

# Complex life cycles in a pond food web: effects of life stage structure and parasites on network properties, trophic positions and the fit of a probabilistic niche model

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**Abstract** Most food webs use taxonomic or trophic species as building blocks, thereby collapsing variability in feeding linkages that occurs during the growth and development of individuals. This issue is particularly relevant to integrating parasites into food webs because parasites often undergo extreme ontogenetic niche shifts. Here, we used three versions of a freshwater pond food web with varying levels of node resolution (from taxonomic species to life stages) to examine how complex life cycles and parasites alter web properties, the perceived trophic position of organisms, and the fit of a probabilistic niche model. Consistent with prior studies, parasites increased most measures of web complexity in the taxonomic species web; however, when nodes were disaggregated into life stages, the effects of parasites on several network properties (e.g., connectance and nestedness) were reversed, due in part to the lower trophic generality of parasite life stages relative to free-living life stages. Disaggregation also reduced the trophic level of organisms with either complex or direct life

cycles and was particularly useful when including predation on parasites, which can inflate trophic positions when life stages are collapsed. Contrary to predictions, disaggregation decreased network intervality and did not enhance the fit of a probabilistic niche model to the food webs with parasites. Although the most useful level of biological organization in food webs will vary with the questions of interest, our results suggest that disaggregating species-level nodes may refine our perception of how parasites and other complex life cycle organisms influence ecological networks.

**Keywords** Community ecology · Wetland · Food web model · Topology · Host–parasite interaction

## Introduction

Twenty-five years ago, ecologists began to argue that the ecological patterns obtained from food webs were only as valid as the methods and data used to construct the webs (Paine 1988; Polis 1991). At the time, most available food webs significantly underrepresented existing biodiversity and there were large inconsistencies in the resolution of nodes and links (Dunne 2006). Importantly, the realization that poor data sets could result in artifactual food web patterns motivated efforts to comprehensively understand how discrepancies in methodology altered observed patterns (Winemiller 1989; Martinez 1991) and initiated a movement to improve the quality of food web data sets (Cohen et al. 1993).

Despite considerable improvements in food web data, most webs do not fully capture the dynamic nature of feeding interactions. Currently, the majority of existing food webs are constructed using taxonomic species as nodes,

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often with the exception of basal groups that are aggregations of taxonomic species (Thompson and Townsend 2000; Ings et al. 2009). This approach to characterizing feeding interactions combines a large amount of variation in trophic interactions among individuals (e.g., owing to ontogenetic stage, body size, sex, reproductive status, or time-of-year) into an approximation at the species level (Woodward 2007; Rudolf 2008). Species with complex life cycles have perhaps the most dynamic trophic interactions because they often exploit distinct niches throughout the course of growth and development, sometimes involving dramatic shifts in both predators and prey from one life stage to another (Wilbur 1980; Werner and Gilliam 1984). The effects of disaggregating complex life cycle species on the structure and dynamics of food webs have not been well studied; however, one of the first empirical assessments indicated that incorporating life stage structure increased the vulnerability of food webs to secondary extinctions (Rudolf and Lafferty 2011). This important result came about largely because many organisms that are represented in food webs as dietary generalists at the species level are in fact ontogenetic specialists at the life stage level, making them highly sensitive to secondary extinction.

Understanding the implications of complex life cycles on food web structure is particularly relevant to the integration of parasites into food web theory because many parasites undergo extreme ontogenetic niche shifts during development (Lafferty et al. 2008). For example, some trematodes in pond ecosystems must sequentially infect snails, amphibians, and predatory birds to complete their life cycle (Fried and Graczyk 1997). In between the three parasitic life stages are two free-swimming, non-feeding stages that can serve as prey to other species (Johnson et al. 2010). The prevalent view of nodes as taxonomic species requires grouping these five life stages together into a node that appears as a dietary generalist feeding on multiple trophic levels (from snails to herons) and is susceptible to an immense diversity of predators (from zooplankton to coyotes). Nonetheless, most prior food web studies to examine the roles of parasites have utilized taxonomic or trophic species as nodes (e.g., Thompson et al. 2005; Lafferty et al. 2006; Hernandez and Sukhdeo 2008; Amundsen et al. 2009; Dunne et al. 2013; but see Huxham et al. 1995). These studies leave open the question of whether life stage structure alters our understanding of how parasites and other complex life cycle species influence most aspects of food webs.

Disaggregating species-level nodes is predicted to alter food webs in a variety of ways. Measures of web complexity, such as connectance and linkage density, can change in unpredictable ways due to disaggregation because it is mathematically possible for the ratio of links to nodes to either increase or decrease with network size. Such changes will depend on the biology of the organisms in the web,

including factors such as diet breadth and predator vulnerability of the taxonomic species relative to life stages. Additionally, incorporating life stages will lead to inherent increases in web size and may cause changes due to the scale dependence of some web properties alone (Schoener 1989; Martinez 1993, 1994). Life stages may also be more appropriate than taxonomic species for particular types of food web analyses. For instance, considerations of trophic levels present a unique challenge for food webs that incorporate parasites or other organisms with complex life cycles. Using traditional indices (e.g., Williams and Martinez 2004), the trophic position of a parasite represented as a taxonomic species would be designated based on all of the hosts used within its life cycle and would likely be overestimated relative to the actual trophic level of each life stage. This problem becomes compounded if predators feed on parasite life stages, which is a prominent link type in most webs with parasites (Thieltges et al. 2013).

Disaggregating species-level nodes into life stages has also been suggested as one way to improve the fit of recent food web models to empirical food web data sets. The niche model (Williams and Martinez 2000) and probabilistic niche model (Williams et al. 2010; Williams and Purves 2011) assume that each organism in the food web feeds along a contiguous or near contiguous feeding interval. Complex life cycle organisms, and particularly parasites, may challenge this assumption at the species level. The distinct niche shifts of most complex life cycle organisms, in terms of both resources and predators, probably result in less contiguous niches than direct life cycle species (Dunne et al. 2013). Parasites are also smaller than their resources and often feed on different hosts that vary greatly in body size and trophic position, which may contribute to decreases in the fit of niche models to food webs that include parasites (Dunne et al. 2013). Consequently, life stage structure may improve the fit of niche models if life stages have a more contiguous feeding interval than taxonomic species.

