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Food-web-based comparison of the drivers of helminth parasite species richness in coastal fish and bird definitive hosts

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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 6 well-resolved coastal food webs that 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; then we investigated the roles 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. Host body size did not affect parasite richness for either host type. 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.

KEY WORDS: Food web · Parasite species richness · Parasitism · Trophic level · Prey range

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

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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 to which it belongs, a factor previously suggested to be associated with parasite species richness (Poulin & Leung 2011, Timi et al. 2011).

Here, we use data on 6 relatively well-resolved coastal food webs that 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 coastal fish and bird definitive hosts when using a food-web-based comparison. Furthermore, we investigated the roles of 3 host properties in driving parasite richness patterns in bird and in fish hosts. We focused on 2 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 3 factors in determining trophically transmitted helminth parasite richness in coastal fish and bird definitive hosts.

MATERIALS AND METHODS

Food webs and host data

We used 6 highly resolved coastal food webs, all in the public domain, that include data on metazoan parasites (Table 1). The first 3 webs (see Hechinger et al. 2011) are from estuarine salt marshes along the North American Pacific coast: Carpinteria Salt Marsh, California, USA; Estero de Punta Banda, Baja California, Mexico; and Bahia Falsa in Bahia San Quintín, Baja California, Mexico. The 3 other food webs are from Flensburg Fjord, a brackish shallow water inlet on the Baltic Sea between Germany and Denmark (Zander et al. 2011), Sylt Tidal Basin, an intertidal bight ecosystem on the North Sea between Germany and Denmark (Thieltges et al. 2011), and Otago Harbour, an intertidal mudflat ecosystem in New Zealand (Mouritsen et al. 2011). Information on how parasite inclusion affects various properties of these food webs is available elsewhere (Thompson et al. 2005, Lafferty et al. 2006, Dunne et al. 2013).

We focused on trophically transmitted helminths (trematodes, cestodes, nematodes and acanthocephalans) in their definitive hosts. For each host species in each food web, we recorded the following

Table 1. Fish and bird species richness (no. of species) and references for data sources of the 6 coastal food webs used for the analyses. Due to the aggregation of bird species into higher taxa in the Flensburg web, we only used the data on fish for this food web

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

variables: (1) its parasite species richness; (2) whether it was a fish or a bird; (3) its prey range, measured as the number of prey species consumed; (4) its body size, measured as maximum body length for fish (from www.fishbase.org) and average body mass for birds (from Dunning 2007); and (5) its short-weighted trophic level (TL), an index suitable for topological networks which has been used in previous analyses of parasite-inclusive food webs (Williams & Martinez 2004, Dunne et al. 2013) and that we found to correlate with other measures of trophic level (preliminary analyses, data not shown). Short-weighted TL is measured as the average of the shortest TL and the prey-averaged TL, with shortest TL calculated as 1 plus the shortest chain length from a consumer to a basal species and prey-averaged TL calculated as 1 plus the mean TL of all the consumer's trophic resources (for more details see Williams & Martinez 2004). Calculations of short-weighted TL were done using Network3D Software (Yoon et al. 2004, Williams 2010). If the same host species occurred in more than one web, each occurrence was treated as a separate entry (or as a separate 'species') in our dataset, as our analyses are web-based and not species-based. Overall, our analyses included 7–21 species of fish hosts and 17–45 species of bird hosts per web, across all webs (Table 1).

Analysis

In a first step, we investigated whether parasite species richness differed both between bird and fish hosts and among the different food webs. In a second step, we studied whether trophic level and prey range differed between bird and fish hosts and among the food webs. Because bird species in the Flensburg food web were aggregated into higher taxonomic categories in the original food web, and not treated as separate species, they were excluded from these analyses. However, we included calculations of mean parasite richness, trophic level and prey range in Flensburg fish hosts in the respective figures for comparison with other webs. We fitted general linear models (GLMs) to parasite species richness (log+1-transformed), prey range (log-transformed) or trophic level, with food web identity and host type (bird versus fish) as fixed factors. Model assumptions were checked using residual plots.

