

CHAPTER 9

Food webs and parasites in a salt marsh ecosystem

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9.1 Background

Our mothers teach us to grill our meats “well done” and chew them thoroughly. Even if mom did not know why she insisted, both are good precautions against parasites. Parasites may be in our food, but they are not in our food webs. Is it necessary to take the precaution of considering them? In this chapter, we argue that parasites affect important properties of food webs and that it may be difficult to fully understand ecosystems without considering parasites.

Food webs depict trophic interactions among networks of consumers, producers, and non-living material. Units in food webs range from specific life-cycle stages of species to broad taxonomic/functional groups. At the most basic level, food webs are static diagrams or matrices of who eats whom (topological webs). Some food webs track flows of energy and matter among links (bioenergetic webs). Other food webs denote the strengths of interactions among species (interaction webs). The food-web framework captures much of the current theory on how habitat heterogeneity, species richness, trophic cascades, indirect mutualism, apparent competition, intraguild predation, environmental change, ecosystem stability, nutrient dynamics, and productivity affect community structure (Paine 1988; Winemiller and Polis 1996). Food webs also aid applied research by providing a better understanding of pest control, environmental contamination, bioremediation, and fisheries management (Winemiller and Polis 1996).

Published food webs vary considerably in quality and detail, but nearly all exclude consumers that are not readily detectable, such as endoparasites and

other infectious agents (Polis 1991; Cohen *et al.* 1993). Indeed, perhaps because they are difficult to detect, typical parasites have been historically lacking from the bulk of ecological theory. However, parasitism is arguably the most prevalent lifestyle among animals (Price 1980; DeMeeùs and Renaud 2002). As ecologists increasingly consider the role of parasites in ecosystems, it is becoming clear that parasites are embedded in food webs and may need to be considered in food-web theory (Polis 1991; Cohen *et al.* 1993; Marcogliese and Cone 1997; Marcogliese 2003). Incorporating parasites, as we have done here, helps illuminate the role of parasitism in natural communities (Dobson *et al.* 2005), and reveals how changes in community structure may affect rates and patterns of parasitism.

Almost all published food webs describe predator-prey links (e.g. lion-gazelle-grass). Food webs of insect parasitoids and their hosts have also been developed because parasitoids are relatively easy to observe when they emerge from their hosts (Lawton 1989). The full food web in any given community will likely contain predator-prey, parasitoid-host and parasite-host interactions, as well as other trophic interactions described below. However, few community food webs have incorporated more than one of these subwebs. In a key exception, Memmott *et al.* (2000) added a parasitoid-host subweb to a rich web of herbivorous insects, plants and predators. They found that adding parasitoids greatly decreased the web's overall connectance (the average proportion of other species with which each species interacts). This was, in part, due to the relatively high host specificity of

parasitoids. Differences between predator-prey and parasitoid-host food webs arise largely because parasitoids are intimate with a single host, while predators have brief interactions with many different prey individuals (Lafferty and Kuris 2002). This comparison illuminates how different types of natural enemies can have different effects on food-web properties.

Analysis of topological predator-prey and parasitoid-host subwebs has led to the discovery of general patterns (Pimm *et al.* 1991). Published webs usually contain three to four trophic levels and an average of less than one predator or parasitoid species per prey or host species. Neither the relative abundance of members in each trophic level, nor the density of linkages varies with the number of species in the web. Finally, omnivory (feeding at more than one trophic level), is less common than would be expected by chance. Such generalizations have received substantial criticism because of the problems concerning data quality associated with the published food webs (Polis 1991).

Rules for assembling topological webs have been inconsistent, and many topological webs seem to reflect authors' conception of what a web should look like rather than direct measurements from nature (Paine 1988; Polis 1991). Studies of interaction webs have generated less contentious predictions, for example, about stability (the ability of a food web to return or maintain equilibrium in the face of disturbance). The stability of a food web is predicted to decrease with (1) diversity, (2) connectance, and (3) the average strength of an interaction (May 1973). With greater species diversity, there are simply more opportunities for instability to arise. Furthermore, strong links allow instability to readily propagate between species. In contrast, many weak interactions may increase ecosystem stability (McCann *et al.* 1998).

Conclusions based on food webs of parasitoids or predators do not necessarily inform us about the role of typical parasites in food webs. At first, the small body size of an individual parasite relative to its host and its generally nonlethal effect implies that a parasite species plays a small role in the flow of energy through a food web. However, parasites have a durable relationship with their host and, unlike predators, their consumption continues over

time. Unlike predators, parasites are very efficient at converting what they consume into reproductive output (Whitlock *et al.* 1966; Ractliffe *et al.* 1969). Even if an individual parasite has a minor impact on the host, when summed over a large population of parasite individuals within the host, the impact may be large. For instance, for lambs with high-intensity infections of *Haemonchus contortus*, the sheep stomach barber-pole worm, the continual export of host energy may result in severe anemia (Ractliffe *et al.* 1969). Such energetic conversion from a host to a parasite infrapopulation (a population of parasites within a host) could profoundly affect food-web dynamics and topography.

Unfortunately, parasite-host links are relatively difficult to elucidate and only a handful of studies have included typical parasites (incorporated as top predators) in food webs (see review in Sukhdeo and Hernandez 2004). In a pioneering study, Huxham *et al.* (1995) incorporated 42 helminth parasites into an 88-species food web for the Ythan Estuary (Aberdeenshire, Scotland). The resulting greater chain lengths and higher proportion of top species were the logically necessary outcomes of affording parasites top-predator status. Also, parasites decreased connectance and increased omnivory (a common food-web statistic) because parasites with complex life cycles usually feed at multiple trophic levels (Huxham *et al.* 1995).

More recently, Thompson *et al.* (2005) explored the role of nine parasite species (as top predators) in a mudflat food web with 67 free-living species and broad categories for basal taxa. In addition to generally supporting the conclusions of Huxham *et al.* (1995), they investigated the effects of each parasite species in the web. They found that parasites only mildly decreased connectance. Only one of the nine parasite species, a trematode, strongly affected the food web, suggesting that generalist parasites with complex life cycles have disproportionate effects on food webs.

Here, we construct a topological food web for an estuary in which we have been studying the role of parasites in ecosystems. We use this food web to help investigate how macroparasites affect community structure. Our goal was to determine how the inclusion of parasites would alter common food-web metrics, such as the number of links,

connectance, and vulnerability (the number of enemy species per prey or host). We not only discovered that parasites significantly changed these food-web metrics, but we also uncovered previously unanalyzed classes of food-web interactions. Explicit inclusion of parasitic interactions serves to increase understanding of community structure, and further integrates the impact of infectious diseases into community ecology.

9.2 Methods

9.2.1 Defining the study system

We have investigated the ecology of larval trematode host-parasite interactions in southern California (USA) and Baja California (Mexico) salt marshes for over two decades, and recently began quantifying host distribution and abundance. Our goal was to develop an accurate and comprehensive topological food web for a small estuary, including information on the parasites.

The study site, Carpinteria salt marsh, is a 93-ha wetland and upland habitat located 19 km east of Santa Barbara, CA (34°2'4" N, 119°31'30" W). The estuary consists of a pickle weed (*Salicornia virginica*) dominated marsh with unvegetated pans, mudflats, and tidal channels that are fed by two seasonal creeks. Although residential and commercial development surrounds the area, the University of California, Santa Barbara Natural Reserve System protects and manages the marsh for scientific research. It serves as the primary site for our long-term studies on ecological parasitology.

Although real food webs may spread over large spatial and temporal scales, topological webs must be constrained by defined limits. We constrained the Carpinteria salt marsh food web to tidally influenced soft sediment and vegetated habitat, excluding several habitats supporting species with trophic links to estuarine species in our web. For example, food and nutrients enter the estuary from streams during the wet season and from the ocean on each incoming tide. Also, many terrestrial birds, mammals, and invertebrates (particularly insects, Cameron 1972) feed along the upland edge of the estuary. Finally, hard substrate at the mouth of the estuary provides habitat for species that are more

characteristic of the open shore. Constraining the food web spatially helped limit the host species pool in the food web to a tractable list.

9.2.2 Naming the players and links

We used species as our preferred taxonomic unit and included known, but unidentified or undescribed "morphospecies." Although we strived to use precise and accurate taxonomy, some members of the food web were grouped into categories (e.g. copepods). We primarily used information from plant transects, bird surveys (R. Hansen, unpublished data), fish seine hauls, and benthic infaunal cores (sieved through either 5 mm or 1 mm mesh) for invertebrates to compile our species lists. For each sampling method, we excluded species that comprised <0.5% of the individuals sampled. We also included species that we knew to be common, but that were not well targeted by our sampling methods. For example, the fish *Mugil cephalus* is abundant in the marsh, yet is notoriously difficult to capture using beach seines. Some top predators that failed the abundance criterion were included because higher trophic levels are relatively important for food webs and species at higher levels are relatively rare.