Our goals in the present study were to examine how node disaggregation influenced the role of parasites, the trophic positions of organisms, and the fit of a probabilistic niche model to an empirical pond food web. To accomplish these aims, we analyzed three versions of a food web from a freshwater pond, each with and without parasites. Version one included taxonomic species for most nodes, excluding some aggregated basal nodes, and is referred to as the “taxonomic species web”; version two included disaggregated nodes only for species that display distinct ontogenetic diet shifts and is referred to as the “niche-shift web”; version three included disaggregated nodes for all species with complex life cycles for which we had diet information for each life stage and is referred to as the “life stage web”. We predicted that the effects of parasites on food web properties would be sensitive to how nodes were defined in the

web due to differences in trophic generality and vulnerability between life stages and species. We also predicted that trophic-level analyses would become more accurate when conducted on food webs with life stage structure because life stages often undergo shifts in diet and many predators specialize on life stages rather than taxonomic species. Lastly, we hypothesized that life stage structure would improve the fit of the probabilistic niche model by making the feeding niches of nodes in the web more contiguous.

## Materials and methods

### Study site

The food web was constructed for Quick Pond within Alameda County in the San Francisco Bay Area of California, USA. The pond is at an elevation of 435 m and is surrounded by grassland and mixed oak habitat that is lightly grazed by domestic sheep during the summer. Quick Pond has a permanent hydroperiod, an early summer surface area of ~2,200 m<sup>2</sup>, and a maximum depth of ~2.5 m. In June 2009, nutrient concentrations in the pond were 53 µg/L total dissolved phosphorus and 1,779 µg/L total dissolved nitrogen.

### Food web construction

The complete food web data set is available online and can be found in Preston et al. (2012). The food web includes detailed information on each node, such as classification, lifestyle, consumer strategy, mobility, residency and body size/biomass information for abundant organisms. It also includes information on each link, including link type (e.g., detritivory, predation, parasitism, etc.) and link evidence (e.g., direct observation, modeled from a similar system, or literature citations when information came from published studies). The species list of free-living organisms came from data collected between 2009 and 2011 and is based primarily on direct observations using visual encounter surveys, dip net and seine net sweeps, stove pipe samples, and zooplankton tows (see also Preston et al. 2013). A few less common invertebrate taxa were added based on surveys at the same site made by Lunde and Resh (2012). Parasites were added into the food web based on evidence from host dissections and in a few instances, from evidence in the literature (<10 % of species). When one parasite life stage was detected, we assumed the other life stages were present. Our parasite quantification likely undersampled certain groups, including phytoplankton, parasites of zooplankton, and non-trematode parasites of birds and mammals [see Preston et al. (2012) for a complete list of undersampled groups and aggregated nodes and the Electronic

supplementary material (ESM) for more details on web construction].

Our analyses involved three different versions of the Quick Pond food web, each of which we analyzed with and without parasites. For consistency with other work (Dunne et al. 2013), we also conducted analyses on versions of the web that included parasites but lacked concomitant links [i.e., links that occur when a parasite is consumed by a predator feeding on infected prey (Johnson et al. 2010)]. All web versions can be extracted from the published data set. We created three versions of the web (the taxonomic species web, niche-shift web, and life stage web) to independently examine the effects of both parasites and of incorporating complex life cycles on web structure. The taxonomic species web is the most aggregated version and every node is either a single taxonomic species, or in some instances an aggregation of trophically similar species [the aggregation of certain poorly resolved nodes (e.g., phytoplankton, bacteria) is common in most previously published food webs (Thompson and Townsend 2000)]. The other two web versions contained nodes that were disaggregated according to life stage characteristics of species with complex life cycles. In the niche-shift web, we disaggregated nodes into life stages only when the species in question underwent distinct ontogenetic diet shifts during the course of development. We quantified the degree of ontogenetic diet shift ( $p$ ) for each node with a complex life cycle following Rudolf and Lafferty (2011):

$$p = \left[ \sum_{i,j=1}^{i,j=S} (k_{ij}/w_{ij}) \right] / S$$

where  $S$  is the number of life stages within a node,  $k_{ij}$  is the number of shared resources used between life stages  $i$  and  $j$ , and  $w_{ij}$  is the number of unique resources used between life stages  $i$  and  $j$ . This index ranges from  $p = 0$ , for an ontogenetic specialist with zero dietary overlap between life stages, to  $p = 1$ , for an ontogenetic generalist with complete dietary overlap between stages. In the niche-shift web, we only divided nodes into life stages when  $p < 0.5$  for that specific node. This restricted the disaggregation of nodes to only species that showed a high degree of dietary specialization between life stages. Finally, in the life stage web we included disaggregated nodes of all complex life cycle species for which we had detailed life stage information, regardless of whether they underwent significant niche shifts between life stages.

### Food web properties

We calculated the number of nodes ( $S$ ), number of links ( $L$ ), linkage density ( $D$ ), connectance ( $C$ ), degree distributions, nestedness, and clustering coefficients for each version of

the Quick Pond food web (i.e., the taxonomic species web, the niche-shift web, and the life stage web, each without parasites, with parasites but no concomitant links, and with parasites and concomitant links). Linkage density quantifies the average number of links per node ( $D = L/S$ ) and connectance quantifies the proportion of observed links out of the total number of links possible ( $C = L/S^2$ ). Both connectance and linkage density are measures of web complexity and much research has examined how they are related to important network properties such as stability (e.g., May 1973; Cohen and Briand 1984; Dunne et al. 2002). We also examined the degree distributions of both free-living and parasitic nodes within each web to examine how the number of links per node (i.e., node degree) changes with node aggregation and the addition of parasites to the web. Average node degree is also equal to the sum of trophic generality (the number of links a node makes with resources) and trophic vulnerability (the number of links predators make with a node) (Schoener 1989). We calculated these values separately for both free-living organisms and their parasites. The aforementioned web properties were calculated with Network3D (Yoon et al. 2004) and the Cheddar package in R (Hudson et al. 2013). We also calculated nestedness, which is the degree to which specialists interact with nested subsets of the species interacting with generalists (Ings et al. 2009). Using the program ANINHADO (Guimaraes and Guimaraes 2006), we calculated the nestedness metric based on overlap and decreasing fill (Ulrich et al. 2009), as well as relative nestedness (Bascompte et al. 2003). Lastly, we calculated clustering coefficients using the networkX package in Python (Hagberg et al. 2008). Clustering coefficients measure the fraction of connected link pairs that are both connected to an adjacent node (Dunne et al. 2002). For consistency with prior studies, we also calculated web properties for the four subwebs within the main food web (Lafferty et al. 2006). Additional information on analyses and results pertaining to the subwebs is provided in the ESM.

