	1	0.091	0.936	0.405	12.1%
	Log body size	1	0.035	0.360	0.591	4.6%
	Residual	3	0.097			
Punta	Trophic level	1	0.017	0.017	0.897	0.1%
	Log prey range	1	2.039	2.121	0.166	11.7%
	Log body size	1	0.892	0.927	0.351	5.1%
	Residual	15	0.962			
Sylt	Trophic level	1	0.007	0.061	0.808	0.3%
	Log prey range	1	0.627	5.792	0.028	25.3%
	Log body size	1	0.002	0.022	0.884	0.1%
	Residual	17	0.108			
Flensburg	Trophic level	1	0.226	1.647	0.235	3.2%
	Log prey range	1	5.724	41.690	<0.001	80.2%
	Log body size	1	0.092	0.671	0.436	1.3%
	Residual	8	0.137			

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Table 4: Results of GLMs testing for the effects of short-weighted trophic level, log prey

range and log body size on parasite richness (log-transformed) of bird species in five different

food webs.

| Food web	Factor	df	MS	F	p	Variance explained
Bahia	Trophic level	1	6.602	11.639	0.002	20.9%
	Log prey range	1	2.593	4.571	0.039	8.2%
	Log body size	1	1.419	2.502	0.122	4.5%
	Residual	37	0.567			
Carpinteria	Trophic level	1	7.191	13.883	<0.001	20.1%
	Log prey range	1	8.922	17.224	<0.001	24.9%
	Log body size	1	0.002	0.005	0.945	0.01%
	Residual	38	0.518			
