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The effects of parasites on the kelp-forest food web

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The effects of parasites on the kelp-forest food web

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
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by

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Morton, Dana N., Antonino, C., Dykman, L., Broughton, F., Kuris, A., Kevin D. Lafferty. In prep. A food web including parasites for southern California kelp forests.

McLaughlin, John P., **Dana N. Morton,** Kevin D. Lafferty. 2020. "Parasites in Marine Food Webs". *Marine Disease Ecology.* (Eds) Behringer, Silliman, & Lafferty. Oxford University Press

Morton, Dana N., Tom W. Bell, and Todd W. Anderson. 2016. Spatial synchrony of amphipods in giant kelp forests. *Marine Biology.* 163: 1-11.

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DATA PRODUCTS

Lafferty, K.D., Rassweiler, A.,Gotschalk, C.C., **Morton, D.N.,** Bell, T.W., Henderikx, F., Kushner, D.J. Sprague, J., Johnson, C. and Washburn, L. 2019. The response of kelp forest organisms to spatial and temporal variation in wave energy in the California Channel Islands. Camarillo (CA): US Department of the Interior, Bureau of Ocean Energy Management. OCS Study BOEM.

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ABSTRACT

The effects of parasites on the kelp-forest food web

by

Dana Nicole Morton

Parasites often track food web linkages through their complex life cycles, but most food webs do not systematically include parasites. Where studied, parasites have strong effects on food web structure. Kelp forests are famous for strong trophic interactions, and their dynamic and open nature make them very different relative to the systems where parasites have been thoroughly studied (salt marsh, sand flat, and lake ecosystems). **The objective of this dissertation was to build a high-resolution topological kelp-forest food web that includes parasites. I used this food web to address the research question: How do parasites affect food-web structure?** Chapter 1 provides background and motivation for this work by reviewing key areas of research in kelp forest ecology and the effects of parasites in food webs. Chapter 2 describes the study system and a free-living food web with 490 species across 23 Phyla, with 546 distinct life stages and 8,759 trophic interactions. Chapter 3 describes the parasites in the food web, which adds 422 species across 10 Phyla (521 life stages) and 2,745 trophic interactions between parasites and hosts to the network for a total of 11,504 links. Adding trophic interactions between predator and parasites (concomitant predation) adds a further 9,536 links to the network. Chapter 4 examines the effects parasite addition on food-web structure. The kelp-forest food web was greatly enriched through resolution of free-living species and parasites, and parasites made up a larger proportion of the kelp-forest food web than any other published food web with parasites. Some of the effects of parasite addition were related to increasing network size and contrasted patterns in other systems (e.g. decreased connectance). On the other hand, other effects (e.g. longest chain length) were consistent with predictions based on other systems and were not due to increased network size alone. Specialist parasites and concomitant links altered the degree distribution independent of network size. Parasite life cycles are embedded throughout diverse patterns of free-living species interactions and must navigate a dense network of predators to infect appropriate hosts. The kelp forest ecosystem provides a diverse source of food and a diverse set of predators for both free-living and parasitic species, and our understanding of kelp forest ecosystems is enriched by including them.

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1. Kelp-forest ecosystems and parasites

1.1 Introduction

Kelp forests are oases of 3-dimensional structure in a desert of empty space. Among the fronds, stipes, and holdfasts of giant kelp are animals looking for food, or trying to prevent becoming food. The species of mammals, birds, fishes, invertebrates and algae found in giant kelp forests are engaged in a complex network of who eats whom. All of this eating and the high productivity of kelp forests has inspired ecologists globally (e.g. Estes and Palmisano 1974, Ojeda and Santelices 1984, Vásquez et al. 1984, Tegner and Dayton 2000, Schiel and Foster 2015, Carr and Reed 2016). Kelp forests along the coast of southern California (San Diego to Point Conception) have been studied more than anywhere else in the world, with more than seven decades of research on predation and grazing (e.g. Limbaugh 1955, Dayton 1985, Foster and Schiel 2010, Reed et al. 2011, Kushner et al. 2013, Lamy et al. 2020) and the cascading indirect effects (e.g. Behrens and Lafferty 2004, Lafferty 2004, Davenport and Anderson 2007) that permeate the kelp-forest food web. Food webs are a common way to describe an ecological network (Borer et al. 2002) and help describe complexity, species interactions, and functioning in ecosystems (Dunne et al. 2002) by visualizing and measuring how species are connected (Dunne et al. 2002, Amundsen et al. 2009, Rudolf and Lafferty 2011). Three food webs and a links database have been published for California kelp forests, but they lack resolution that would allow for network analysis and comparison with other food webs (Graham 2004, Graham et al. 2008, Byrnes et al. 2011, Beas-Luna et al. 2014). Here, I add to this extensive knowledge base by building a kelp-forest food web that systematically resolves the free-living and parasitic species that dominate biodiversity in this system.