### Trophic levels and omnivory

We calculated short-weighted trophic level for each node, which is equal to the average of a node's shortest trophic level (1 + the shortest chain to a basal taxon) and its prey-averaged trophic level (1 + the mean trophic level of the consumer's resources) (Williams and Martinez 2004). We used these values to obtain a mean trophic level per web and to investigate changes in trophic levels due to disaggregation that occurred for organisms with complex life cycles and for organisms with direct life cycles. For organisms with complex life cycles, we compared the trophic level of the species in the taxonomic species web with the corresponding life stages in the life stage web. We calculated

larval trophic positions as the mean of all larvae when a species had multiple larval stages. We also compared the trophic level of direct life cycle species between the taxonomic web and the life stage web to examine effects of prey disaggregation. We used the trophic-level designations to calculate omnivory, which is the fraction of species feeding on multiple trophic levels [defined as having a trophic position that is not within 0.05 of an integer value (Thompson et al. 2007)]. For calculations of trophic level and omnivory, we grouped non-feeding life stages of heterotrophs (e.g., some adult flies and larval parasite stages) within their previous feeding life stage. This adjustment was made because non-feeding life stages would otherwise be assigned a trophic level of zero, equivalent to a basal taxon, despite the fact that they are heterotrophs. We decided to not remove the non-feeding life stages for these analyses because they frequently have a completely different suite of predators than other stages and this adds valuable information to the web.

### Probabilistic niche model and intervality

We examined the fit of the probabilistic niche model to all of the aforementioned web versions. The probabilistic niche model uses the links in the food web to infer latent niche roles and probabilistically interval feeding ranges (Williams et al. 2010; Williams and Purves 2011). The model was recently applied to seven food webs with parasites, using trophic species as nodes (Dunne et al. 2013), and can be used to accurately detect and reproduce structure in food webs (Williams and Purves 2011). The goodness of fit is determined by the fraction of links predicted correctly, calculated as the average probability of existence assigned to observed links, when the number of expected links is close to the number of observed links. We used Markov chain Monte Carlo to search for a maximum likelihood solution to the model (after Williams et al. 2010; Williams and Purves 2011).

To aid in the interpretation of the probabilistic niche model results, we also calculated intervality directly (Stouffer et al. 2006; Zook et al. 2011). Interval food webs are defined either by contiguous diets or contiguous predators, where an optimal latent ordering of species can be constructed such that each species' diet (or each species' predators) are consecutive within the ordering. Intervality is measured as the number of gaps (non-links) in those intervals, given some optimal ordering of species. Each missing species from the interval is counted as a single gap. The probabilistic niche model seeks to embrace the "quasi-intervality" commonly found in food webs (Stouffer et al. 2006), and so more flexibly captures this structure by allowing for gaps peripheral to the main interval of each species. We calculated intervality separately as consumer

gaps and diet-range gaps using the Cheddar package in R (Hudson et al. 2013).

**Results**

Food web versions

Complex life cycles and ontogenetic diet shifts were prevalent within the Quick Pond food web. The taxonomic species web included 63 nodes made up of five basal groups, 43 free-living species and 15 parasites. Twenty of the 43 free-living nodes and 12 of the 15 parasite nodes were organisms with complex life cycles for which we had feeding information for each life stage. The free-living organisms with complex life cycles were primarily insects and amphibians. The parasites with complex life cycles were primarily protists and helminth worms that obligately infect multiple host species. Disaggregating the complex life cycle organisms with distinct diet shifts at each life stage (i.e., the niche-shift web with  $p < 0.5$  for each node) resulted in an increase in network size to 105 nodes, of which 42 were parasite life stages. Disaggregating the nodes further, such that all life stages became a distinct node (the life stage web), increased the total number of nodes to 113. The entire increase in node count between

the niche-shift web and the life stage web was the result of disaggregating free-living insects and amphibians that did not undergo distinct diet shifts between life stages (all of the parasites with complex life cycles underwent distinct diet shifts; i.e.,  $p < 0.5$ ).

Food web properties

Disaggregating the nodes of the web led to obvious increases in the number of links (from 1,088 to 1,432 to 1,905, respectively); however, this effect did not lead to consistently positive or negative changes in most web metrics. For connectance, linkage density, clustering coefficients and nestedness, the lowest metric was associated with the niche-shift web, which has an intermediate number of nodes (Table 1). This pattern was consistent whether we included concomitant links or not (Table S1). Disaggregating the nodes from the taxonomic species web to the niche-shift web resulted in a decrease of connectance from 0.27 to 0.13 (Table 1). Disaggregating the nodes further resulted in a connectance of 0.15, reflecting the higher node degree of the added life stages in the life stage web (i.e., dietary generalists with complex life cycles). Linkage density showed the largest decrease in the niche-shift web because only species with high resources specificity were disaggregated in this web (Table 1; linkage density = 17.3,

**Table 1** Food web properties and probabilistic niche model (PNM) results for three versions of the Quick Pond food web, each with and without parasites

	Taxonomic species web		Niche-shift web		Life stage web	
	–Parasites	+Parasites	–Parasites	+Parasites	–Parasites	+Parasites
Number of nodes	48	63	63	105	71	113
Observed links	597	1,088	714	1,432	1,038	1,905
Linkage density	12.4	17.3	11.3	13.6	14.6	16.9
Connectance	0.26	0.27	0.18	0.13	0.21	0.15
Clustering coefficient	0.63	0.63	0.45	0.53	0.55	0.56
Nestedness ( $N^*$ )	1.3	1.8	0.6	0.6	1.1	0.9
Nestedness (NODF)	40.4	50.0	29.1	27.0	33.2	30.1
Mean trophic level	1.8	4.4 (5.1)	1.8	3.6 (3.6)	1.9	3.7 (3.9)
Fraction omnivores	0.71	0.83 (0.88)	0.8	0.91 (0.84)	0.75	0.92 (0.89)
Mean consumer gaps	4.1	6.8	4.6	8.5	5.8	9.8
Mean diet-range gaps	3.9	6.8	6.1	7.5	7.2	8.8
PNM results						
$f_L$	0.73	0.66	0.62	0.54	0.64	0.57
Expected links	606	1,101	732	1,408	1,043	1,972
Observed links	597	1,088	714	1,432	1,038	1,905