Following these initial analyses, we investigated the relative contributions of host prey range, host trophic level and host body size to variation in parasite species richness among host species. As the initial analyses revealed significant interaction terms (host type × food web), indicating that the effect of host type was conditional on food web identity, we analysed all food webs separately. In addition, we treated fish and bird hosts separately for 3 reasons. First, our goal was to evaluate the respective effects of different predictors of helminth species richness independently in the 2 types of hosts, necessitating that they be treated separately. Second, helminth species richness values were generally higher in birds (see 'Results'); therefore, pooling them for a combined analysis would have resulted in a bimodal distribution of the response variable. Finally, because of data availability, we had to use different metrics of body size for birds (mass) and fish (length), forcing these to be analysed separately. For these analyses, we considered data from fish hosts from the Flensburg food web but omitted data from bird hosts because of the species aggregation mentioned above. We could not include taxonomic or phylogenetic information to the analyses as there was insufficient replication of taxa for the 2 host types within individual webs. General linear models (GLMs) were fitted to log+1-transformed helminth species richness values, with host prey range (log-transformed), host trophic level and host body size (log-transformed) as fixed factors. Model assumptions were verified using residual plots. In addition, we checked for collinearity among these variables, and found relatively weak correlations (based on R^2 values) between variables in 6 out of the 33 comparisons (see Table A1 in the Appendix). For all GLMs we calculated the proportion of variance (V) explained by the different factors (SS = sum of squares) as $V = SS_{factor}/SS_{total} \times 100$. For all analyses we used a significance threshold of $p < 0.05$.

RESULTS

Mean parasite species richness of trophically transmitted helminths was significantly lower in fish hosts compared with bird hosts in all 5 food webs investigated (Fig. 1, Table 2). However, the effect of host type depended on the identity of the food web as indicated by the significant interaction term, resulting from varying magnitudes of the difference between values in fish and bird hosts among the webs (Fig. 1, Table 2). Finally, mean parasite species richness in bird and fish hosts also significantly differed among the 5 food webs (Fig. 1, Table 2).

Further analyses revealed that the mean prey ranges as well as the mean trophic levels of fish and bird hosts differed among webs. However, the effect of host type was not consistent among webs, as indicated by the significant interaction terms (Table 2). In some food webs, fish and bird hosts showed similar values of prey ranges and trophic level, whereas in others fish or bird hosts had higher values than their respective counterpart (Fig. 2). Although not integrated in the statistical analyses, mean parasite richness as well as mean trophic level and mean prey range of fish hosts in the Flensburg web were within the range of values observed in the other webs (Figs. 1 & 2).

The separate analyses of the factors driving parasite richness in bird and fish hosts within each food web revealed different patterns for the 2 host types. In fish hosts, prey range was the only factor that had a significant positive effect on parasite species richness in hosts in 2 of the 6 food webs (Sylt & Flensburg), while in another the effect was marginally significant (Carpinteria; p = 0.089; Fig. 3, Table 3). This effect was particularly strong in the Flensburg web, where it explained 80% of the variance (Table 3). In contrast, neither trophic level nor host body size showed a significant effect on parasite richness (Table 3). Additional analyses indicated mild collinearity (based on R^2 values) only in 2 out of the 18 comparisons (Table A1 in the Appendix), and was thus considered not to affect the analyses.

In bird hosts, prey range had a significant (positive) effect on parasite richness in all food webs apart from Otago, where it was marginally significant (0.059; Fig. 4, Table 4). In addition, trophic levels had a significant positive effect on parasite richness in all food webs apart from Otago (Fig. 5, Table 4). However, in most food webs the effect of prey range was stronger (explaining 8.2 to 44.4% of the variance) than that of trophic level (8.5–20.0%; Table 4). Only in the Bahia food web was trophic level a stronger predictor of parasite richness than prey range (20.9 versus 8.2%; Table 4). In contrast, host body size had no effect in any of the 5 food webs (Table 4). Additional analyses indicated weak collinearity (based on R^2 values) in only 4 out of the 15 comparisons (Table A1 in the Appendix), and was 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 difference between fish and birds 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 local-