Most marine food webs focus on interactions among well-studied, conspicuous organisms like large fishes. For instance, when building a food web for the Santa Barbara Channel Islands kelp forest, Graham (2004) used the diver survey species lists from the Channel Islands National Park Kelp Forest Monitoring (CINP KFM) program. This meant that although fish were resolved to the species level, many invertebrates in the food web became aggregated, underrepresented, or altogether ignored. Graham et al. 2008 generated a qualitative food web with relationships of conspicuous species gleaned from the literature. Byrnes et al. (2011) published a second kelp-forest food web from the species lists generated by the Santa Barbara Coastal Long-Term Ecological Research (SBC LTER) group. This network was resolved to the species level, but also focused on fish, large invertebrates, and macroalgae. To better parameterize kelp-forest models, Beas-Luna et al. (2014) assembled a broader literature on interactions among kelp forest species including non-trophic interactions, such as competition and habitat associations in a well-documented (but not maintained) database. With these three efforts, we know more about the kelp-forest food web than just about any other ecosystem.

The next obvious way to improve the kelp-forest food web is to add the small invertebrate species that can be important consumers of detritus and parasites of larger species. Most amphipod species are detritivores (Guerra-Garcia et a. 2014), and diverse species of amphipods are prey for fishes (Hobson and Chess 2001), but they are often aggregated to one or very few nodes in published webs. Though less apparent than detritivores, parasites have strong effects on diversity, biomass, and food-web complexity (Dunne et al. 2013, McLaughlin 2018, Lafferty et al. 2006). However, only eight published marine food webs include parasites (Dunne et al. 2013, Hechinger et al. 2011, Mouritsen et al. 2011, McLaughlin 2018). These marine food webs with parasites are all for soft-bottom systems, like salt marshes (Dunne et al. 2013). These salt-marsh food webs served as a model for how to improve the kelp-forest food webs through the non-biased inclusion of taxa without regard for taxon or life-style. Taking a systematic approach not only expanded the role of small invertebrates in the kelp-forest food web, it increased resolution at every trophic level, leading to perhaps the most complex and complete marine food web yet created.

1.2 Objective

My objective was to build well a resolved food web for the kelp forests of the Santa Barbara Channel that includes both free-living and parasitic species.

2. Free-living web

2.1 Introduction

A food web starts with a list of nodes for a given location and time period, and then determines which of the potential feeding links among nodes occur. Kelp-forest ecosystems are more complex than many ecosystems for which food webs have been built, but the extensive knowledge base and research history in southern California provided me with the necessary foundation for this work. Santa Barbara Channel kelp forests were ideal for this work due to monitoring by the Channel Islands National Park and the SBC Long Term Ecological Research programs. I started by compiling a list of free-living kelp-forest species from several sources. Because species often change their food and predators as they grow, I partitioned these species into different life stages. Therefore, most nodes in the web were resolved to species and life stage. I included metadata for taxonomic relationships, and three functional traits (habitat niche, life-style, and consumer strategy) for each node (Appendix Table 1). These traits, in combination with predator and prey relationships resolved in the food web, help define the functional roles of nodes, which make it possible for others to analyze the effects of species loss or gain, changing thermal environments, and changing habitat features (e.g. the dynamics of canopy-forming kelps). Links between nodes were then obtained from published diets, direct observation, or inference.