Numbers for mean trophic level and fraction omnivores outside parentheses apply to versions of the food web without concomitant predation links and numbers in parentheses apply to versions of the food web with concomitant predation links. See the Electronic supplementary material for additional results for web versions that lack concomitant predation links

NODF Nestedness metric based on overlap and decreasing fill,  $N^*$  relative nestedness,  $f_L$  fraction of links predicted correctly by the probabilistic niche model

13.6, and 16.9 for the three webs). Clustering coefficients and nestedness followed a similar pattern to connectance and linkage density where the lowest value was obtained in the niche-shift web (Table 1). This finding is consistent with the idea that clustering coefficients tend to increase with node degree (Dunne 2006) and nestedness generally increases with connectance (Thebault and Fontaine 2010). All webs displayed significantly nested patterns of interactions relative to null matrices, regardless of life stage structure or whether parasites and concomitant links were included.

The effects of parasites on web structure were influenced by the treatment of complex life cycles within the web. Adding parasites and concomitant links into the webs increased the number of links by 82 % (taxonomic species web), 100 % (niche-shift web), and 84 % (life stage web) (Table 1). Of the increase in link number, 40 % was due to concomitant links in the taxonomic species web, 37 % was due to concomitant links in the niche-shift web and 32 % was due to concomitant links in the life stage web (Table S1). In the taxonomic species web, inclusion of parasites increased connectance slightly from 0.26 to 0.27 and this effect was primarily driven by the high connectance of the predator–parasite subweb (Table S2). In the niche-shift and life stage webs, however, connectance decreased with inclusion of parasites from 0.18–0.13 to 0.21–0.15, respectively (Table 1). The decrease was slightly stronger in the webs lacking concomitant links (Table S1). Nestedness demonstrated a similar pattern, in which inclusion of parasites increased nestedness in the taxonomic species web, but decreased it slightly in the disaggregated niche-shift and life stage webs (Table 1). Unlike connectance and nestedness, linkage density increased in all web versions with the inclusion of parasites, except for the two disaggregated webs that lacked concomitant links (Table S1). The magnitude of increase in the taxonomic species web (39 %) was ~ two times larger than the increases in the niche-shift web (20 %) and the life stage web (15 %) (Table 1). Parasites increased clustering coefficients in the two webs with life stage structure and concomitant links (Table 1), but decreased clustering coefficients in the same webs lacking concomitant links (Table S1). Concomitant links from a predator to a parasite, in combination with a host parasite link, represent a form of clustering, so this result is not surprising.

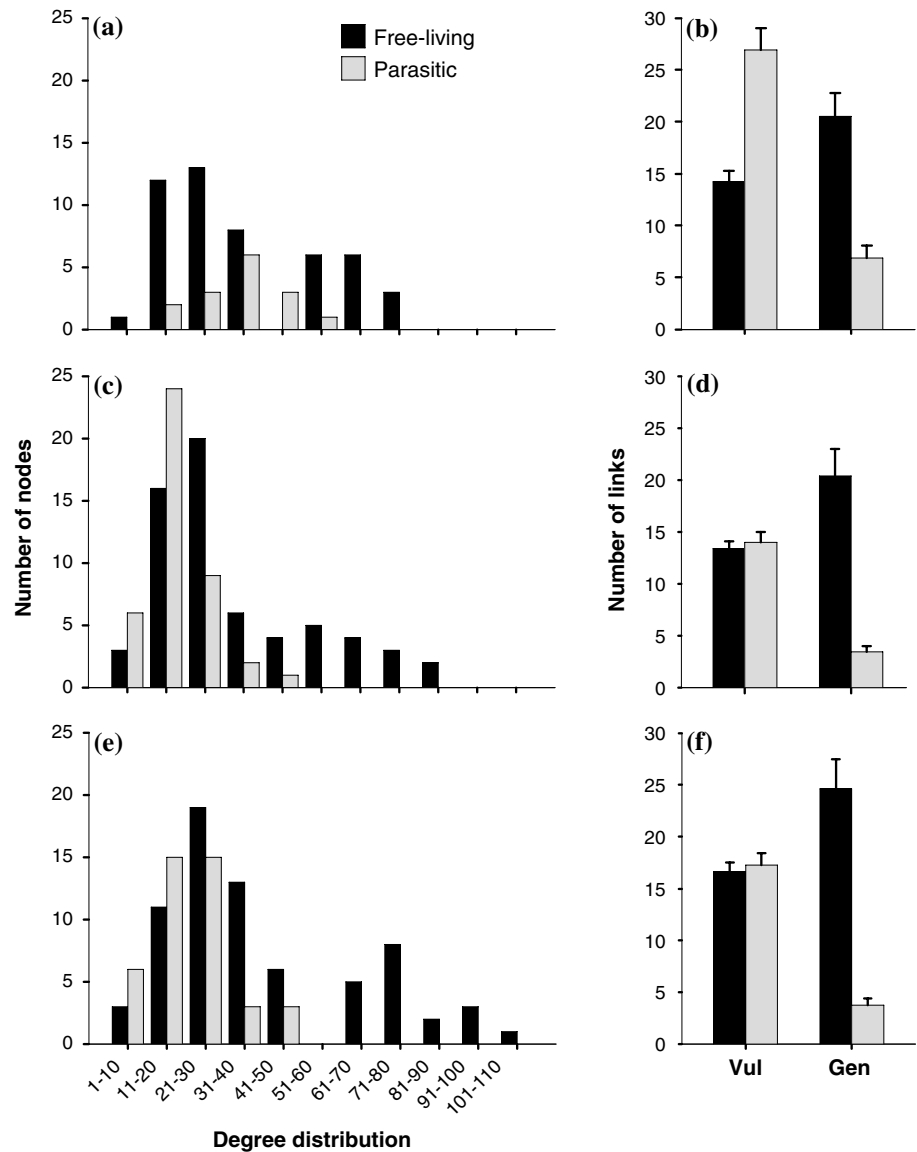
Examining the degree distributions (i.e., the number of incoming and outgoing links per node) helped explain the contrasting effects of parasites on web structure across the three web versions (Fig. 1). In the taxonomic species web with parasites and concomitant links, the average node degrees of free-living organisms ( $k = 34.8$ ,  $SE = 2.7$ ) and of parasites ( $k = 33.8$ ,  $SE = 2.8$ ) were similar and inclusion of parasites into the web raised the overall node degree