Topological food webs consist of an $n \times n$ matrix of n species, with predators as columns and prey as rows (Cohen 1978). Binary entries (e.g. 0 or 1) in the matrix indicate whether a predator eats a prey. To add links to the matrix, we consulted published information on diets (Morris *et al.* 1980; Barry *et al.* 1996; Love 1996; CLO 2002). In many cases, the diet descriptions were broad enough (e.g. "fish") to require our discretion in assigning them to particular species. In addition, we incorporated our unpublished data on diet and gut contents, which we often obtained in conjunction with parasitological examinations. We conservatively extrapolated diet information from other locations to the same or analogous food sources found in Carpinteria salt marsh. For some species, we generated diet items of unstudied species from those of similar, well-studied species.

Food webs based on observations are only as complete as the observations are exhaustive. We decided to improve our food web by logically

inferring links when specific data were unavailable. Parasites can be useful indicators of host diets (Marcogliese and Cone 1997). For parasites acquired with food, the living parasite stays in the gut far longer than the digested food item, providing a sensitive indicator of host diet (Marcogliese 2003). The opposite logic also applies; a species that serves as an intermediate host for a parasite known to occur in a particular predator is likely to be prey for that predator (Huxham *et al.* 1995; Marcogliese 2003). For this reason, we expanded a host's diet list when a parasite's presence indicated that the host consumed a particular prey item. For example, in our system, the trematode *Cloacitrema michiganensis* parasitizes American coots. These waterfowl forage largely on vegetation. Because the trematode encysts on opercula of the horn snail, *Cerithidea californica*, American coots likely ingest horn snails incidentally while feeding on vegetation. Mallards have similar diets to coots and we assumed that they also ate horn snails. In our results (Appendices 1–4), we distinguish between confirmed and inferred links.

To determine host–parasite links, we used published lists of parasites for the hosts in our study, when such information was available for the region (Russell 1960; Martin 1972; Love and Moser 1983; Huspeni and Lafferty 2004). We also used our unpublished parasite observations. We discuss each of the host–parasite groups in turn, below.

Published reports and our observations indicate that a variety of ecto- and endoparasites commonly infect estuarine fishes. In particular, metacercarial cysts of digenean trematodes frequently infect fishes in Carpinteria salt marsh. Non-digenean trematode parasites recorded from our samples included worms in the gut (camellianid nematodes) and tissue (larval tetraphyllidean and trypanorhynchian cestodes, larval acanthocephalans) and ectoparasites of the skin (dactylogyrid and gyrodactylid monogeneans, ergasilid copepods) mouth (cymothoid isopods), and gills (ciliophoran protozoans and gyrodactylid monogeneans). With the exception of ciliates, we did not include any protozoan, bacterial, or viral parasites of fishes.

For birds, we primarily included intestinal helminth parasites based on published and unpublished dissection data, but we additionally inferred

parasitism in birds from diet (see Box 9.1). Birds also serve as hosts for a wide range of viruses, bacteria, and protozoans, as well as a high abundance and diversity of ectoparasitic arthropods. We limited our treatment of these taxa to the assumption that each bird species was infected by one species of *Plasmodium* (avian malaria) (Bennett *et al.* 1993). Vector control efforts have found 10 species of mosquitoes in and around the marsh (Ferren *et al.* 1996); two of these species (*Aedes taeniorhynchus* and *Culex tarsalis*) are common in the marsh and feed on birds. *C. tarsalis* transmits arboviruses and avian malaria to birds. Bird ectoparasites, micropredators, and blood parasites play a more important and diverse role than our food web implies (Janovy 1997).

We also did not consider some potentially important parasites of invertebrates. Although poorly studied, bacteria, viruses, protozoa, and fungi probably parasitize most invertebrates. We included some protozoan parasites of invertebrates, but did not include others we have encountered in similar wetlands. For example, we have evidence from other wetlands that apicomplexan protozoans parasitize clams and crabs. We also did not include symbiotic species for which insufficient information is available to determine whether the symbionts are parasites or commensals. Examples include ciliates that live in the mantle cavity of the high marsh snail, *Assiminea californica*, and two species of copepods that live on the cuticle of thalassinidean ghost shrimp. Some of the trematode metacercariae encyst on the outside of hard-shelled invertebrates. These parasites do not have trophic links with their second intermediate hosts and we did not count them as such. However, we note this association in our table and matrix as they help indicate life cycles and do form predator–parasite links. It is not clear how incomplete parasite information affects our results, but inclusion of parasites that use few hosts (like parasitoids or feather lice) would reduce the linkage density in the parasite–host subweb.

9.2.3 Incorporating parasites into the web

How should parasites be included in food webs? Published food webs usually equate parasites with top predators. This perspective has contributed

Box 9.1 Identifying complex life cycles from food webs

So, you want to put parasites in your food web? The best source of information is to dissect samples of the free-living species in the web and identify all parasites to species, or at least to morphospecies. This requires a lot of expertise and effort and it is no surprise that no study has completely accomplished it. In most systems, there will be some published information on parasites from the host species encountered. Because hosts range widely and may pick up parasites from other regions or habitats, one should carefully review host–parasite accounts to be sure that they are likely to occur in the food web under study. The use of hypothetical parasite–host links is often necessary to fully incorporate parasites into food webs (Huxham *et al.* 1995). Even if a comprehensive parasite list is available, one will be forced to guess about some of the links between hosts and parasites, especially for rare or difficult to sample hosts. For example, the trematodes in our system are generalists in birds and it is difficult to obtain birds for parasite analysis. Most of our trematodes have been reported from a wide range of avian final hosts. In addition, experimental infections have repeatedly demonstrated their ability to infect a variety of other hosts, including ducks, pigeons, chickens, and even cats, rats, and mice (Martin 1972).

Thus, the ingestion of intermediate hosts (fish, crustaceans, mollusks, and annelids) should be the primary determinant of parasitism in birds. We therefore assumed that if a bird ate a prey that served as second intermediate host for an avian trematode, the bird could successfully acquire that parasite. For example, the trematode *C. michiganensis* has been reported from nine bird species in our web. This trematode encysts on the shells of burrowing clams and exoskeletons of ghost shrimp, suggesting that the additional eight species of bird that prey on these second intermediate hosts also serve as final hosts for *C. michiganensis*. We did not make such assumptions for non-avian predators. For example, raccoons eat a wide range of prey, but appear to serve as hosts only for a few of the avian trematodes (Lafferty and Dunham, 2005).

We had 64 confirmed instances of trematode–bird links in our system and diet information added an additional 236 probable trematode–bird links. Food webs can greatly aid the development of predicted host–parasite associations, as they reveal what links expose predators to parasites. The specificity of the parasite for the predator host ultimately determines whether exposure leads to transmission.

substantial insight to food-web theory, but there are drawbacks. Sometimes food-web theory (cascade and niche models) arranges consumers on a body size axis, and assumes that consumers are larger than prey, a strategy that may provide illogical roles for parasites (Dobson *et al.* 2005). Instead of blending parasites into the predator–prey subweb, we organized the food web into four subwebs. The first was the predator–prey subweb, which corresponded to nearly all published food webs.

The second subweb was the parasite–host subweb. By adding parasites to a subweb, instead of as top predators in the predator–prey web, it was possible to compute statistics for predator–prey interactions that remain comparable to previously published food webs.

The third subweb included predators that feed on parasites, a component missing from all previous food webs. For example, some consumers feed on free-swimming trematode cercariae. We extrapolated limited laboratory observations on fishes to several potential links (we are currently verifying

this aspect of the food web). More importantly, predators unintentionally eat the parasites of their prey, resulting in either parasite transmission or parasite death (Box 9.2). We suspect that in cases where transmission is possible, when a predator eats an infected prey, most of the parasites fail to transmit and the predator digests them. For example, less than 10% of ingested metacercariae establish in a coral reef fish; the rest perish (Aeby 2002). Therefore, we included predation on parasites as independent links in the food web.