Otago	Trophic level	1	0.691	1.370	0.263	7.1%
	Log prey range	1	2.163	4.290	0.059	22.3%
	Log body size	1	0.289	0.574	0.462	3.0%
	Residual	13	0.504			
Punta	Trophic level	1	3.866	6.999	0.012	8.5%
	Log prey range	1	18.246	33.035	<0.001	40.0%
	Log body size	1	0.813	1.472	0.232	1.8%
	Residual	41	0.552			
Sylt	Trophic level	1	1.767	5.741	0.024	10.1%
	Log prey range	1	7.777	25.262	<0.001	44.4%
	Log body size	1	0.276	0.895	0.353	1.6%
	Residual	25	0.308			
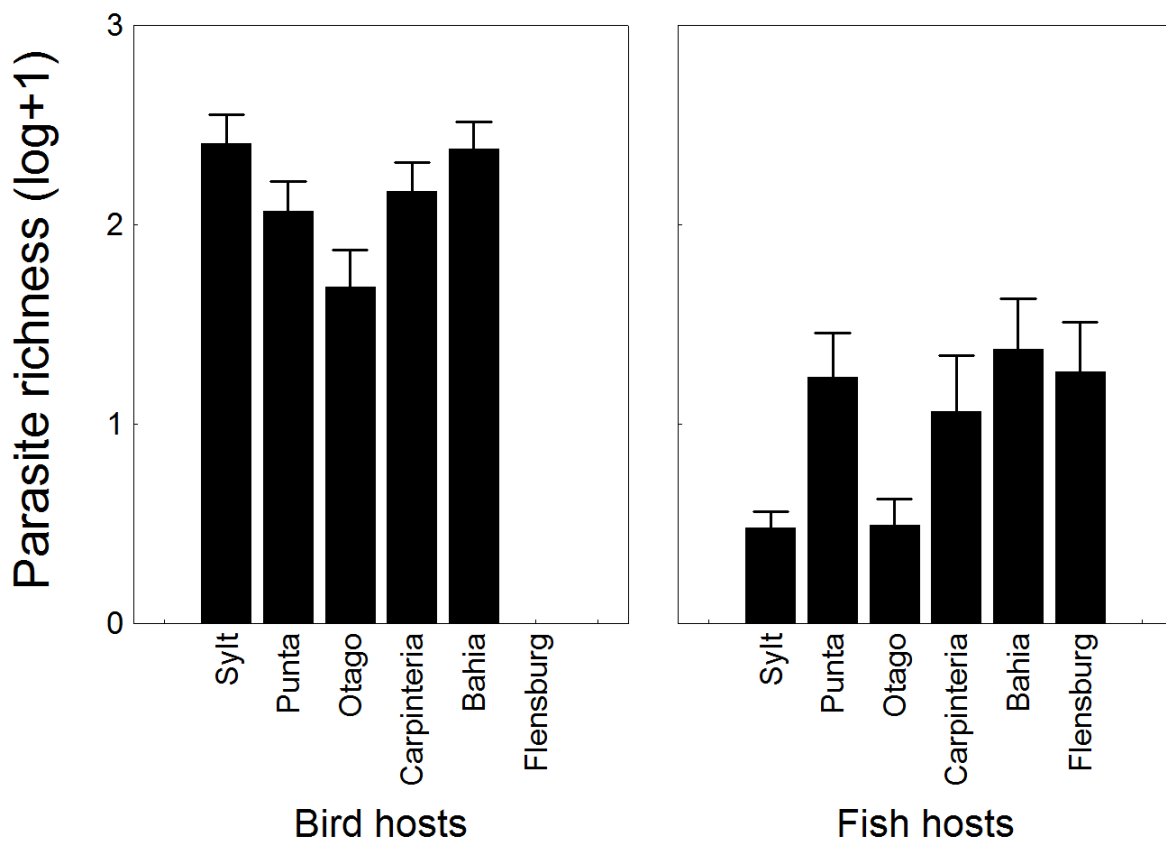