(all nodes in the web) by nearly ten links per node [from 24.9 ( $SE = 2.0$ ) to 34.5 ( $SE = 2.2$ )]. For the niche-shift web, in contrast, the average node degree of free-living organisms ( $k = 33.8$ ,  $SE = 2.6$ ) was nearly twice that of parasites ( $k = 17.5$ ,  $SE = 1.3$ ) and inclusion of parasites increased the overall node degree of the web by less than five links per node. The pattern in the life stage web was similar to that observed in the niche-shift web. The changes in node degree were caused by differences in trophic generality and vulnerability between free-living organisms and parasites. In the taxonomic species web, trophic generality of parasites was more than three times lower than it was for free-living organisms while vulnerability was nearly two times higher (Fig. 1). In the niche-shift and life stage webs, vulnerability of parasites and free-living nodes was roughly equivalent but trophic generality was more than five times lower (Fig. 1). This result reflects the higher resource specificity of parasite life stages relative to free-living life stages. Unsurprisingly, the inclusion of parasites caused a large decrease in average node degree in the webs lacking concomitant links. The trophic vulnerability of parasites was reduced by 50 % in the life stage web, 64 % in the niche-shift web and 70 % in the life stage web when concomitant links were removed. Similarly, the trophic generality of free-living species was reduced by 20, 30 and 30 %, in the three web versions when concomitant links were removed.

#### Trophic levels and omnivory

The inclusion of parasites caused increases in mean trophic level and omnivory in all web versions whether concomitant links were included or not; however, the magnitude of change depended on how life stages were treated in the web (Table 1). In the taxonomic species web, the inclusion of parasites caused the frequency distribution of trophic positions to shift to higher values than in the disaggregated webs (Fig. 2). In the taxonomic species web with parasites but lacking concomitant links, mean trophic level increased from 1.8 to 4.4 with the inclusion of parasites, whereas in the niche-shift and life stage webs the increases were smaller (1.8–3.6 and 1.9–3.7, respectively; Table 1). These increases indicate that the trophic position of parasites themselves and predation on free-living parasite stages (as opposed to only concomitant predation) are important in increasing the trophic levels in the web. As expected due to elevated rates of predation on parasites, the increases in trophic level with parasite inclusion were greater in the taxonomic species and life stage webs that included concomitant links (although concomitant links had no effect on mean trophic level in the niche-shift web; Table 1). Omnivory showed the greatest increase with the addition of parasites in the life stage web. The changes in trophic level

**Fig. 1** The degree distributions (left panels) and trophic vulnerability and generality (right panels) for parasites (light bars) and free-living organisms (dark bars) in the three versions of the Quick Pond food web. Panels **a** and **b** correspond to the taxonomic species web; **c** and **d** correspond to the niche-shift web; **e** and **f** correspond to the life stage web. Trophic vulnerability (*Vul*) and generality (*Gen*) are means (+ SE). Concomitant predation links have been omitted from the web versions used in this figure



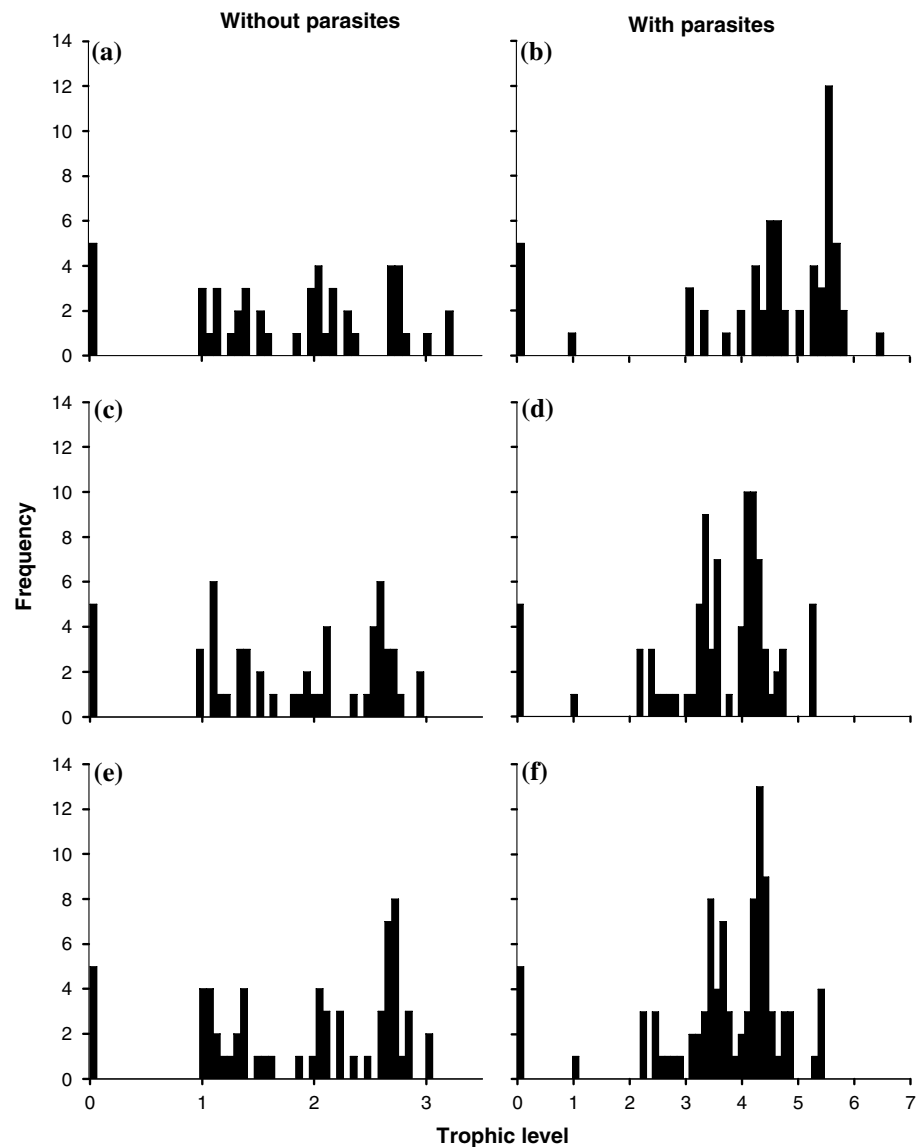
and omnivory reflect the assignment of trophic positions to species relative to corresponding life stages. For invertebrates, amphibians and parasites, the species-level node in the taxonomic species web was always assigned a higher trophic position than the larval and adult nodes in the disaggregated webs (Fig. 3). Direct life cycle organisms followed a similar pattern because the trophic position of their prey decreased with node disaggregation. For amphibians and parasites, the adult stages fed at a higher trophic position than the larvae, but there was no difference for invertebrate stages (Fig. 3).