The fourth subweb included parasite–parasite trophic interactions, another unrecognized subweb. These were primarily interactions among trematodes that share the same first intermediate host snail species (*C. californica*). Multispecies infections of larval trematodes within an individual snail often result in competitive exclusion through intraguild predation among larval trematodes (Kuris 1990; Sousa 1993; Lafferty *et al.* 1994; Huspeni and Lafferty 2004). There were two other parasite–parasite interactions. A picornavirus infects and

Box 9.2 Parasite transmission and host abundance

A link is just the beginning. It represents a complex consumer–resource interaction that plays out in time and space at individual and population levels. Links, therefore, can be starting points for interesting theoretical and empirical studies. Linkages in food webs can influence directly transmitted diseases as well as those with complex multiple-host life cycles, but links between parasites and hosts are particularly tenuous. This is because links may not be sufficient to maintain transmission if the abundance of hosts is low. If the frequency of contact between infected and susceptible hosts is lower than the death or cure rate of infected hosts, the prevalence of disease will decrease. Such a process eventually dampens epidemics. Infrequent contact between hosts can also prevent initiation of epidemics. Predators can make it difficult for directly transmitted parasites of prey to persist by keeping prey populations at low density, thereby reducing transmission. This is an important consideration as two-thirds of the predator–prey links in the Carpinteria salt marsh food web lead to the death of parasites. For example, Hudson *et al.* (1992) found that predators limited the abundance of the

parasitic nematode, *Trichostrongylus tenuis*, by feeding on infected grouse. Loss of infected individuals stabilizes grouse populations. Without predators, grouse populations exhibit cyclic fluctuations. These cycles are predominantly caused by a nematode-induced reduction in host fecundity (Hudson *et al.* 1998). Similarly, predators can keep sea urchin populations at low levels, but where fishing reduces urchin predators, urchins become abundant and bacterial epidemics are more common (Lafferty 2004). Thus, food-web linkages indirectly influence host contact rates, permitting infectious disease to act as a density-dependent mortality source. Sometimes, parasites strengthen trophic links by increasing host susceptibility to predation by other hosts in the life cycle. This reduces the minimum host-threshold density, allowing parasites to exploit less common hosts (Dobson 1988). While exhaustive knowledge of host–parasite links is itself difficult to obtain, this is actually the easy part to tackle. Understanding the dynamics associated with these links requires intensive study and is the key challenge for understanding the role of parasites in communities.

kills the entoniscid isopod that parasitizes shore crabs (Kuris *et al.* 1979) and avian malaria parasites (*Plasmodium* spp.) infect mosquitoes.

Huxham *et al.* (1995) point out that life-cycle stages of parasites differ substantially in their ecology such that each stage could be considered a separate trophic species. We treated different stages of a parasite's life cycle as one species, but coded our results so the different stages could be distinguished in subsequent analyses. Treating each stage as a separate species would decrease linkage density.

9.2.4 Food-web metrics

To assess the effects of parasitism on food-web properties, we calculated several metrics of webs with and without parasites. However, since it was intuitively obvious that including parasites increases food chain length, we did not calculate this property. We did measure vulnerability to predators and parasites, and averaged this within each trophic level of the free-living species. We also calculated several linkage statistics for the complete

web and for each subweb. These were: potential number of links, observed number of links, expected number of links (based on past studies of predator–prey webs), observed connectance and expected connectance (based on past studies of predator–prey webs).

The potential number of links, L_p , in a symmetrical matrix of $S \times S$ species (such as a predator–prey subweb, parasite–parasite subweb, or complete web) is equal to the number of cells in the matrix (S^2). This power relationship causes the potential number of links to increase sharply with species richness. For a subweb comprised of two separate species lists (such as X parasites and Y hosts), the number of cells in the matrix is XY , not S^2 , and $L_p = XY$. Only a fraction of the potential links in a food web occurs. The observed number of links, L_o , is simply the sum of the links observed in a web (excluding those few cases, mentioned above, where parasites encyst on the outside of a host and extract no energy). Connectance is a commonly used food-web statistic that indicates linkage density. Observed connectance, C_o , is the proportion of potential links realized, or $C_o = L_o/L_p$.

9.2.5 Assembling the web

For the basal trophic level, one “species” was carrion, two “species” were detritus, and five “species” were functional groupings of plants. We divided the producer component of the food chain into (1) phytoplankton, (2) epipellic fauna (mostly microalgae, foraminiferans, and bacteria), (3) macroalgae (*Ulva* sp., *Enteromorpha* sp., and *Gracilaria* sp.), (4) submergent vascular plants (*Ruppia maritima*), and (5) five common emergent vascular plants (Table 9.1).

Many species feed on bacterial and fungal decomposers. This part of the food web has very high diversity and several trophic levels within the bacterial and phage guilds (Breitbart *et al.* 2004), which we were forced to greatly simplify. Because this part of the food web has no linkage with the parasites in our web, however, simplifying it does not greatly alter our conclusions. We divided the detrital food web into (1) terrestrial and (2) marine “detritus.” Isotope studies have found that detritus from vascular plants (e.g. *S. virginica*) contributes to the diet of semiterrestrial detritivores (*Traskorchestia traskiana* and *Melampus olivaceus*), while algal sources supply food for the remaining detritivores that feed in the water (Page 1997). Seventy-five free-living consumers were included in the predator-prey subweb. These were divided into trophic levels, where a predator’s trophic level was one level above the highest trophic level of its prey.

Of the 74 invertebrate species reported from the estuary, 8 large invertebrates and 11 small invertebrates met our criteria for abundance and habitat use. We also added 12 species that were common, but inadequately sampled: three crabs, two amphipods, a fly, mosquito larvae, a water boatman, two high intertidal snails, a deep dwelling mud shrimp, and a mussel. Of the 22 reported fish species, five met the criteria for abundance and habitat use. We added two predators (leopard shark and round stingray) and mullet (for reasons noted above). Of the 118 reported bird species, 32 met our criteria for abundance and habitat use. To this list, we added three top predators (Northern harrier, Cooper’s hawk and osprey), a scavenger (turkey vulture) and the secretive clapper rail as these species were likely important to the web in a manner disproportionate to their abundance. The other terrestrial

Table 9.1 List of basal food items, including detritus and carrion.

L is a taxonomic letter code, # is the rank-order species/item abundance within the letter code, and T is the trophic level (basal taxa are 0). Basal taxa, unlike other taxa, were lumped into broad groups. D = detritus, K = carrion, P = plant

Common name	Details	L	#	T
Marine detritus		D	1	0
Terrestrial detritus	From vascular plants	D	2	0
Carrion		K	1	0
Macroalgae	<i>Enteromorpha</i> , <i>Ulva</i> , <i>Gracilaria</i>	P	1	0
Epipellic flora	Mostly diatoms	P	2	0
Pickleweed	<i>Salicornia virginica</i>	P	3	0
Jaumea	<i>Jaumea carnosa</i>	P	4	0
Salt grass	<i>Distichlis spicata</i>	P	5	0
Alkali heath	<i>Frankenia salina</i>	P	6	0
Shore grass	<i>Monanthochloe littoralis</i>	P	7	0
Submergent vascular	<i>Ruppia cirrhosa</i>	P	8	0
Phytoplankton	Undocumented	P	9	0

vertebrate that commonly foraged in the intertidal was the raccoon (*Procyon lotor*).

The binary matrix was too large to present as a single table so we describe the food web in three ways. The first is a set of tables organized taxonomically (Tables 9.1–9.5). These tables provide a common and scientific name for each species, as well as a trophic level and species coding consisting of a letter (taxon specific) and number (rank-order abundance within taxon from most abundant (1) to least abundant). We then broke down the matrix by subweb in Appendices 9.1–9.4. From the tables, we created a traditional web diagram to illustrate the predator–prey subweb (Fig. 9.1). We created Fig. 9.2 by adding the host–parasite subweb to the predator–prey subweb. Here, parasites were oriented along the right vertical axis to better distinguish the parasite–host subweb from the predator–prey subweb.