2.2 Research motivation

Kelp forests along the coast of California have been subject to many changes in the last few decades (Dayton et al. 1992, Eckert et al. 2000, Bell et al. 2015) and these changes are likely to continue and increase in frequency. Dramatic shifts in kelp biomass have occurred historically during ENSO events (Ebeling et al. 1985, Dayton and Tegner 1984, Edwards 2004, Rogers-Bennet and Catton 2019), and recently kelp forests in the Santa Barbara Channel (SBC) and northern California have experienced extreme heat waves in the form of "the Blob" coupled with ENSO events (Cavanaugh et al. 2019, Rogers-Bennet and Catton 2019). Fish assemblages have been showing signs of "tropicalization", coupled with declines in diversity, as conditions warm (Holbrook et al. 1997, Freedman 2019). The invasive alga *Sargassum horneri* has spread throughout southern CA and influences the benthic community (Marks et al. 2015, Caselle et al. 2017). Several disease outbreaks have also affected kelp-forest assemblages, including the black abalone die-off (Ben-Horin 2013, Lafferty and Kuris 1993), sea urchin microbial disease (Behrens and Lafferty 2004, Lafferty 2004), and two sea-star wasting epizootics followed by partial recovery (Eckert 2000, Hewson 2014). Some SBC kelp forests are now Marine Protected Areas (MPAs), which benefit commercially targeted species (Caselle et al. 2015, Hamilton and Caselle 2015) and may alter system responses to species invasion (Caselle et al. 2017). Due to larger-scale protections, formerly extirpated species like giant black seabass (House et al. 2016) and sea otters (Lafferty and Tinker 2014) are returning. An improved food web will help us predict how kelp forests may respond to these changes.

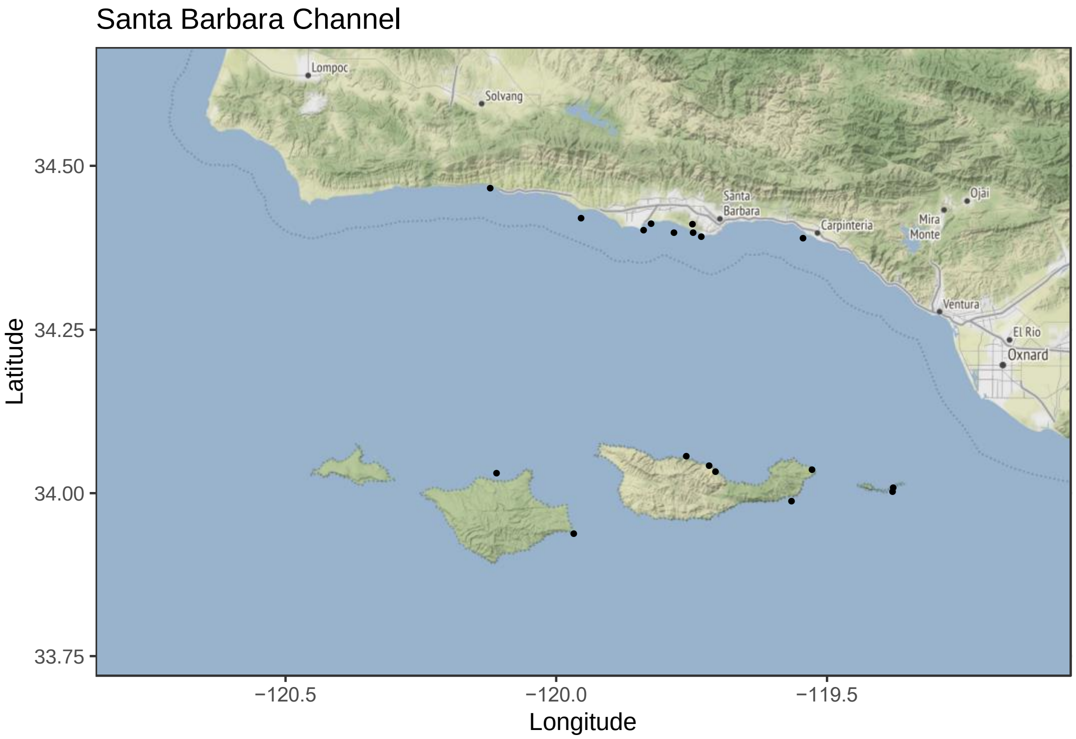
2.3 Objective

Create a high-resolution topological food web for free-living species in Santa Barbara Channel kelp forests.