Probabilistic niche model and intervality

The fit of the probabilistic niche model, as measured by the fraction of links predicted correctly, decreased in all web versions with the inclusion of parasites (Table 1).

Model fit also decreased with disaggregation from the taxonomic species web to the niche-shift web, but then increased slightly from the niche-shift web to the life stage web. Webs that included concomitant links universally resulted in a better fit than webs without concomitant links (Table S1). Niche structure can be approximately assessed through the direct intervality measures. Including parasites decreased intervality (i.e., increased gaps) in terms of both contiguous consumer ranges and contiguous diet ranges for all versions of the food web, consistent with the niche model fit results (Table 1). The magnitude of these changes for consumer gaps was largest in the two disaggregated webs (i.e., these have more gaps with parasites). For diet-range gaps, the magnitude of change with parasite inclusion was largest in the taxonomic species web. Visualizations of the trophic niche space occupied by organisms in the food web show an increase in the number of gaps and a

**Fig. 2** Frequency distributions of nodes at different trophic positions within the three versions of the Quick Pond food web. Panels **a** and **b** correspond to the taxonomic species web; **c** and **d** correspond to the niche-shift web; **e** and **f** correspond to the life stage web. The *left panels* show each web without parasites and the *right panels* show each web with parasites. Trophic positions were calculated using the equation for short-weighted trophic level. Trophic levels of 0 represent basal non-feeding nodes (e.g., primary producers), trophic levels of 1 represent herbivores, and trophic levels >2 represent predators. Concomitant predation links have been omitted from the web versions used in this figure



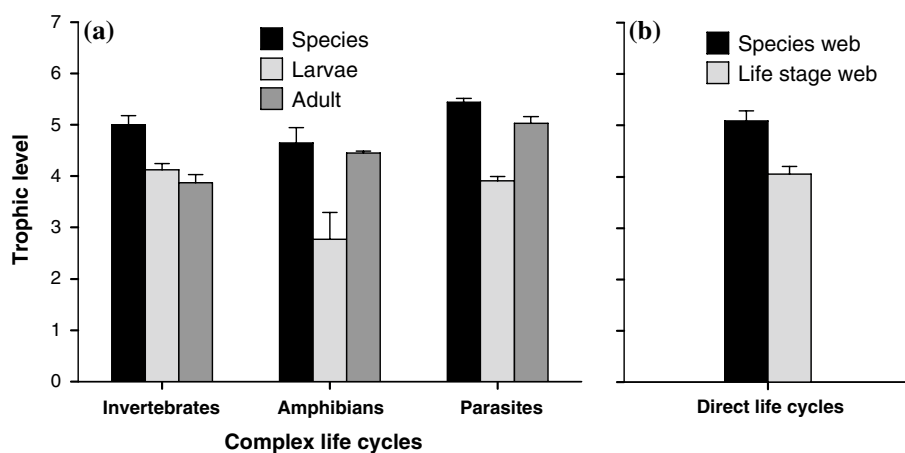
decrease in contiguous feeding niches with web disaggregation (Fig. 4). Although some contiguous feeding ranges appear in the niche-shift web and life stage web, particularly for parasites, there is a large increase in the number of peripheral links that lie outside contiguous feeding intervals (Fig. 4). This effect may be due to the increase in the number of available prey nodes with disaggregation (i.e., predators have a wider range of suitable prey items leading to a less contiguous feeding interval). This result may also partly be due to the scale dependence of model fit (Dunne et al. 2013).

## Discussion

Organisms with complex life cycles present unique challenges in food web studies due to the wide variation in

feeding interactions that occur during their growth and development. Using life stages as nodes in food webs may add valuable information, yet the consequences of utilizing this approach are not obvious. Here we examined how the disaggregation of species-level nodes influences the perceived role of parasites in a pond food web, with particular emphasis on the analysis of trophic positions and the fit of a probabilistic niche model to the empirical web. Our main findings were that (1) the effects of parasites on web properties were highly sensitive to the level of node aggregation, (2) disaggregation of species-level nodes into life stages provided more accurate analyses of trophic positions in food webs with parasites and other complex life cycle organisms, and (3) node disaggregation did not improve the fit of the probabilistic niche model to the food web with parasites, contrary to predictions. Although the unique aspects of our food web must be considered in extending





**Fig. 3** Changes in trophic level with node disaggregation for organisms with **a** complex life cycles (invertebrates, amphibians and parasites) and **b** for predators with direct life cycles (reptiles, birds and mammals). **a** Bars represent the species-level (black bars) node from the taxonomic species web and the larval (light gray bars) and adult

(dark gray bars) nodes from the life stage web. **b** Bars represent the species-level nodes from the taxonomic species web (black bar) and the life stage web (light gray bar). Concomitant predation links have been omitted from the webs used in this figure. All bars are means (+SE)

these results to other systems (e.g., the high proportion of species with complex life cycles), our results nonetheless highlight the need to carefully consider whether the types of nodes used in a food web are best suited to addressing the ecological questions of interest.