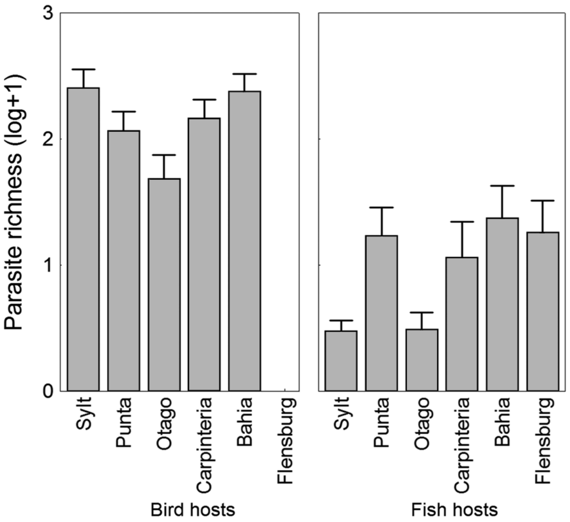

Fig. 1. Mean number of trophically transmitted parasite species (parasite richness; log-transformed; +SE) found in bird and fish definitive hosts in 6 coastal food webs. For the Flensburg food web, data were only available for fish hosts

Table 2. Results of general linear models (GLMs) testing for the effects of food web identity (5 different webs), host type (fish or bird) and an interaction term between the 2 fixed factors for 3 different response variables: log parasite richness, short-weighted trophic level and log prey range of each predator

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		

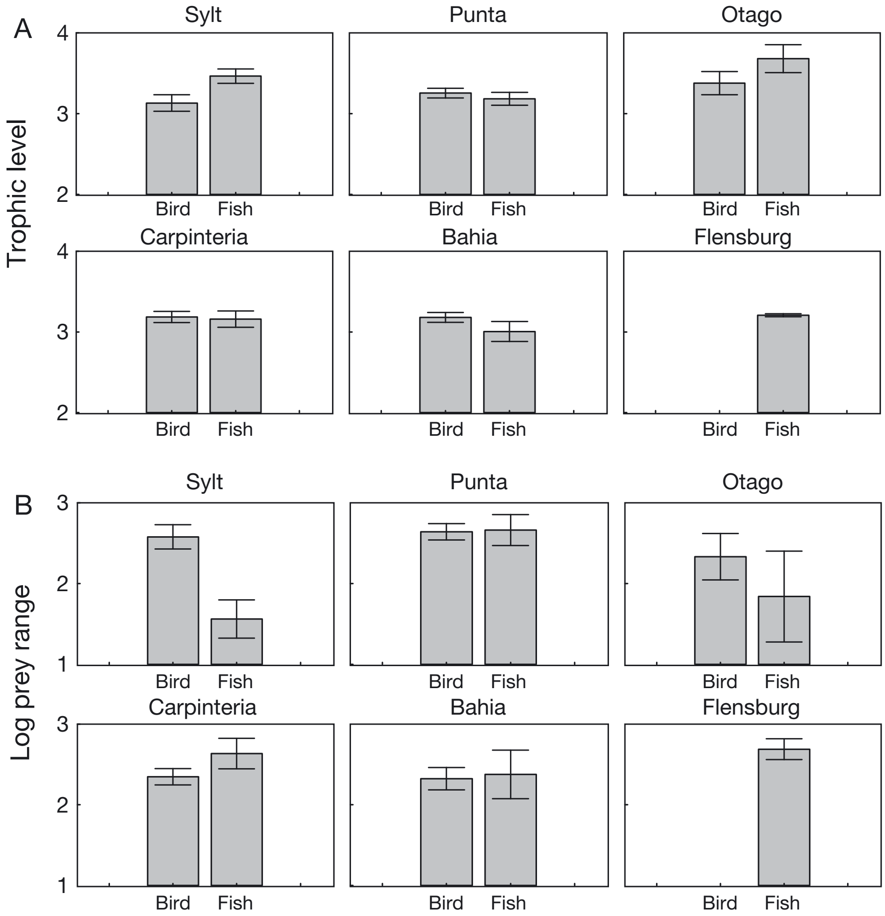

Fig. 2. (A) Mean short-weighted trophic level and (B) mean log prey range (both ±SE) of bird and fish species in the 6 food webs. For the Flensburg food web, data were only available for fish hosts. Note the truncated *y*-axes

ities. The significant interaction term (food web versus 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 can be related not only 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: although in some webs birds showed higher values than fish, it was the opposite in others or there was no difference between the 2 host types. Hence, at the level of entire food webs, none of the factors considered here (host trophic level and prey range) seems to be a universal driver of the difference in parasite richness between bird and fish hosts.