2.4 Site description

I defined “kelp forest” as rocky reef habitat within the 5-20 m depth range that supports dense stands of giant kelp, *Macrocystis pyrifera*. Nodes in the web included species that used the water column and benthic zones within kelp forests as feeding habitat, including transient kelp-forest visitors, but excluding rare and vagrant species. For this study, I considered the Santa Barbara Channel (SBC) to include the mainland region between Point Conception (-120.476º longitude, 34.455 º latitude) and Point Mugu (-119.065 º longitude, 34.079º latitude), as well the northern and southern sides of the four northern Channel Islands (Figure 2.1). Although the SBC is a subset of the Southern California Bight, its strong west-east gradient in cold to warm temperature means the study system includes many of the kelp forest species in California (e.g. Hamilton et al. 2010). This means the SBC kelp-forest food web is a large "metaweb", characterizing kelp forest meta-communities, rather than a site-specific web. In other words, the network includes cold water and warm water species that might not necessarily co-occur at a single site. However, one can generate a site-specific food web by removing species from the metaweb that do not occur at a particular location.

Figure 2.1. The study region extending from Point Conception to Point Mugu and including the four islands that delineate the Santa Barbara Channel (from east to west: Anacapa, Santa Cruz, Santa Rosa, San Miguel). Black dots indicate sites where sampling for parasites occurred (see Chapter 3, Appendix Table 4). Map citation: Google Maps via *ggmap* in R.



2.5 Data sources

Published data sets and species' range boundaries were used to create species lists. The initial list of fishes, algae, and invertebrates was assembled from the Channel Islands National Park Kelp Forest Monitoring program (CINP KFM) and the SBC Long Term Ecological Research program (SBC LTER). I added to these lists using primary literature, technical reports (e.g. NOAA, USFW), personal observations, expert opinion, crowd-sourced observations (e.g. eBird.org), guidebooks, and grey literature. I sampled the local kelp forest zooplankton and the algae-associated small-invertebrate community, because these organisms were not well represented in the literature (see below). Published diet observations, direct observations, and inference were used to determine feeding links.

2.6 General sampling methods

Zooplankton tows

I conducted vertical zooplankton tows within kelp forests at two island locations (on the same date) and two mainland locations (repeated tows, four dates at one site, three of those dates at a second site, including one nighttime sampling date), for eight site by date samples (Appendix Table 2). While the vessel was at anchor within a kelp forest, a 30 cm diameter, 200 micron plankton net was dropped to the bottom and pulled to the surface at a rate of 0.33 m per second. Care was taken not to scrape the net against kelp plants. The collection jar attached to the net was weighted with a small lead weight to ensure that the net did not collect organisms on the way down to the bottom. The depth and time of collection were recorded (Appendix Table 2). Collected organisms were frozen until sorting. All organisms were counted and identified to species when possible, but some groups were identified to

Order or Family, and then cross-checked with lists of known local species. If this was not possible, specimens were assigned to morphospecies, indicating they appeared to be a unique species based on morphology. Representative specimens from each species or morphospecies were photographed and measured.

Benthic substrates

Giant kelp holdfasts were sampled for free-living invertebrates. In the field, holdfast circumference and two slant height measures were taken, as well as basal stipe circumference. A subsample of approximately 25% of the holdfast was collected in a large plastic zip bag and weighed in the lab ($n = 8$). The samples were processed for organisms > 200 microns. All organisms were counted and identified to species or morphospecies when possible. Some groups were identified to Family, and then matched to lists of known local species. Representative specimens from each species or morphospecies were measured.

Taxon-specific methods: Gastropods

Small gastropods are a diverse but overlooked group that lives in benthic turf algae. Algal clumps were collected haphazardly by either laying down a m_2 quadrat and collecting all algae within the quadrat, or by collecting clumps and weighing at the lab. All gastropods were removed by hand under a stereomicroscope, counted, identified to species or morphospecies, measured, and photographed.