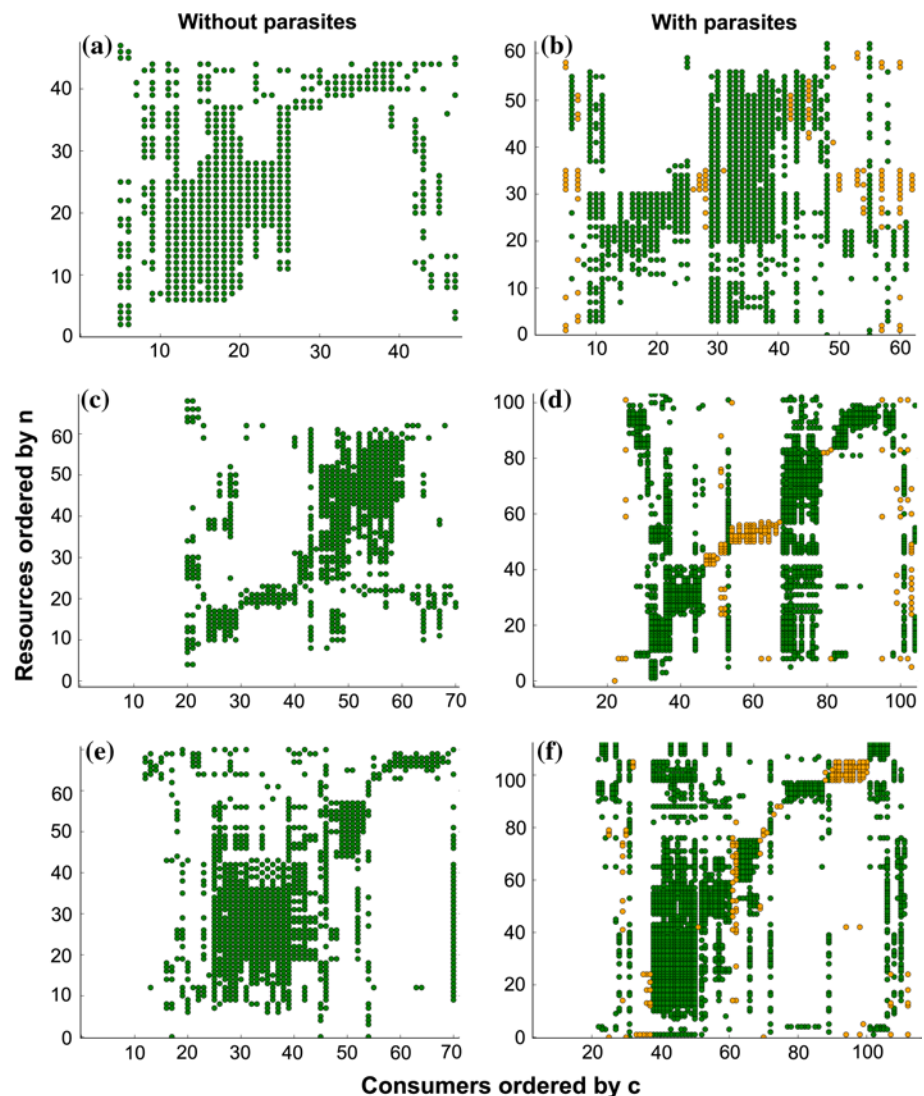
Incorporating parasites as taxonomic species increased most structural metrics associated with web complexity, largely consistent with findings from previous studies (Lafferty et al. 2006; Hernandez and Sukhdeo 2008; Amundsen et al. 2009; Dunne et al. 2013). Parasite inclusion led to an 82 % increase in the total number of links and concurrent increases in connectance, linkage density and nestedness in the taxonomic species web that included concomitant links. While it is often assumed that changes in food web properties with the inclusion of parasites are due to unique aspects of parasite biology, it is important to distinguish between unique effects of parasites and generic effects driven by increases in network size (Dunne et al. 2013). To date, the most unique effects of parasites in food webs have been associated with robustness (Rudolf and Lafferty 2011; Lafferty 2012), the relative frequency of certain motifs, and the contiguity of feeding intervals (Dunne et al. 2013). Our results for most web properties within the taxonomic species web (e.g., connectance) are largely consistent with expected changes due to network size.

In contrast to the taxonomic species web, the addition of parasites to the disaggregated webs altered web properties in ways that were not consistent with scale dependence. When we disaggregated species-level nodes to capture variability in feeding relationships between life stages, the effects of parasite inclusion on connectance and nestedness were reversed relative to the taxonomic species

web. Analyses of the degree distributions suggested that this result was associated with differences in the generality and vulnerability of parasite life stages relative to free-living life stages. Life stages of parasites had a higher vulnerability to predators but a much lower trophic generality (i.e., high host specificity) at the life stage level compared to free-living species. These differences effectively equalized the average node degree (i.e., the number of incoming and outgoing links) for free-living organisms and parasites within the taxonomic species web. In contrast, within the two disaggregated webs, the reduced generality of parasite life stages led them to have a much lower average node degree relative to free-living organisms. Despite increases in linkage density, the number of observed links in these web versions did not increase in proportion with the number of possible links added by parasite life stages, leading to a decrease in connectance with the inclusion of parasites. Similarly, the inclusion of parasites increased nestedness in the taxonomic species web but decreased nestedness in the disaggregated webs. This finding is consistent with recent results demonstrating that connectance has a strong positive relationship with nestedness (Thebault and Fontaine 2010). It is possible that disaggregation may also obscure a nested structure because networks composed of specialists tend to show greater nestedness than networks rich in generalists (Lima et al. 2012).

Disaggregating nodes into life stages was particularly useful for analyses involving trophic positions and omnivory in the food web. Organisms with distinct life stages, and particularly parasites, feed at varying trophic levels throughout development. The traditional approach of grouping these life stages led to an overestimation of