Figure 1: Mean number of trophically transmitted parasite species (parasite richness; log-transformed; ±SE) found in bird and fish definitive hosts in six coastal food webs. For the Flensburg food web, data were only available for fish hosts.
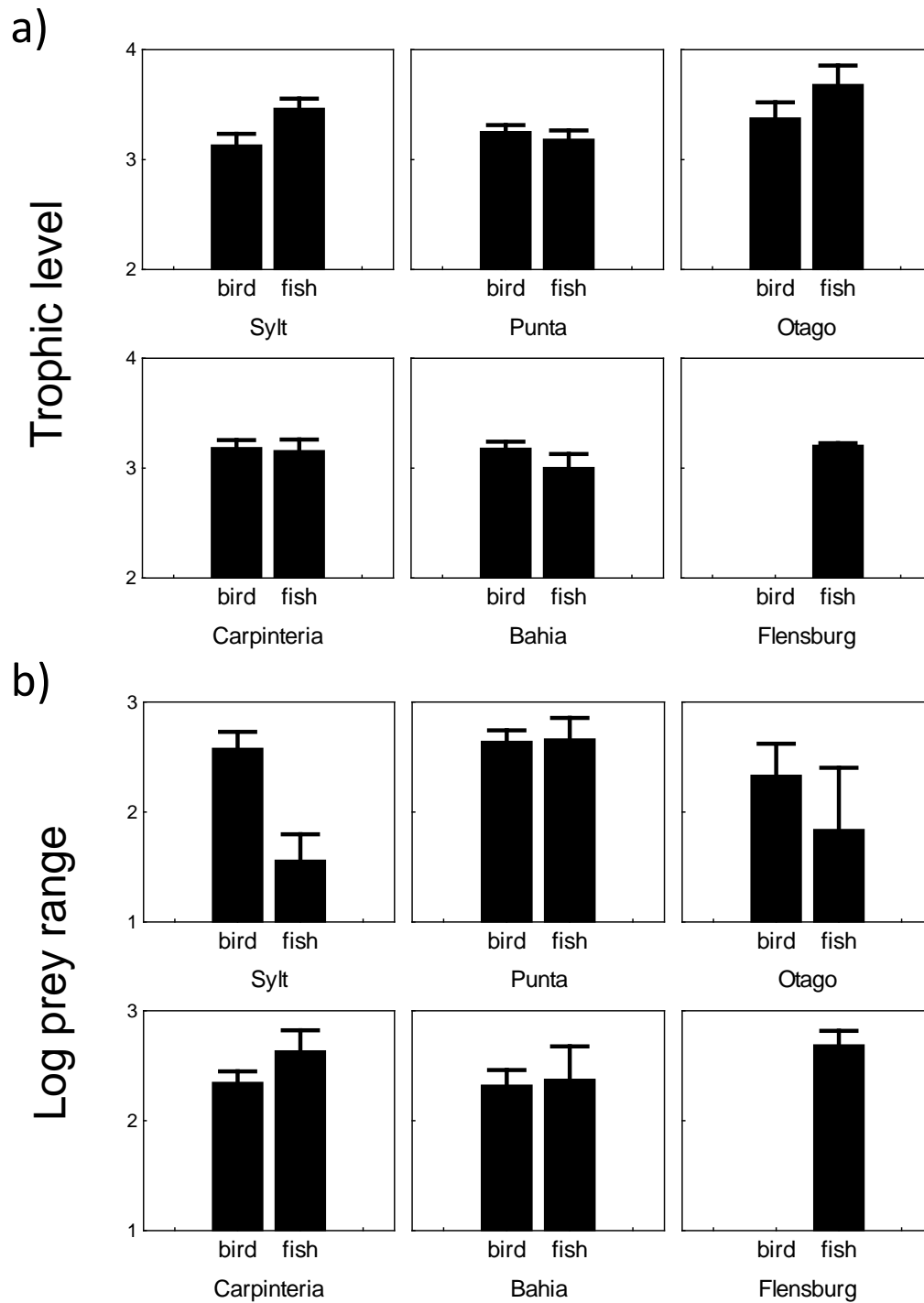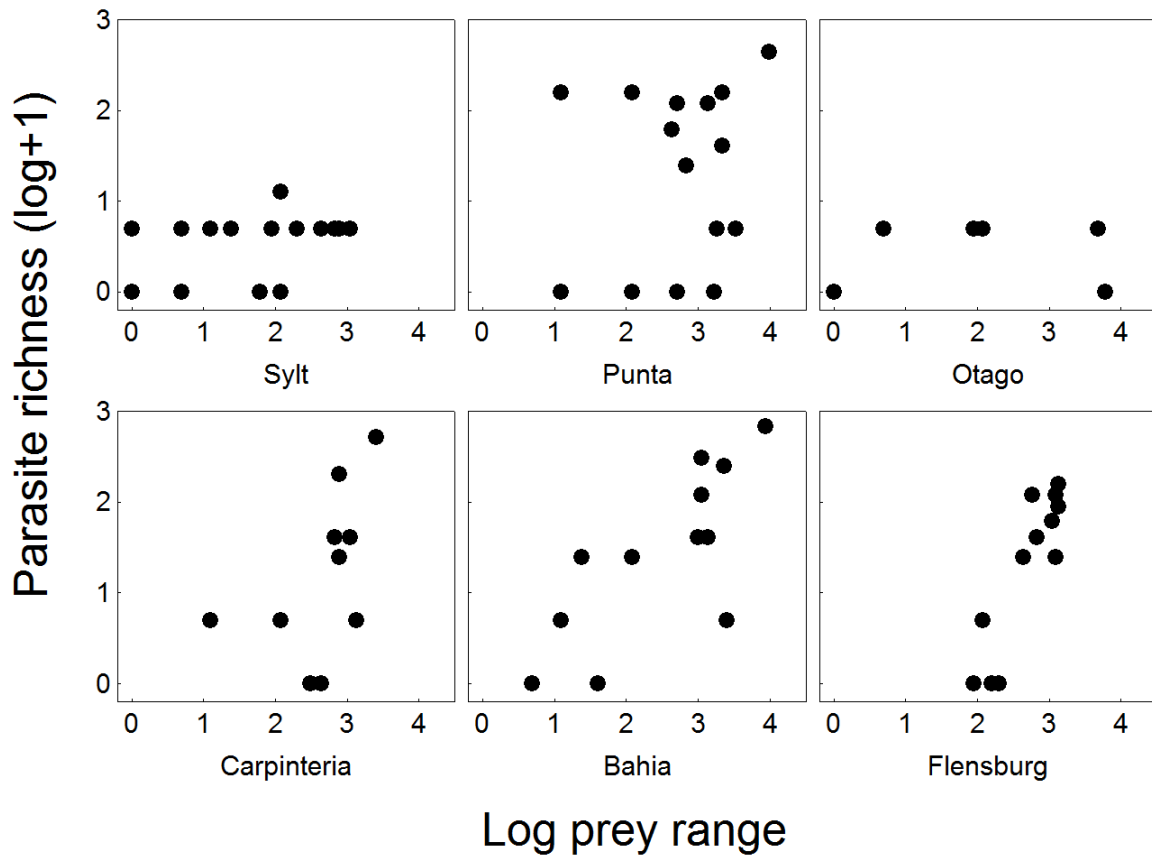
Figure 2: a) Mean short-weighted trophic level and b) mean log prey range (both ± SE) of bird and fish species in the six food webs. For the Flensburg food web, data were only available for fish hosts. Note the truncated y-axes.
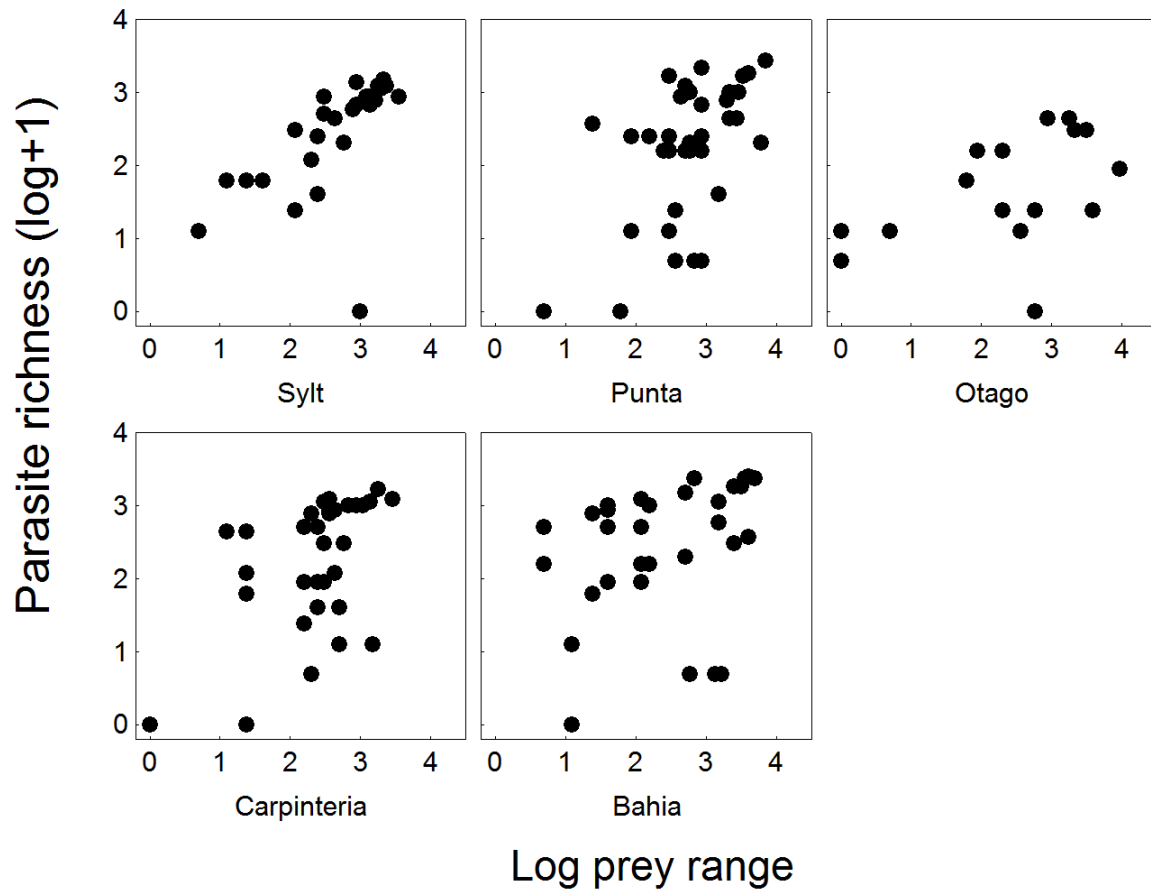
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440