2.7 Node list assembly

Species was the preferred taxonomic unit, and life stages were included as separate nodes if that life stage was present in the system and had distinct trophic interactions from the adult stage. I assigned each node a justification code (see below), confidence level, literature reference, and locality of the reference.

Life stages as nodes

Species were partitioned into life-stage nodes (e.g., larva, juvenile, adult) if a species changed its trophic position from one stage to the other. Whether or not a distinct life stage was resident in the kelp forest was indicated by various data sources (e.g. observations of rockfish recruits in surveys). However, some life stages were inferred from species life history. For example, amphipods brood offspring and have crawl-away juveniles. These juveniles remain in the kelp forest (rather than having a pelagic phase), and due to their small size are subject to different predators than adults (e.g. adults are eaten by fishes, while juveniles are eaten by hydroids). This is justification for juvenile amphipods being a distinct node from adult amphipods. On the other hand, many species have planktonic larvae that develop outside of the kelp forest, so only the adult stages were included at the species level. When comparing this food web with others (which rarely separate species into life stages), it is easy to collapse life stage nodes into species nodes.

Justifications for node inclusion

Because food webs based on monitoring data lack many kelp-forest species, I used multiple lines of evidence to justify whether or not to include a node in the food web. Free-living species were included if they were known from the SBC, and were indicated by the data sources described above (e.g. reports, surveys, published papers, guidebooks, expert opinion, etc.). Species lists from regional guidebooks included non kelp-forest species, so these lists were compared with species lists from long-term monitoring surveys. I excluded most rare species (<1% frequency of detection in surveys, or those described as “rare” qualitatively). For instance, if a species listed in a field guide seemed detectable by monitoring groups (e.g. large mid-water fishes), but was not detected in SBC surveys, it was not included in the food web. Exceptions were made for species that are difficult to detect (cryptic species, or species not normally counted) or important even when rare (top predators). For instance, if a species listed in a guidebook was from a group that was not surveyed by monitoring programs in detail (e.g. species resolution of most sponges), inclusion might be based on detection in other literature, consultation with local experts, or personal observations. Larval parasites in prey species were used as evidence for the presence of final-host species (e.g. finding shark tapeworm larvae in a fish indicates a shark is likely present in the system). The justifications for including a node in the food web were included as metadata, as well as the localities of the species observation and references, and then used to determine a categorical confidence score.

Assignment of node confidence

Depending on the evidence for including a node, I rated confidence from 1-4, with 1 being the most confident. Nodes that were observed by monitoring surveys or this study were assigned a confidence value of 1 (62.3% of free-living nodes). Nodes that were known from the SBC through other sources (e.g. guide books, published literature), but that were not reported in surveys were included with a confidence value of 2 (27.8% of free-living nodes). For example, gammarid amphipods were not monitored at the species level in monitoring surveys, but other studies in the region provide lists of species present. Species known from the broader Southern CA bight and with reported ranges north to Point Conception or beyond were included with a confidence value of 3 if they were from a taxonomic group that may not have been sampled effectively by methods utilized in the SBC (5.9% of free-living nodes). This included several sponge species that were not monitored at the species level by monitoring programs. Transient species indicated by expert opinion and crowd-sourced observations, as well as some life stages that were inferred to be present (e.g. juvenile gammarid amphipod species) were also assigned confidence values of 3. Some life stages that were inferred to be present were included with a confidence value of 4 (4% of free-living nodes) because confidence in the adult stage was 2. Readers can use confidence scores to filter their own node list.

Additional Node Metadata

Additional metadata for each node includes species functional group (e.g. predator, herbivore, detritivore, omnivore, autotroph, filter-feeder), taxonomic information (phylum, class, order, family), habitat association (e.g. holdfast, water column, rock surface), small-scale habitat association (e.g. rock, water-column, macroalgae, etc.), body size (in either grams or mm), range, thermal association, and consumer strategy (e.g. autotroph, omnivore, detritivore, filter-feeder, carnivore) were recorded for each node. See Appendix Table 1 for all metadata columns and possible values.