9.3 Results

The potential number of links (excluding the diagonal) in the 87×87 predator–prey subweb was 7569. We observed 505 trophic links (Appendix 9.1). There was an average of 6.7 prey species per predator species. Diet breadth increased and peaked at intermediate trophic levels. This may partly be explained by our grouping of basal taxa, which reduced the number of prey species available for lower trophic levels. As expected, omnivory

Table 9.2 Invertebrates. A = annelid (and a nemertean), C = crustacean, G = gastropod, I = insect, V = bivalve. Other codes as in Table 9.1

Common name	Scientific name	L	#	T
Oligochaete	Unidentified	A	1	1
Polychaete	<i>Capitella capitata</i>	A	2	1
Phoronid	Unidentified	A	3	1
Nemertean	<i>Geonemertes</i>	A	4	2
Spionid	<i>Polydora nuchalis</i>	A	5	1
Polychaete	<i>Eteone lightii</i>	A	6	1
Tube amphipod	<i>Corophium</i>	C	1	1
Copepods	Unidentified harpacticoids	C	2	1
Ostracods	Unidentified	C	3	1
Aquatic amphipod	<i>Anisogammarus confervicolus</i>	C	4	1
Beach hopper	<i>Traskorchestia traskiana</i>	C	5	1
Lined shore crab	<i>Pachygrapsus crassipes</i>	C	6	4
Yellow shore crab	<i>Hemigrapsus oregonensis</i>	C	7	3
Fiddler crab	<i>Uca crenulata</i>	C	8	1
Ghost shrimp	<i>Neotrypaea californiensis</i>	C	9	1
Mud shrimp	<i>Upogebia macginittiorum</i>	C	10	1
Horn snail	<i>Cerithidea californica</i>	G	1	1
Bubble snail	<i>Acteocina inculta</i>	G	2	1
Olive snail	<i>Melampus olivaceus</i>	G	3	1
Assiminean snail	<i>Assiminean californica</i>	G	4	1
Water boatman	<i>Trichocorixia reticulata</i>	I	1	1
Brine fly larva	<i>Ephydra</i> sp.	I	2	1
Brine fly adult	<i>Ephydra</i> sp.	I	3	1
Mosquito larva	See Appendix 9.2, 15–6	I	4	1
Bent-nosed clam	<i>Macoma nasuta</i>	V	1	1
Littleneck clam	<i>Protothaca staminea</i>	V	2	1
Jackknife clam	<i>Tagelus</i> spp.	V	3	1
False Mya	<i>Cryptomya californica</i>	V	4	1
European mussel	<i>Mytilus galloprovincialis</i>	V	5	1

Table 9.3 Fishes. F = fish. Other codes as in Tables 9.1 and 9.2

Common name	Scientific name	L	#	T
Topsmelt	<i>Atherinops affinis</i>	F	1	1
Arrow goby	<i>Clevelandia ios</i>	F	2	2
California killifish	<i>Fundulus parvipinnis</i>	F	3	3
Staghorn sculpin	<i>Leptocottus armatus</i>	F	4	5
Long-jaw mudsucker	<i>Gillichthys mirabilis</i>	F	5	5
Mullet	<i>Mugil cephalus</i>	F	6	1
Round stingray	<i>Urobatis halleri</i>	F	7	5
Leopard shark	<i>Triakis semifasciata</i>	F	8	6

increased from the first to the sixth trophic level (1.0, 1.5, 2.5, 3.0, 3.6, 4.4 average trophic levels fed on, respectively). Omnivory creates a disparity between the trophic level on which a predator typically fed,

Table 9.4 Mammal and birds. R = raccoon, B = bird. Other codes as in Tables 9.1–9.3

Common name	Scientific name	L	#	T
Raccoon	<i>Procyon lotor</i>	R	1	5
Willet	<i>Catoptrophorus semipalmatus</i>	B	1	5
Black-bellied plover	<i>Pluvialis squatarola</i>	B	2	5
American coot	<i>Fulica americana</i>	B	3	2
Western sandpiper	<i>Calidris mauri</i>	B	4	4
Dunlin	<i>Calidris alpina</i>	B	5	4
Least sandpiper	<i>Calidris minutilla</i>	B	6	4
California gull	<i>Larus californicus</i>	B	7	5
Whimbrel	<i>Numenius phaeopus</i>	B	8	5
Mallard	<i>Anas platyrhynchos</i>	B	9	2
Mew gull	<i>Larus canus</i>	B	10	5
Marbled godwit	<i>Limosa fedoa</i>	B	11	5
Forster's tern	<i>Sterna forsteri</i>	B	12	4
Ring-billed gull	<i>Larus delawarensis</i>	B	13	5
Dowitcher	<i>Limnodromus</i> spp.	B	14	4
Western gull	<i>Larus occidentalis</i>	B	15	5
Bonaparte's gull	<i>Larus philadelphia</i>	B	16	5
Semipalmated plover	<i>Charadrius semipalmatus</i>	B	17	3
Great blue heron	<i>Ardea herodias</i>	B	18	6
Killdeer	<i>Charadrius vociferus</i>	B	19	2
Snowy egret	<i>Egretta thula</i>	B	20	6
Long-billed curlew	<i>Numenius americanus</i>	B	21	5
Greater yellowlegs	<i>Tringa melanoleuca</i>	B	22	3
Black-crowned night heron	<i>Nycticorax nycticorax</i>	B	23	6
Green heron	<i>Butorides virescens</i>	B	24	4
Double-crested cormorant	<i>Phalacrocorax auritus</i>	B	25	6
Great egret	<i>Ardea alba</i>	B	27	5
Surf scoter	<i>Melanitta perspicillata</i>	B	28	6
Pied-billed grebe	<i>Podilymbus podiceps</i>	B	29	4
Belted kingfisher	<i>Ceryle alcyon</i>	B	30	5
Bufflehead	<i>Bucephala albeola</i>	B	31	4
American avocet	<i>Recurvirostra americana</i>	B	32	2
Green-winged teal	<i>Anas crecca</i>	B	33	6
Clapper rail	<i>Rallus longirostris</i>	B	34	1
Turkey vulture	<i>Cathartes aura</i>	B	35	5
Cooper's hawk	<i>Accipiter cooperii</i>	B	36	5
Northern harrier	<i>Circus cyaneus</i>	B	37	6
Osprey	<i>Pandion haliaetus</i>	B	37	6

and the trophic level to which it was assigned (based on the highest trophic level of its prey). Hence, while the top trophic level of the average species was 3.2, the average trophic level at which a species fed was 2.1. As expected, species at higher trophic levels were preyed on by fewer species than were species at lower trophic levels (by definition species at the top trophic levels have no predators).

Table 9.5 Parasites. C = crustacean, I = insect, L = leech, N = nematode, O = other, T = trematode, W = tapeworm. Other codes as in Tables 9.1–9.4. Note that several free-living crustacean and insect species occur in other tables. No trophic level is defined for parasites in our food web

Common name	Scientific name	L	#
Entoniscid isopod	<i>Portunion conformis</i>	C	11
Isopod	<i>Nerocila californica</i>	C	12
Bopyrid isopod	<i>Orthione</i> sp.	C	13
Copepod	<i>Ergasilus auritius</i>	C	14
Mosquito	<i>Aedes taeniorhynchus</i>	I	5
Mosquito	<i>Culex tarsalis</i>	I	6
Leech	Unidentified glossiphoniidae	L	1
Nematode	<i>Proleptus obtusus</i>	N	1
Nematode	Unidentified	N	2
Nematode	<i>Spirocamallanus pereirai</i>	N	3
Nematode	<i>Baylisascaris procyonis</i>	N	4
Acanthocephalan	Unidentified	O	1
Nemertean	<i>Carcinonemertes epialti</i>	O	2
Monogene	<i>Gyrodactylus</i> sp.	O	3
Ciliate	<i>Trichodina</i> sp.	O	4
Gregarine	Eugregarine 1	O	5
Gregarine	Eugregarine 2	O	6
Virus	Picornavirus	O	7
Malaria	<i>Plasmodium</i> sp.	O	8
Dodder	<i>Cuscuta salina</i>	P	10
Bird's beak	<i>Cordylanthus maritimus</i>	P	11
Trematode	<i>Euhaplorchis californiensis</i>	T	1
Trematode	<i>Himasthla rhigedana</i>	T	2
Trematode	<i>Probolocoryphe uca</i>	T	3
Trematode	<i>Himasthla species B</i>	T	4
Trematode	<i>Renicola buchanani</i>	T	5
Trematode	<i>Acanthoparyphium</i> spp.	T	6
Trematode	<i>Catantropis johnstoni</i>	T	7
Trematode	Unidentified Rencolid	T	8
Trematode	<i>Parorchis acanthus</i>	T	9
Trematode	<i>Austrobilharzia</i> sp.	T	10
Trematode	<i>Cloacitrema michiganensis</i>	T	11
Trematode	<i>Phocitrema ovale</i>	T	12
Trematode	<i>Renicola cerithidicola</i>	T	13
Trematode	Unidentified Cyathocotyloid	T	14
Trematode	<i>Stictodora hancocki</i>	T	15
Trematode	<i>Mesostephanus appendiculatus</i>	T	16
Trematode	<i>Pygidiospoides spindalis</i>	T	17
Trematode	Unidentified microphallid	T	18
Trematode	<i>Hysteroleicitha</i> sp.	T	19
Trematode	<i>Parvatrema</i> sp.	T	20
Trematode	Unidentified Microphallid	T	21
Trematode	<i>Galactosomum humbargari</i>	T	22
Cestode	Unidentified Tetracystidae	W	1
Cestode	Unidentified Tetracystidae	W	2
Cestode	Unidentified Trypanorhynch	W	3
Cestode	Unidentified Dilepidid	W	4

The number of species in each trophic level did not conform to the expectation that diversity should decline at top trophic levels (levels 1–6 had 29, 6, 4, 9, 18, and 9 species, respectively, Fig. 9.2). However, for birds, which were the only speciose taxon with data on relative abundance, species feeding at lower trophic levels tended to be more abundant than species feeding at higher trophic levels (correlation between average trophic level at which a species fed and that species' abundance $R = -0.46$, $N = 37$, one-tailed $P = 0.002$).