That fish nevertheless showed consistently lower levels of parasite richness than birds may be caused by other factors not studied here. For example, the larger body mass and longer intestinal tract of birds have been suggested to underlie the bird–fish difference in parasite richness (Kennedy et al. 1986, Gregory et al. 1996). In our study, we could not test for an effect of body mass because of the lack of available data for fish, but this may be relevant because many fish species in the food webs used for our analyses are small benthic fish (e.g. Gobiidae). In addition, the

Table 3. 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 fish species in 6 different food webs

Food web	Factor	df	MS	*F*	p	Variance explained (%)
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			
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			
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			
Carpinteria	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			
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			
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			

observed pattern may be related to the fact that coastal food webs such as the ones used for our analyses are dominated by trematodes (Mouritsen & Poulin 2002). In these ecosystems, trematodes predominantly use birds as definitive hosts whereas fish act mainly as intermediate hosts (e.g. Thieltges et al. 2006). Hence, the observed pattern may, at least in part, be related to the respective biology of the parasites involved. Alternatively, it could be an artefact resulting from the way parasite inclusive food webs are usually assembled. Although parasite data for fish are often based on extensive sampling of hosts in the respective food webs, data for birds are more difficult to obtain because of the generally high legal protection status of birds; thus, data assembly must rely on lower host sample sizes accompanied by additional inference from observations of larval parasite life cycle stages in intermediate hosts and general knowledge of parasite life cycles in the respective systems. This may introduce a bias in the accuracy of parasite species richness values, but given the well-known dominance of

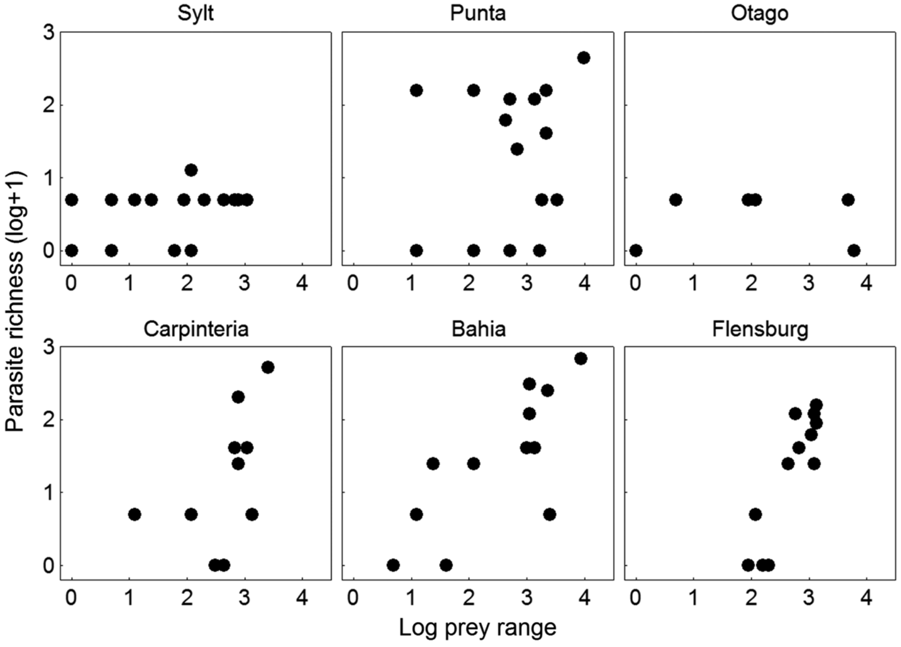

Fig. 3. Relationship between prey range of a fish species (log-transformed) and the number of trophically transmitted parasite species (parasite richness; log+1-transformed) found in the same fish species in 6 coastal food webs

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 5 different food webs

Food web	Factor	df	MS	*F*	p	Variance explained (%)
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			
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			
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			
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			
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			

trematodes using birds as definitive hosts in coastal ecosystems (Mouritsen & Poulin 2002), it is highly likely that the observed pattern reflects more a biological reality than a methodological artefact. However, the potential extent of methodological artefacts and the exact mechanisms driving the observed pattern at the level of entire food webs remain to be investigated. In particular, it would be valuable to explore innovative non-invasive methods of investigating parasite infections in birds to be able to obtain more empirical data on actual parasite richness in birds.