**Fig. 4** The observed links of the three versions of the Quick Pond food web, with each consumer node ( $i$ ) ordered by latent feeding position ( $c_i$ ) and each resource node ( $j$ ) ordered by latent niche position ( $n_j$ ). Panels **a** and **b** correspond to the taxonomic species web; **c** and **d** correspond to the niche-shift web; **e** and **f** correspond to the life stage web. The *left panels* show each web without parasites and the *right panels* show each web with parasites. *Green dots* indicate resource links for free-living consumers and *orange dots* indicate resource links for parasite consumers. Concomitant predation links are included in the web versions used in this figure (color figure online)



the trophic level of the species relative to its individual life stages. In some cases, the trophic position of a taxonomic species was two to three trophic positions above the larval trophic level, and in all cases the species-level trophic position exceeded that of both the larval and adult stages in the disaggregated food webs. This likely overestimated the trophic position in the taxonomic species food web that included parasites. In the life stage web lacking concomitant predation links, 23 % of the remaining links still involved predation on parasites, primarily representing cases of predation on free-living parasite stages. In the case of complex life cycle parasites, most of these predator-parasite links occur with life stages of parasites that feed on a relatively low trophic level [e.g., predation on trematode cercariae (Orlofske et al. 2012)]. The net effect of the overestimation of parasite trophic positions, coupled with a large proportion of predator-parasite links, serves to overestimate the mean trophic level of the entire food

web. In a web version with concomitant links, the number of predator-parasite links was 36 % of the total and the mean trophic level of the web increased to 5.1, indicating that concomitant links further compound this problem when they are included. We verified this interpretation by conducting the analyses of trophic position on a version of the food web without links between predators and parasites, and indeed the overestimation found in the taxonomic species web with parasites was eliminated. This same scenario (i.e., overestimation of the trophic position of complex life cycle species) is likely with all complex life cycle organisms and provides one impetus to consider using life stage structure for questions related to trophic levels and omnivory. We also note, however, that our findings may be sensitive to the measure of trophic position that is utilized (Williams and Martinez 2004).

Contrary to predictions, the fit of a probabilistic niche model to the empirical webs with parasites did not improve

as a result of disaggregating species-level nodes. Niche models are based on the assumption that food webs are interval and organisms feed within a relatively contiguous feeding range (Williams et al. 2010). It has been posited that parasites, due to their complex life cycles and potential for host specificity, may reduce the intervality of food webs because they have a broad feeding niche with many gaps or secondary feeding niches (Dunne et al. 2013). As a result, we predicted that disaggregating species-level nodes into life stages would improve the fit of the probabilistic niche model because each life stage is likely to have a more narrow niche breadth than the species as a whole. Our results, however, did not support this hypothesis, as model fit decreased with node disaggregation and the inclusion of parasites decreased model fit in all three food webs by a similar amount. Two possible explanations, which are not mutually exclusive, may underlie these findings. First, Dunne et al. (2013) found that fit of the probabilistic niche model tends to decrease with increasing food web size. Disaggregating species-level nodes inherently increases web size, so this mechanism may contribute to the decrease in model fit. Second, the contiguous-diet intervality metrics show that the number of gaps increased with disaggregation, whether parasites were included or not, which likely makes it more difficult for the model to fit probabilistically contiguous intervals for consumers. The increase in diet-range gaps, which increased more with disaggregation than consumer gaps, probably reflects the increase in prey availability due to life stage structure.

Describing the structural characteristics of food webs has been of interest because of hypothesized relationships between structure and measures of network stability, such as robustness, persistence, and resilience (Ives and Carpenter 2007; Rooney and McCann 2012). An important question within the field of disease ecology is whether parasites have a net positive or negative effect on network stability. Analyses of past webs have indicated that parasites increase certain metrics (e.g., connectance) associated with network stability (Lafferty et al. 2006; Hernandez and Sukhdeo 2008; Amundsen et al. 2009) and engage in many weak interactions, which have been suggested to further enhance stability (McCann et al. 1998). Yet parasites also possess traits associated with network instability; complex life cycle parasites are highly susceptible to secondary extinctions (Lafferty and Kuris 2009; Chen et al. 2011; Lafferty 2012) and diseases occasionally induce extinctions of their hosts directly (e.g., Skerratt et al. 2007). Our results contribute to this discussion by highlighting how the effects of parasites on connectance and nestedness are sensitive to the way nodes are defined, underscoring the need to carefully consider how web construction alters perceived outcomes. While the role of connectance in web stability is still a topic of debate, there is increasing evidence that high

levels of nestedness can destabilize food webs (Thebault and Fontaine 2010). Understanding how parasites influence network stability is a promising avenue for future theoretical and empirical work.

The observed differences in the three versions of the Quick Pond food web emphasize the need to carefully consider which level of biological organization (e.g., trophic species, taxonomic species, life stages) is best tailored to the aims of a particular web analysis. Cohen et al. (1993) made the recommendation that taxonomic species-level nodes should be disaggregated into more resolved units when a change in diet occurs with increasing size or life stage. This is essentially our approach in the niche-shift web, where ontogenetic stages are only divided when there is a significant diet shift between stages. This approach has the advantage of incorporating valuable information on the variation in predators and prey throughout development and does not lead to redundancy in links if the only species disaggregated are those that show shifts in predators and/or diet [a criticism of disaggregating nodes based on life stage alone (Huxham et al. 1995)]. In our analyses, disaggregating nodes into life stages made assigning trophic levels and calculating omnivory more accurate, particularly for food webs with parasites. However, care must be taken in comparing food webs with and without life stages because disaggregating species-level nodes leads to numerous inherent changes in web structure, as observed here and elsewhere (Pimm and Rice 1987; Rudolf and Lafferty 2011). One drawback of separating species into life stages is that different stages are effectively treated as separate populations even though the success of one stage is tightly coupled to the success of the previous stage. For web analyses that include quantitative population metrics, this drawback may offset any advantages of dividing taxonomic species into life stages. Clearly defining life stages or ontogenetic niche shifts can also be challenging across the diversity of taxa included in food webs. Here, we incorporated a somewhat arbitrary delineation in diet between life stages in the niche-shift web. More precise definitions of niche shifts that are readily applicable in a food web context would be useful.

As the field of food web ecology advances in new directions, two promising avenues involve integrating multiple types of species interactions (e.g., mutualism, parasitism, predation) into the same network (e.g., Van Veen et al. 2008; Fontaine et al. 2011) and examining how variability in linkages beyond the species level influences network structure and function (Ings et al. 2009). By considering individual life stages in a food web that incorporates both predator–prey and host–parasite interactions, our study highlights how network properties and the observed roles of functional groups are sensitive to the “rules” used in building the network. Further analyses of food webs from

other ecosystems are needed to test whether these patterns are generally applicable across other systems. Understanding how subtleties in food web construction influence observed patterns in feeding interactions will be useful in examining a wide range of food web questions, including responses of networks to ecosystem change (Tylianakis et al. 2008) and the movement towards more quantitative webs that incorporate measures of interaction strength and energy fluxes (Cohen et al. 2003; Berlow et al. 2004).

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