The frequency of interactions between the predator–prey subweb and parasitism became apparent after considering that 216 of the 321 links between birds and prey and 6 of the 72 links between fish and prey allow the transmission of at least one parasite species from intermediate to final host species.

The parasite–host subweb consisted of 47 parasite species and 87 potential host species (ignoring basal taxa), or 4089 potential links (Appendix 9.2). There were 615 parasite–host links in this subweb, not including the 21 cases where non-feeding parasites encysted on the outside of hosts. The average number of host species per parasite species (14.0) was considerably higher than the average number of prey species per predator species (6.7). The number of parasite species per host species increased with trophic level, with top predators having more parasite species than intermediate species.

The predator–parasite subweb also had 4089 potential links (Appendix 9.3). There were 910 links between predators and parasites driven by the consumption of infected hosts. One-third (338) of these links could lead to parasite transmission. That is, the predator also served as a host for the parasite. In addition, four fishes and three clams had the potential to eat the free-swimming cercarial stage of 19 of the 22 trematode species, providing 139 additional links. Twenty-eight of these were redundant with other predator–parasite links, leading to a total of 1021 predator–parasite links.

The parasite–parasite subweb had 2209 potential links (Appendix 9.4). In addition to the picornavirus–entoniscid and *Plasmodium*–mosquito links, there were 170 intraguild predation links between trematode species, for a total of 172 parasite–parasite links.

There were 2313 links out of the 17,956 potential links in the overall food web (the four combined subwebs).

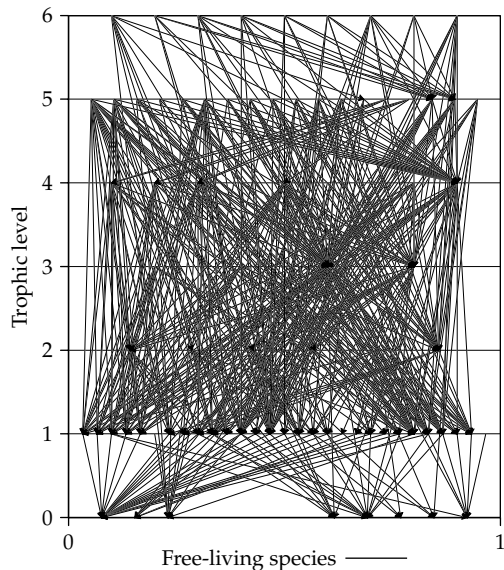


Figure 9.1 Traditional food-web diagram corresponding to the predator–prey subweb. Arrows connect predators to prey (arrow heads located on the prey). Species are arranged vertically by trophic position (basal through 6) and horizontally within a trophic level by the alphanumeric coding in the tables.

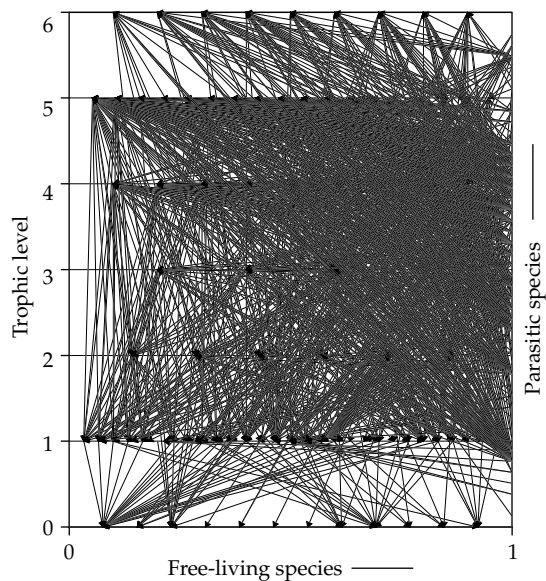


Figure 9.2 Like Fig. 9.1, but including the parasite–host subweb. Parasites aligned on the right vertical axis. Arrows leading from parasites to hosts indicate parasitism.

9.4 Discussion

Including parasites in the Carpinteria salt marsh food web adds new insight to this food web and others. The most general insight is the recognition of three new subwebs that are likely present in all communities. Here, these subwebs contain more than two-thirds of the links.

The inclusion of a parasite–parasite subweb was the greatest departure from previously published webs; our familiarity with larval trematode community structure predisposed us to consider this subweb. For example, the diverse guild of trematodes using the horn snail is characterized by high levels of interspecific competition and intraguild predation (Kuris 1990; Sousa 1993; Lafferty *et al.* 1994). Connectance in parasite–parasite webs will depend on the life-history strategy of the parasites. Typical parasites do not often interact trophically with other parasites. In contrast, parasitic castrators and parasitoids often compete for limited host resources through intraguild predation (Kuris 1974; Lafferty and Kuris 2002). The trematodes that dominate the Carpinteria salt marsh food web affect many aspects of the ecosystem. As parasitic castrators, they reduce snail density (Lafferty 1993a) and size at maturity (Lafferty 1993b). They convert snail reproductive tissue into free-swimming cercariae available to zooplankters and filter feeders. They also increase predation on some second intermediate hosts through behavior modification (Lafferty and Morris 1996).

Many links were a consequence of including a guild of trematodes that have broad final-host specificity. Other types of parasites (e.g. single-host life cycle and host-specific groups such as feather lice) may yield subwebs with less connectance than the predator–prey subweb. This was the case for the parasitoid–host subwebs of Memmott *et al.* (2000), which had low connectance due to high host specificity. Host specificity, therefore, should be the key to determine how parasites affect connectance. The increased diversity and connectance that parasites impart to the Carpinteria salt marsh food web could alter the web's stability, depending on the strengths of the interactions between hosts and parasites. Weak links with long loops characterize trophic interactions of parasites with complex life cycles, and this should increase stability (Dobson

et al. in press). In addition, infectious diseases tend to disproportionately impact common species, helping to maintain their rarer competitors, thereby promoting coexistence and stability (Dobson *et al.* in press). Interaction webs with parasites will be necessary to fully explore these hypotheses.

Parasites may also alter the interaction strengths in the predator-prey subweb if predators select diseased prey (Packer *et al.* 2003). For instance, experimental removal of helminth parasites in natural populations reveals how easily predators capture parasitized snowshoe hares (Murray *et al.* 1997) and red grouse (Hudson *et al.* 1992), relative to unparasitized conspecifics. Furthermore, many parasites require the ingestion of an intermediate host by a final host to complete their life cycle. Some parasites that achieve transmission via food-web links alter the behavior or appearance of intermediate hosts to increase their risk of being preyed on by final hosts (Lafferty 1999). For example, a common trematode species in snails at Carpinteria salt marsh, *Euhaplorchis californiensis*, uses the third most common fish species, *Fundulus parvipinnis*, as a second intermediate host. Larval *E. californiensis* encyst on the fish's brain and manipulate behavior, rendering infected fish 10–30 times more likely to be eaten by one of the 15 bird species in the Carpinteria salt marsh food web that serve as a final host for the adult worm (Lafferty and Morris 1996).

Similarly, predator-parasite links may alter the interaction strength of parasite-host links. If predators are an important source of parasite mortality in prey, some parasites might have a hard time persisting in predator-rich food webs. This challenge appears to be one explanation for the evolution of complex life cycles. Parasites must be under tremendous pressure to form parasite-host links with the predators of their hosts (Lafferty 1999). When predators strongly prefer parasitized prey (but do not serve as hosts), complex interactions in models of host and parasite populations can result. These include oscillations, alternate stable states, and parasite extinction (Hall *et al.* 2005). However, in more productive environments, predators that do not prefer parasitized prey can cause extinction of hosts followed by extinction of their host-specific parasites (Hall *et al.* 2005).

Some studies show how parasite links can alter food webs. In particular, the invasion and eradication

of Rinderpest (a morbillivirus related to measles) in East African ungulates illustrates how one infectious disease strongly affected a food web by altering the density of abundant hosts (Sinclair 1979; Plowright 1982; Dobson 1995; Tompkins *et al.* 2001). Rinderpest arrived with cattle in 1889 and the resulting epidemics caused mass mortality in domestic and wild artiodactyls throughout Africa. This led to reductions in abundance of their predators (Plowright 1982). A vaccine was introduced into cattle and, by 1961, native ungulate populations experienced rapid recovery (Plowright 1982; Spinage 2003). The increased prey base led to increases in lion and hyena populations, which then preyed heavily on gazelles and displaced wild dogs. Canine distemper is currently reducing predator densities in Africa with further resultant alterations to food webs (Roelke-Parker 1996).