A clearer pattern emerged from the analyses of the drivers of parasite richness within individual food webs, which were run separately for fish and bird hosts. For both fish and birds, host prey range had a significant effect on parasite richness, although its relevance was more consistent among the food webs in birds than in fish. In general, the broader the range of prey consumed by a host species, the higher the numbers of parasites associated with this species was. Because the parasite species considered here are all trophically transmitted, this pattern was expected. With an increase in prey range, predators should face a higher risk of consuming a prey species that serves as an intermediate host for a trophically transmitted parasite. Indeed, this relationship has been found in previous analyses and seems to be a

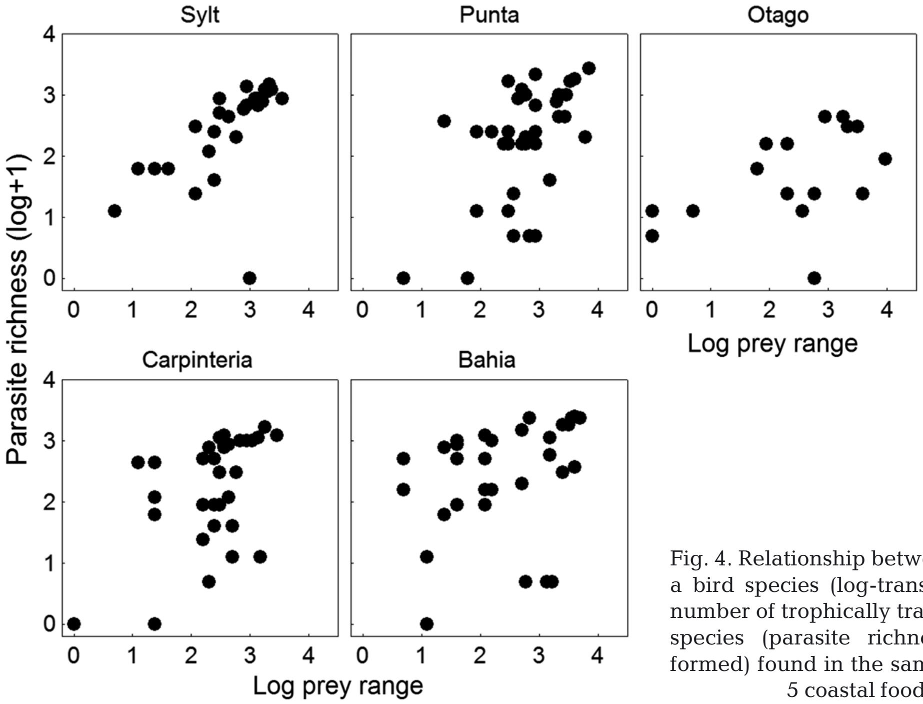

Fig. 4. Relationship between prey range of a bird species (log-transformed) and the number of trophically transmitted parasite species (parasite richness; log+1-transformed) found in the same bird species in 5 coastal food webs