441 **Figure 3:** Relationship between prey range of a fish species (log-transformed) and the

442 number of trophically transmitted parasite species (parasite richness; log+1-transformed)

443 found in the same fish species in six coastal food webs.
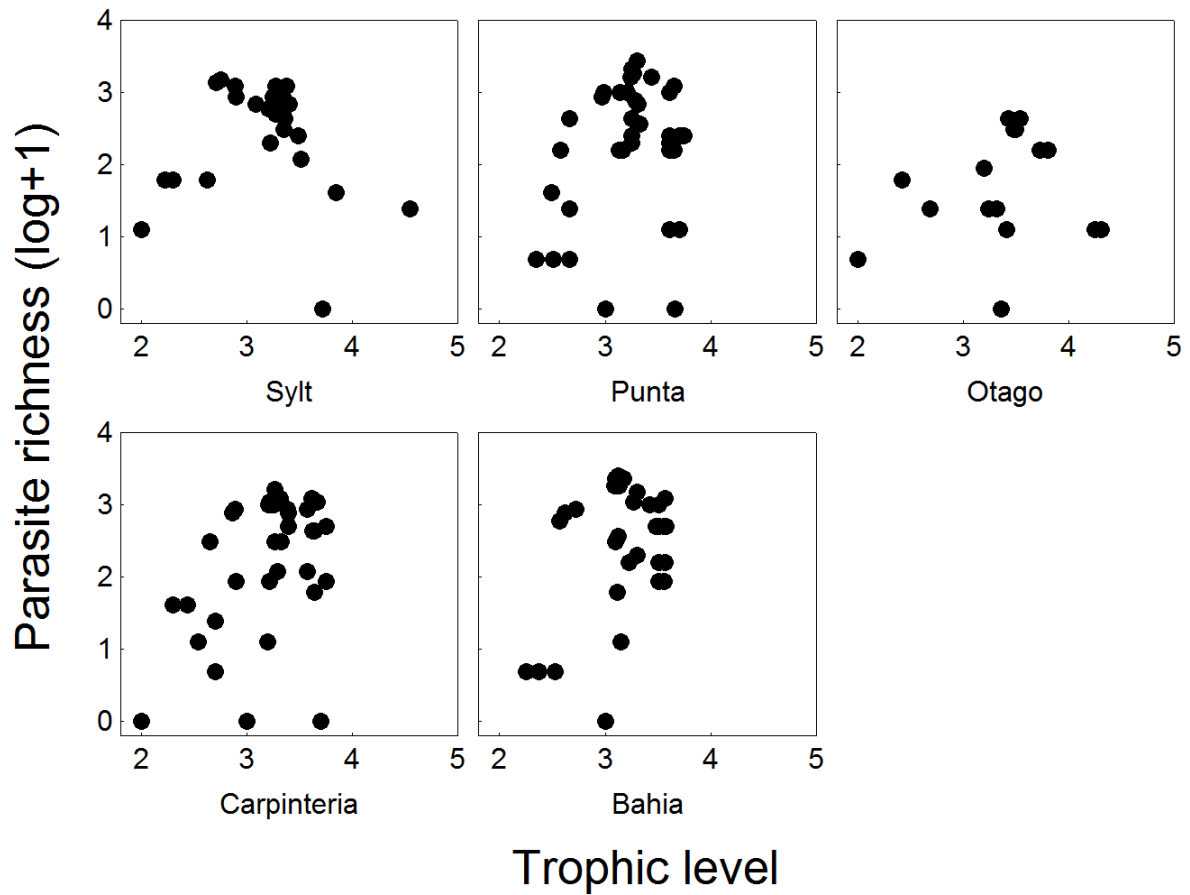
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447 **Figure 4:** Relationship between prey range of a bird species (log-transformed) and the

448 number of trophically transmitted parasite species (parasite richness; log+1-transformed)

449 found in the same bird species in 5 coastal food webs.