The Carpinteria salt marsh food web could be expanded to include meroplanktonic food items in the predator-prey subweb, such as the free-swimming larval stages produced by most of the five annelids, four decapod crustaceans, five bivalves, and six bony fishes in our example. Similarly, trematode life-cycle stages that use mollusks as first intermediate hosts produce many free-swimming cercariae. These motile larvae do not feed while they seek out the next host in the life cycle. The vast majority of cercariae likely fail to infect a host and either become prey or contribute to detritus. Thus, inclusion of cercarial productivity as a planktonic component of food webs strengthens connectance. It is notable that trematodes could comprise half the species richness of the larval zooplankton community in this estuary and biomass could be considerably more than half of the larval zooplankton standing crop (Stevens 1996). It is also possible that increases in the abundance of planktivores could reduce transmission of cercariae.

Food-web structure can also affect what types of parasites can persist (Marcogliese 2002). Parasites that exploit trophic transmission will depend on the presence of trophic linkages among host species (Dobson *et al.* in press). A species-rich, well-connected, predator-prey web will facilitate the completion of more types of complex life cycles. Even simple changes can affect parasite communities if they permit the completion of new life cycles. For instance, when a few pairs of great crested grebes

colonized Slapton Ley (Devon, UK) in the early 1980s, a new link (grebe-fish) permitted completion of the life cycles of a cestode linked with copepod, fish and bird hosts, and a trematode linked with snail, fish, and bird hosts (Kennedy and Watt 1994). Both parasites greatly impacted the dominant fish intermediate host and led to significant changes in the fish community (Kennedy and Watt 1994).

Parasites with complex life cycles are good indicators of food-web linkages in an ecosystem. To the extent that food-web linkages indicate ecosystem functionality, parasites can also be good environmental indicators (Lafferty 1997). At our study site, habitat restoration was followed by an increase in the abundance and diversity of the larval trematodes in horn snails, presumably because the improved habitat fostered foraging opportunities for a diverse assemblage of final-host birds (Huspeni and Lafferty 2004).

9.5 Conclusion

The Carpinteria salt marsh food web is far more complicated than a typical predator-prey subweb. Invisibility and small size make it hard to adequately include parasites in food webs, but it seems unwise to completely ignore them. Including parasites strongly affected characteristics of the Carpinteria salt marsh food web. Most notably, in contrast to parasitoid-host subwebs, our parasite subwebs had a large number of links and disproportionately added to food-web connectance. Further incorporation of parasites into food webs will increase our appreciation of their role in ecosystems.

Acknowledgments

We thank T. Huspeni, E. Dunham, C. Boch, L. Mababa, F. Mancini, M. Pickering, A. Kaplan, and members of our research group for their extensive assistance in the field and laboratory. This manuscript has benefited from support received from the National Science Foundation through the NIH/NSF Ecology of Infectious Disease Program (DEB-0224565) and US EPA STAR EaGLE Coastal Initiative through the Pacific Estuarine Ecosystem Indicator Research Consortium, US EPA Agreement EPA/R-82867601. The UCSB Natural Reserve System provided access to field sites.

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Appendix 9.1

Predator–prey subweb. Interactions for predator trophic levels 1–6 depicted as predator [prey trophic level: prey *i*, prey *j*]. Prey listed in bold = known links. Regular font = putative links. Italics = links inferred from parasitism. Letter codes and numbers correspond to groups and species/item numbers as defined in Tables 9.1–9.5.

First trophic level (all prey in trophic level 0): A1–2,5,6,C1–2[**D1**], A3[**D1**, **P2**, **P9**], B34[**K1**], C3[**D1**, **P2**], C4[**D1**, **P1–2**], C5[**D2**], C8[**D1**, **D2**, **P1–2**], C9–10[**D1**, **P5**], F1,6[**D1**, **P1**], G1[**D1**, **P2**], G2[**D1**, **P2**], G3[**D2**], G4[**D2**], I1[**D1**, **P2**], I2[**D1**], I3[**D1**, **K1**], I4[**P1–2**], V1[**D1**, **P2**, **P9**], V2[**P2**, **P9**], V3–5[**P9**].

Second trophic level: A4[1: A1–3, A5–6, C1–4], B3[0: **P1**, **P3–4**; 1: C4, V1], B9[0: **P1**, **P3–8**; 1: C4, G2, I2, V1], B19[1: C5, I3], B32[0: P3, P9; 1: A1, C4, G2, I2], F2[1: **C1–2**, C3–4, I1].

Third trophic level: B17[1: **A1–2**, A3, A5–6, **C1**, **I3**, **V1**, **V5**; 2: A4], B22[1: **A1**, A2–3, A5–6; 1: G1, **I3**; 2: A4, **F2**], C7[0: **D1–2**, **K1**, **P1–2**, **P8**; 1: **A1–3**, **A5–6**, G2, I2, V1–5; 2: **A4**], F3[1: A1–3, A5–6, C2–4, G2, G4, I1–2, I4; 2: A4].

Fourth trophic level: B4[1: **A1–2**, A3, A5–6, **C1**, **C3**, **G1–2**, **I3**, V1, V4–5; 2: A4; 3: C7], B5[1: A1–3, A5–6, C1, C4–5, G1, V1–2; 2: A4; 3: F3], B6[1: **A1–2**, A3, A5–6, C2–5, G1, I2–3, V1; 2: A4; 3: F3], B12[1: F1; 2: F2; 3: F3], B14[1: **A1–2**, A3, A5–6, **C1**, **C3–4**, **G1–3**, **I2**, V1–3; 2: A4, **F2**; 3: C7, F3], B24[1: F1; 2: F2; 3: **F3**], B29[1: F1; 3: **F3**], B31[1: A1–3, A5–6, **C3**, G1, I1, I3; 2: A4, F2; 3: F3], C6[0: **D1–2**, **K1**, **P1–3**, **P8**; 1: **A1–3**, **A5–6**, C4, C8, **G1–2**, G3, I2, V1–5; 2: **A4**; 3: C7].

Fifth trophic level: B1[A1–2, A3–6, **C1**, **C3**, C4, **C5**, **C8–10**, G1, I2, I4, V1–3, V4, V5; 2: A4, **F2**; 3: C7; 4: **C6**], B2[1: **A1–2**, A3, A5–6, **C1**, C4–5, C8, G1, **I3**, V1–2, V4–5; 2: **A4**, **F2**; 3: C7; 4: C6], B7[0: K1; 1: F1, V1–3, V5; 3: C7, F3; 4: C6], B8[1: C8, **G3**; 3: C7; 4: **C6**], B10[0: K1; 1: **F1**, V1–3, **V5**; 3: C7; 4: **C6**], B11[1: **A1–2**, A3, A5–6, **C1**, **C3–5**, C8, **G3**, V1–2; 2: A4, F2; 3: C7; 4: **C6**], B13,16[0: K1; 1: F1, V1–3, V5; 3: C7; 4: C6], B15[0: **K1**];

1: **F1**, V1–3, **V5**; 3: **C7**; 4: **C6**, B21[1: **C8–10**, V3, **V4**; 2: **F2**; 3: **C7**; 4: **C6**], B27[1: C4, C8–10, G1, V1, **V2**, V3, **V5**; 3: **C7**; 4: **C6**], B30[1: C4, C8, **G1–2**, V1–2, **V5**; 3: **C7**; 4: **C6**], B33[1: C8, G1, G3; 3: **C7**; 4: **C6**], B35[4: B4–6], B36[4: B4–6, B14], F4[1: **C1**, C3, **C4**, C5, C8, **C9–10**; 2: **F2**; 3: **C7**, **F3**; 4: **C6**], F5[1: C2–4, **C5**, C8–10; 2: **F2**; 3: **C7**, **F3**; 4: **C6**], F7[1: C8–10, V1–3; 2: **F2**; 3: **C7**; 4: **C6**], R1[0: **K1**, 1: C8, F1; 2: B3, B9, B19; 3: **C7**; 4: **C6**; 5: B33].