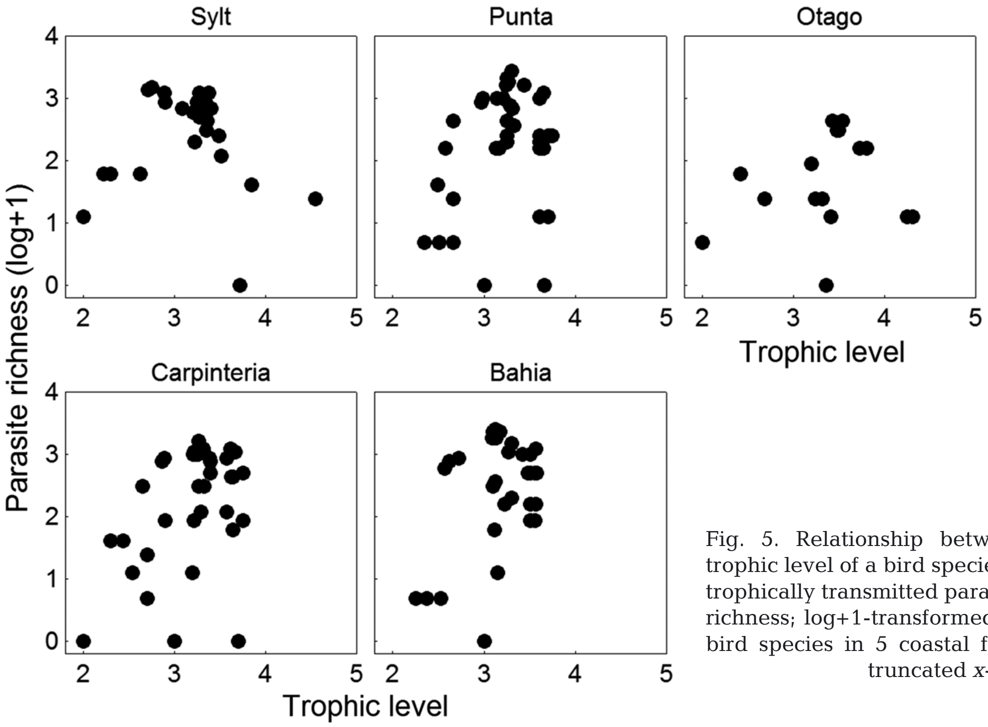

Fig. 5. Relationship between short-weighted trophic level of a bird species and the number of trophically transmitted parasite species (parasite richness; log+1-transformed) found in the same bird species in 5 coastal food webs. Note the truncated *x*-axes

universal pattern of parasite transmission in food webs (Chen et al. 2008, Thieltges et al. 2013). However, the strength of this relationship differed among the food webs in our study. For example, prey range explained 80% of the variance in fish parasite richness in the Flensburg web while it was not significant or only marginally significant as a predictor in 4 out of the 6 food webs. In contrast, for bird parasites, prey range was a significant or marginally significant driver of parasite richness in all 5 food webs. This may point to a stronger importance of prey range for parasite transmission in bird than in fish hosts, though the relatively low numbers of fish species may have compromised our power to detect this relationship in fish. Hence, more well-resolved food webs including fish and bird parasites will be needed to verify that prey range is indeed a stronger driver for bird than for fish parasites.

In contrast to prey range, trophic level only had a significant effect on parasite richness in birds but not in fish hosts. In 4 of the 5 webs, bird parasite richness was positively correlated with trophic level, the latter explaining 8–21% of the variance in parasite richness. This difference in the importance of trophic level between bird and fish hosts may be due to their different role in the biology of the main parasite taxa in the food webs analysed. As discussed above, trematodes are the dominant parasites in intertidal ecosystems and mainly use birds as their definitive hosts, with fish more often serving as intermediate hosts (Mouritsen & Poulin 2002). Birds feeding at a higher trophic level will thus face a greater likelihood of feeding on fish (and other taxa) that serve as intermediate hosts for parasites, leading to the observed pattern. This reflects the observation from a previous study that the proportion of larval taxa in fish hosts is highest in small fish hosts with low trophic levels, i.e. parasites utilise mainly those hosts as intermediate hosts because they offer the highest chance to be consumed by larger definitive hosts at a higher trophic level (Poulin & Leung 2011). That parasite infection risk for a predator indeed increases with its trophic level has previously been shown for hosts in the Carpinteria food web (Lafferty et al. 2006). Similarly, a comparative study of fish parasite communities using trophic levels from FishBase (www.fishbase.org) has found a positive correlation between trophic level and average taxonomic distinctness of the parasite assemblage in a fish (Luque & Poulin 2008). However, our study is now the first to (1) corroborate this pattern for several food webs using food-web-generated measures of trophic level (instead of literature data), and (2) investigate differences in its relevance for bird and fish hosts. Although trophic level was a significant factor determining bird parasite richness in most food webs, it was a weaker driver of parasite richness compared with prey range in all food webs apart from the Bahia food web. This suggests that parasite richness in a host is more strongly determined by the number of prey species it consumes than by its position in the food chain. It would be informative to investigate in the future whether the different influence of trophic level for bird and fish hosts also holds true for other food webs from terrestrial and freshwater ecosystems.