450

Figure 5: Relationship between short-weighted (SW) trophic level of a bird species and the number of trophically transmitted parasite species (parasite richness; log+1-transformed) found in the same bird species in 5 coastal food webs. Note the truncated x-axes.

ELECTRONIC APPENDIX

Table S1: Results of checks for collinearity of the three factors (host trophic level, prey range and body size) included as predictors in the separate analyses for each food web and host type (fish or birds). Shown are the result of linear regressions (r^2, r and p-value) and the regression formula in case of significant relationships.

Fish

SW TL vs. log prey range

Sylt	$r^2 = 0,128$; r = -0,358; p = 0,111
Punta	$r^2 = 0,087$; r = 0,2945; p = 0,220
Otago	$r^2 = 0,252$; r = -0,502; p = 0,251
Carpinteria	$r^2 = 0,017$; r = -0,130; p = 0,702
Bahia	$r^2 = 0,027$; r = -0,164; p = 0,591
Flensburg	$r^2 = 0,006$; r = -0,079; p = 0,807

SW TL vs. log body size

Sylt	$r^2 = 0,066$; r = 0,257; p = 0,260
Punta	$r^2 = 0,261$; r = 0,511; p = 0,025; y = -1,628 + 1,677*x
Otago	$r^2 = 0,028$; r = 0,167; p = 0,721
Carpinteria	$r^2 = 0,357$; r = 0,597; p = 0,052
Bahia	$r^2 = 0,098$; r = 0,313; p = 0,297
Flensburg	$r^2 = 0,174$; r = 0,417; p = 0,178

Log prey range vs log body size

Sylt	$r^2 = 0,023$; r = 0,153; p = 0,507
Punta	$r^2 = 0,025$; r = 0,158; p = 0,519
Otago	$r^2 = 0,030$; r = -0,172; p = 0,711
Carpinteria	$r^2 = 0,0001$; r = 0,009; p = 0,980
Bahia	$r^2 = 0,637$; r = -0,798; p = 0,001; y = 5,818 - 0,869*x
Flensburg	$r^2 = 0,249$; r = -0,499; p = 0,099

Birds

SW TL vs. log prey range

Sylt	$r^2 = 0,273$; r = 0,5223; p = 0,004; y = 0,166 + 0,770*x
Punta	$r^2 = 0,024$; r = -0,1562; p = 0,305
Otago	$r^2 = 0,001$; r = -0,0239; p = 0,927
Carpinteria	$r^2 = 0,000$; r = 0,005; p = 0,976
Bahia	$r^2 = 0,119$; r = -0,344; p = 0,027; y = 4,837 - 0,790*x

SW TL vs. log body size

Sylt $r^2 = 0,041$; $r = -0,204$; $p = 0,289$
Punta $r^2 = 0,042$; $r = 0,206$; $p = 0,175$
Otago $r^2 = 0,316$; $r = -0,562$; $p = 0,019$; $y = 9,632 - 0,941*x$
Carpinteria $r^2 = 0,003$; $r = 0,052$; $p = 0,741$
Bahia $r^2 = 0,015$; $r = 0,121$; $p = 0,451$

Log prey range vs log body size
Sylt $r^2 = 0,111$; $r = -0,333$; $p = 0,078$
Punta $r^2 = 0,002$; $r = -0,045$; $p = 0,768$
Otago $r^2 = 0,061$; $r = -0,247$; $p = 0,340$
Carpinteria $r^2 = 0,076$; $r = -0,275$; $p = 0,077$
Bahia $r^2 = 0,108$; $r = -0,329$; $p = 0,036$; $y = 7,041 - 0,442*x$

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