Sixth trophic level: B18[1: **F1**, F6; 2: **F2**; 3: **F3**; 5: F4–5], B20[1: **C8**, **F1**, **I3**; 2: **F2**; 3: **C7**, **F3**; 4: **C6**; 5: F4–5], B23[1: **C8**, F1; 2: **F2**; 3: **C7**, **F3**; 4: **C6**; 5: F4–5], B25[1: F1, F6; 2: **F2**; 3: **F3**; 5: F4–5], B26[1: F1, F6; 2: **F2**; 3: **F3**; 5: F4–5], B28[1: C4, C8, F1; 2: **F2**; 3: **C7**, **F3**; 4: **C6**; 5: F4–5], B37[1: F1, **F6**; 3: **F3**; 5: F4–5], F8[1: C8–10, F1, V1–3; 2: **F2**; 3: **C7**, **F3**; 4: **C6**; 5: F4

Appendix 9.2

Parasite–host subweb. Superscripts denote the following: 1 = parasite-1st intermediate host link; 2 = parasite-2nd intermediate host link; 3 = parasite-final host link. The superscript 2' indicates a metacercaria that excysts on the outside of the host and does not feed on the host. These are not counted as links in the parasite–host food web but are presented to illustrate life cycles (although they are included in the predator–parasite subweb). Excluded from the table are: (1) the two adult mosquitoes (I5–6) whom we assume feed on raccoons and all the birds, and (2) *Plasmodium* (avian malaria) which we assume infects all bird species and uses the mosquito *C. tarsalis* as a vector. Other codes as in Appendix 9.1.

Trophically transmitted parasites: N2[1: **V3**¹; 5: F7³; 6: F8³], N3[1: **C2**¹, **F1**³, **F6**³; 2: **F2**³; 3: **F3**³; 5: **F4–5**³], N4[6: **R1**], O1[2: **B19**³; 3: **B17**³; 4: **B14**³; 5: **B1**³], T19[1: C2², G2¹; 5: **F5**³], T20[1: **V3**²; 4: B14³; 5: B1³, B7³, B10³, B13³, B15–16³, B21³, B27³], T21[1: **G4**¹; 4: C6²; 5: B1¹, B22¹, B7–8¹, B10–11¹, B13¹, B15–16¹, B21¹, B27¹, B30¹, B33¹], T22[1: **F1**²], W1[1: **V3**²; 5: F7³; 6: F8³], W2[5: F7³; 6: F8³], W3[3: F3²; 5: F4²; 6: F8³], W4[3: F3²; 4: B5–6³, B12³, B14³, B24³, B29³, B31³, C6³; 6: B18³, B20³, B23³, B25–6³, B28³, B37³].

Trematodes that use *C. californica* as a 1st intermediate host: T1[1: **G1**¹; 3: **F3**²; 4: B5–6³, B12³, B14³, B24³, B29³, **B31**³; 5: B7³, B18³, B20³, B23³, B25–6³, B28³, B37³], T2[1: **C8**², **C10**², **G1**¹, **G1**²; 3: **C7**²; 4:

B4³, **B14**³, **C6**²; 5: **B1–2**³, B7–8³, B10–11³, B13³, B15–16³, **B21**³, B27³, B30³, B33³; 6: B20³, B23³, B28³], T3[1: **C8**², **G1**¹; 3: **C7**²; 4: B4³, B14³, **C6**²; 5: **B1–2**³, B7–8³, B10–11³, B13³, B15–16³, B21³, B27³, B30³, **B33**³; 6: B20³, B23³, B28³], T4[1: **A5**², **G1**¹, **G2**²; 2: B32³; 3: **B17**³, **B22**³; 4: B4–5³, **B6**³, **B14**³, B31³; 5: B1–2³, B11³, B30³], T5[1: **G1**¹; 3: **F3**²; 4: **B5–6**³, **B14**³, B24³, B29³, B31³; 5: **B7**³, **F5**³; 6: B18³, B23³, B25–6³, B28³, B37³], T6[1: **A2**², **A5**², **G1**¹, **G1**², V1–4²; 2: B3³; 3: B17³, B22³; 4: **B4**³, B5–6³, **B14**³, **B31**³; 5: B1–2³, B7³, B10–11³, B13³, B15–16³, B21³, B27³, B30³, B33³], T7[1: **G1**¹, **G1**²; 3: B22³; 4: **B4–5**³, B6³, **B31**³; 5: **B1–2**³, B27³, B33³], T8[1: **A2**², **A5–6**², **G1**¹; 3: B17³, B22³; 4: B4–6³, B14³, B31³; 5: B1–2³, B11³], T9[1: **C8**², **C9**², **G1**¹, **G1**², V1², V3²; 3: B17³, **B22**³, **C7**²; 4: **B4–6**³, **B14**³, B31³, **C6**²; 5: **B1–2**³, B7³, B8³, B10–11³, B13³, **B15–16**³, B21³, B27³, B30³, **B33**³; 6: B20³, B23³, B28³], T10[1: **G1**¹; 4: **B4–5**³, B12³, **B14**³, **B31**³; 5: **B1–2**³, B13³, B15³], T11[1: **C8**², **C9**², **G1**¹, **G1**², V1², V3²; 3: B17³, **B22**³, **C7**²; 4: **B4–6**³, **B14**³, B31³, **C6**²; 5: **B1–2**³, B7³, B8³, B10–11³, B13³, **B15–16**³, B21³, B27³, B30³, **B33**³; 6: B20³, B23³, B28³], T12[1: **G1**¹; 3: B22³, **F3**²; 4: B5–6³, **B12**³, B14³, B24³, B29³, B31³; 5: B1–2³, B7³, B10–11³, **B13**³, **B15–16**³, B21³, **F5**²; 6: B18³, B20³, B23³, B25–6³, B28³, B37³], T13[1: **G1**¹; 3: **F3**²; 4: **B5–6**³, B12³, **B14**³, B24³, B29³, B31³; 5: **B7**, **F5**²; 6: B18³, B23³, B25–6³, B28³, B37³], T14[1: **G1**¹; 3: B22³, **F3**²; 4: B5–6³, B12³, B14³, B24³, B29³, B31³; 5: B1–2³, B7³, B10–11³, B13³, B15–16³, B21³, **F5**²; 6: B18³, B20³, B23³, B25–6³, B28³, B37³], T15[1: **G1**¹; 2: B3³; 3: **B22**³, **F3**²; 4: B5–6³, B12³, B14³, B24³, B29³, B31³; 5: **B1–2**³, B7³, B10–11³, B13³, B15–16³, B21³, **F5**², R1³; 6: B18³, B20³, B23³, B25–6³, B28³, B37³], T16[1: **G1**¹; 3: B22³; 4: B12³, B14³, B24³, B29³, B31³; 5: B1–2³, B7³, B10–11³, B13³, B15–16³, B21³, **F5**², R1³; 6: B18³, B20³, **B23**³, B25–6³, B28³, B37³], T17[1: **G1**¹; 3: B22³, **F3**²; 4: B5–6³, B12³, B14³, B24³, B29³, B31³; 5: B1–2³, B7³, B10–11³, B13³, B15–16³, B21³, **F5**²; 6: B18³, B20³, **B23**³, B25–6³, B28³, B37³], T18[1: C4², **G1**¹; 4: B4³, B14³, C6²; 5: B1–2³, B7³, B8³, B10–11³, B13³, B15–16³, B21³, B27³, B30³, B33³; 6: B20³, B23³, B28³].

Nontrophically transmitted parasites depicted as parasite[host trophic level: host]. C11[3: **C7**³], C12[1: **F1**³, **F6**³; 6: F8³], C13[1: **C10**¹], C14[1: **F1**³, **F6**³; 2: **F2**³; 3: F3³; 5: **F4–5**³], L1[5: **F4–5**³], N1[1: **C9**¹; 5: F7³; 6: F8³], O2[3: **C7**³], O3–4[1: F1³, **F6**³; 2: F2³; 3: F3³; 5: F4³, F5³], O5[1: **A2**³], O7[4: **C6**³].

Parasitic plants. P10[O: P3–P7], P11[O: P3,P5]

Appendix 9.3

Predator-parasite subweb. Superscripts denote the following: 5 = cercarial (water column) feeding; 6 = vector feeding; 7 = predation by a non-host (no parasite transmission); 8 = predation with parasite transmission. Other codes and notations as in Appendices 9.1 and 9.2.

First trophic level: V1–V3[T1–19⁵].

Second trophic level: A4[O5⁷, N3⁷, T4⁷, T6⁷, T8⁷, T18–19⁷], B3[T6⁸, T9⁸, T11⁷, T18⁸], B9[T18⁸, T19⁷], B32[T18⁸, T19⁷], F2[N3⁸, T1–19⁵, T19⁷].