Finally, an unusual finding of our study is that for both fish and bird species, parasite species richness did not correlate with host body size. This goes against the general trend uncovered in previous comparative studies (e.g. Poulin 1995, Gregory et al. 1996, Luque & Poulin 2008) and confirmed recently by meta-analysis (Kamiya et al. 2014). The main difference between the present study and earlier comparative analyses is that ours is food-web based, and simultaneously accounts for diet breadth (prey range) and trophic level, factors notoriously difficult to quantify for any host species in studies that do not have a local focus. Our results indicate that the diversity of the host's diet (fish & birds) and its trophic level (birds) outweigh its body size as a determinant of helminth species richness. Such overriding effects of other factors may also explain the fact that individual comparative studies sometimes fail to detect an effect of body size (e.g. Poulin et al. 2011, Lima et al. 2012). However, by using maximum body sizes for fish in our study, we may have overestimated average body masses for fish species that may also occur as juveniles in coastal waters, which are known to often serve as nursery grounds for fish (Horn et al. 1998). Unfortunately, actual body size data of all fish included in the webs are not available, and it remains to be investigated whether using actual body size data would change the outcome of the analyses.

In conclusion, our food-web-based comparisons showed that parasite richness differed between bird and fish hosts, with higher mean parasite richness in birds than in fish. Although there was no consistent driver of parasite richness at the level of entire food webs, parasite richness significantly increased with host prey range in bird and, to a lesser extent, in fish hosts within individual food webs. For birds but not fish, parasite richness also significantly increased with the trophic level of a host. These results suggest that host prey range and trophic level seem to be more consistent drivers of trophically transmitted helminth parasite richness in coastal bird than in fish definitive hosts, and it will be informative in the future to assess whether this pattern also holds true for food webs from other ecosystems. Future research may also include the effects of other potential drivers (e.g. host population size) on parasite richness. In addition, one could further investigate whether the observed patterns also hold true for parasite infection levels (e.g. prevalence or intensity). However, a prerequisite for such analyses will be well-resolved parasite-inclusive food webs for which all of these data are available. This will be a challenging task, but such analyses would significantly advance our current understanding of the drivers of parasite infections in food webs.

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Appendix

Table A1. Results of checks for collinearity of the 3 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 the case of significant relationships. SW: short-weighted; TL: trophic level

	r^2	r	p	Regression formula
Fish				
SW TL vs. log prey range				
Sylt	0.128	−0.358	0.111	
Punta	0.087	0.2945	0.220	
Otago	0.252	−0.502	0.251	
Carpinteria	0.017	−0.130	0.702	
Bahia	0.027	−0.164	0.591	
Flensburg	0.006	−0.079	0.807	
SW TL vs. log body size				
Sylt	0.066	0.257	0.260	
Punta	0.261	0.511	0.025	$y = -1.628 + 1.677x$
Otago	0.028	0.167	0.721	
Carpinteria	0.357	0.597	0.052	
Bahia	0.098	0.313	0.297	
Flensburg	0.174	0.417	0.178	
Log prey range vs. log body size				
Sylt	0.023	0.153	0.507	
Punta	0.025	0.158	0.519	
Otago	0.030	−0.172	0.711	
Carpinteria	0.0001	0.009	0.980	
Bahia	0.637	−0.798	0.001	$y = 5.818 - 0.869x$
Flensburg	0.249	−0.499	0.099	
Birds				
SW TL vs. log prey range				
Sylt	0.273	0.5223	0.004	$y = 0.166 + 0.770x$
Punta	0.024	−0.1562	0.305	
Otago	0.001	−0.0239	0.927	
Carpinteria	0.000	0.005	0.976	
Bahia	0.119	−0.344	0.027	$y = 4.837 - 0.790x$
SW TL vs. log body size				
Sylt	0.041	−0.204	0.289	
Punta	0.042	0.206	0.175	
Otago	0.316	−0.562	0.019	$y = 9.632 - 0.941x$
Carpinteria	0.003	0.052	0.741	
Bahia	0.015	0.121	0.451	
Log prey range vs. log body size				
Sylt	0.111	−0.333	0.078	
Punta	0.002	−0.045	0.768	
Otago	0.061	−0.247	0.340	
Carpinteria	0.076	−0.275	0.077	
Bahia	0.108	−0.329	0.036	$y = 7.041 - 0.442x$

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