Third trophic level: B17[O5⁷, T4⁷, T6⁸, T8–9⁸, T11⁸], B22[C14⁷, O3–5, N3⁷, T1–5⁷, T6–8⁸, T9–11⁷, T12⁸, T13⁷, T14⁸, T15⁷, T17–18⁸], C7[O5⁷, N2⁷, T4⁷, T6⁷, T8–9⁷, T11⁷, T19–20⁷, W1⁷], F3[C14⁷, O5⁷, N3⁸, T1–19⁵, T4⁷, T6⁷, T8⁷, T19⁷].

Fourth trophic level: B4[O7⁷, O2⁷, O5⁷, T1–2⁷, T3–4⁸, T5–7⁷, T8⁸, T9–17⁷, T19⁷], B5[O3–5⁷, N3⁷, T1⁸, T2–3⁷, T4, T5⁷, T6⁸, T7⁷, T8⁸, T9–11⁷, T12⁸, T13⁷, T14–15⁸, T16⁷, T17–18⁸], B6[O3–5⁷, N3⁷, T1⁸, T2–6⁷, T7–8⁸, T9–11⁷, T12⁸, T13⁷, T14–15⁸, T16⁷, T17–18⁸, T19⁷], B12[C12⁷, C14⁷, O3–4⁷, N3⁷, T1⁸, T5⁸, T12⁷, T13–17⁸, T22⁷, W3⁷, W4⁸], B14[O7⁷, C14⁷, O2–5⁷, N2–3⁷, T1⁸, T2⁷, T3⁸, T4–7⁷, T8⁸, T9–11⁷, T12⁸, T13⁷, T14–18⁸, T19⁷, T20⁸, W1⁷, W3⁷, W4⁸], B24[C7⁷, C14⁷, O3–4⁷, N3⁷, T1⁷, T5⁸, T12–17⁸, T22⁷, W3⁷, W4⁸], B29[C7⁷, C14⁷, O3–4⁷, N3⁷, T1⁷, T5⁸, T12–17⁸, T22⁷, W3⁷, W4⁸], B31[C14⁷, O3–5⁷, N3⁷, T1–3⁷, T4–5⁸, T6–7⁷, T8–9⁸, T10–11⁷, T12–17⁸, W3⁷, W4⁸], C6[C11⁷, O7⁷, O2⁷, O5⁷, O8⁷, T1–20⁷, W1⁷].

Fifth trophic level: B1[C11⁷, O7⁷, C13–14⁷, O1–6⁷, N2–3⁷, T1–18⁸, T20⁷, T21⁸, W1⁷], B2[C11⁷, O7⁷, C14⁷, O2–6⁷, N3⁷, T1⁷, T2–4⁸, T5–7⁷, T8–9⁸, T10–11⁷, T12⁸, T13⁷, T14–18⁸, T21⁸], B7[O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N2–3⁷, T1–3⁸, T5–6⁸, T9⁸, T11–17⁸, T20⁸, T21⁸, T22⁷, W1⁷], B8[C11⁷, O7⁷, O2⁷, O6⁷, T2⁷, T3⁸, T9⁷, T11⁷, T18⁷, T21⁸], B10[O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N2–3⁷, T2–3⁸, T6⁸, T9⁸, T11–12⁸, T14–18⁸, T20–21⁸, T22⁷, W1⁷], B11[C11⁷, O7⁷, C14⁷, O2–6⁷, N3⁷, T2–4⁸, T6⁸, T8⁸, T9⁷, T11⁷, T12⁸, T14⁸, T15⁷, T16–18⁸, T21⁸], B13[O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N2–3⁷, T2–3⁸, T6⁸, T9⁸, T11⁸, T12⁷, T14–T18⁸, T20–21⁸, T22⁷, W1⁷], B15[O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N2–3⁷, T2–3⁸, T6⁸, T9⁷, T11⁸, T12⁷, T14–T18⁸, T20–21⁸, T22⁷, W1⁷], B16[O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N2–3⁷, T2–3⁸, T6⁸, T9⁸, T11⁸, T12⁸, T14–T18⁸, T20–21⁸, T22⁷, W1⁷], B21[C11⁷, O7⁷, C12⁷, C13–14⁷, N1⁷, O2–4⁷, O6⁷,

N2–3⁷, T2–3⁸, T6⁸, T9⁸, T11⁸, T12⁸, T14–T18⁸, T20–21⁸, W1⁷], B27[C12⁷, C13⁷, N1⁷, O2⁷, O6⁷, N2⁷, T1⁷, T2–3⁸, T4–5⁷, T6–7⁸, T8⁷, T9⁸, T10⁷, T11⁸, T12–17⁷, T18⁸, T20–21⁸, W1⁷], B30[C11⁷, O7⁷, C14⁷, O2⁷, O6⁷, T1⁷, T2–4⁸, T5⁷, T6⁸, T7–8⁷, T9⁸, T10⁷, T11⁸, T12–17⁷, T18⁸, T19⁸, T21⁸], B33[C11⁷, O7⁷, C14⁷, O2–4⁷, O6⁷, N3⁷, T1–7⁸, T9⁸, T12–18⁸, T19⁷, T21⁸, W3⁷, W4⁸], B35[O8⁷, T1–15⁷, T17⁷, W4⁸], B36[O8⁷, O1⁷, T1–17⁷, T20⁷, W4⁸], F4[C11⁷, O7⁷, C13–14⁷, N1⁷, O2–4⁷, O6⁷, N3⁷, T1–3⁷, T1–19⁵, T5⁷, T9⁷, T11–18⁷, T21⁷, W3–4⁷], F5[C11⁷, O7⁷, C13–14⁷, N1⁷, O2–4⁷, O6⁷, N3⁷, T1–3⁷, T1–19⁵, T5⁷, T9⁷, T11–18⁷, T19⁸, T21⁷, W3–4⁷], F7[C11⁷, O7⁷, C13–14⁷, N1⁸, O2–4⁷, O6⁷, N2⁸, N3⁷, T2–3⁷, T6⁷, T9⁷, T11–12⁷, T14–18⁷, T20–21⁷, W1⁸], R1[C11⁷, O7⁷, C12⁷, C14⁷, O2–4⁷, O6⁷, N3, T2–3, T6⁷, T9⁷, T11–12⁷, T14–15⁷, T16⁸, T17–18⁷, T21–22⁷].

Sixth trophic level: B18,25–26,37[C12⁷, C14⁷, L1⁷, O3–4⁷, N3⁷, T1⁸, T5⁸, T12–18⁸, T19⁷, T22⁷, W3⁷, W4⁸], B20[C11⁷, O7⁷, C12⁷, C14⁷, L1⁷, O2–4⁷, O6⁷, N3⁷, T1–3⁸, T5⁷, T9⁸, T11–12⁸, T13⁷, T14–18⁸, T19⁷, T21⁸, T22⁷, W3⁷, W4⁸], B23[C11⁷, O7⁷, C12⁷, C14⁷, L1⁷, O2–4⁷, O6⁷, N3⁷, T1–3⁸, T5⁸, T9⁸, T11–18⁸, T19⁷, T21⁸, T22⁷, W3⁷, W4⁸], B28[C11⁷, O7⁷, C12⁷, C14⁷, L1⁷, O2–4⁷, O6⁷, N3⁷, T1–3⁸, T5⁸, T9⁸, T11–18⁸, T19⁷, T21⁸, T22⁷, W3⁷, W4⁸], F8[C11⁷, O7⁷, C12⁷, C13–14⁷, L1⁷, N1⁸, O2–4⁷, O6⁷, N2⁸, N3⁷, T1–3⁷, T5⁷, T9⁷, T11–18⁷, T20–22⁷, W1⁸, W3⁸, W4⁷].

Appendix 9.4

Parasite–parasite subweb. Most species interact via intraguild predation (as described in Kuris and Lafferty 1994). Other codes and notations as in Appendices 9.1–9.3.

Trematode–trematode interactions: T1[T3, T5, T7–8, T12–17, T18], T2[T1, T3–8, T11–17, T18], T3[T5, T7, T13, T16, T18], T4[T1, T3, T5–9, T11–17, T18], T5[T3, T8, T13–14, T16, 18], T6[T1, T3, T5, T7–8, T11–17, T18], T7[T3, T5, T8, T13–14, T16, T18], T8[T3, T5, T7, T13–14, T16], T9[T1–8, T11–17, T18], T11[T1, T3, T5–8, T12–17, T18], T12[T1, T3, T5, T7–8, T13–17, T18], T13[T3, T5, T8, T14, T16, T18], T14[T3, T5, T7–8, T13, T16, T18], T15[T1, T3, T5, T7–8, T12–14, T16–17, T18], T16[T1, T3, T5, T7–8, T12–15, T17, T18], T17[T1, T3, T5, T7–8, T12–16, T18], T18[T3, T5, T7, T13, T16].

Other parasite–parasite interactions: O7[6: C11³], O8[6: I6³].