2.8 Link assignment

Given N nodes in the node list, there are N_2 potential feeding links (including cannibalism). Many of these potential feeding interactions are easy to exclude based on logic (e.g., algae don’t eat animals). Because links in previously published kelp-forest food webs contained errors, I constructed links from scratch using primary sources where possible. Where possible, this food web reports links at the stage level, but these links could be aggregated to the species level, or even the group level for comparison with other food webs. Each link was assigned a literature reference, locality of the observation, justification code, and confidence level.

Justifications for link inclusion

Links were assigned using several data sources and logic. A systematic literature review was conducted in Google Scholar to collect diet records for each free-living species (including synonyms) using standardized search terms ("Genus species" [diet* OR feed* OR prey]). If these search terms did not yield results, the search was expanded to records of the species (“Genus species”). I also used direct observations from gut contents. In many cases, diet information was not available at the species level, creating the possibility of false negative links (e.g., failing to report a diet item due to lack of direct observation). To reduce the probability of false negative links, the search was expanded to the next higher taxonomic level where information was available, under the assumption that diets are often taxonomically conserved. Such links were inferred by assessing both the compatibility of the interaction (e.g., body size ratios, diet generality), as well as the probability of encounter between the species. For example, if two species were known to encounter each other through shared habitat and behaviors, and general feeding habits of the consumer were compatible with the resource species, a link was inferred. Parasite presence was also used to infer links between free-living consumers and resources when life cycles of parasites were known. The presence of a trophically transmitted parasite in a host indicates that the intermediate host of the parasite was ingested by that host, so a link between those two hosts would be inferred. For some understudied species, expert opinion was used to inform trophic links. I report the strongest justification code for each link in the food web and all relevant references. For example, if I observed a link directly that was also reported by literature studies, I indicate I used direct observation to justify the link. The references for that link would indicate that it was observed directly in this study and would also list relevant literature. For inferences, I list all references that provide the logical basis for an inference (e.g. descriptions of foraging behavior, diet of related species).

Assignment of confidence levels

Although inferring links from logic reduces the frequency of false negative links, it also increases the possibility of reporting false positive links (reporting links that do not in fact occur). To help indicate confidence, links were assigned a code from 1-4 based on the strength of the justification for the link, with 1 being the most confident, 4 being the least. Links from the literature were assigned a confidence code based on the proximity between SBC and the region where the interaction was observed. Any links indicated by direct observations, or other studies conducted within the SBC were assigned a confidence value of 1. Links indicated by literature conducted within the greater southern California region were assigned a confidence level of 2, if the links were species-specific. Species-specific links in the literature that were from outside southern CA were assigned a confidence value of 3. Some non-species-specific links from within the SBC or southern CA were also assigned a confidence value of 3 if there was evidence that the species involved matched those in this web. Links that were inferred from only a single line of indirect evidence were assigned a confidence level of 4. Therefore, the confidence score should correlate inversely with the probability that a proposed link is a false positive, and indicates where more study is needed.

Additional link metadata

In addition to metadata on locality, literature source, justification, and confidence (Appendix Table 3), I categorize links based on different types of trophic interactions (Table 2.1, Appendix Table 3). For instance, links where a consumer kills the resource were coded as predator-prey interactions, while links where a consumers eats a small portion of a resource individual without killing it (e.g. herbivores) were assigned as grazer-resource (often called micropredator) interactions.

Table 2.1 Types of consumer interactions, following the framework of Lafferty and Kuris 2002. Consumer strategy determined by the number of victims consumed, the fate of the victims consumed, and whether the effect of consumption is intensity dependent.

Trophic Interaction Type	Victim death required?	Victim fitness:	Intensity dependent effect on victim?
Number of victims (per life stage) > 1			
Predation	Yes	0	No
Micropredation / grazing	No	> 0	Yes / No
Number of victims (per life stage) = 1			
Typical parasite	No	> 0	Yes
Trophically transmitted parasite	Yes	0	Yes
Parasitic castration	No	0	No
Pathogen infection	No	> 0	No

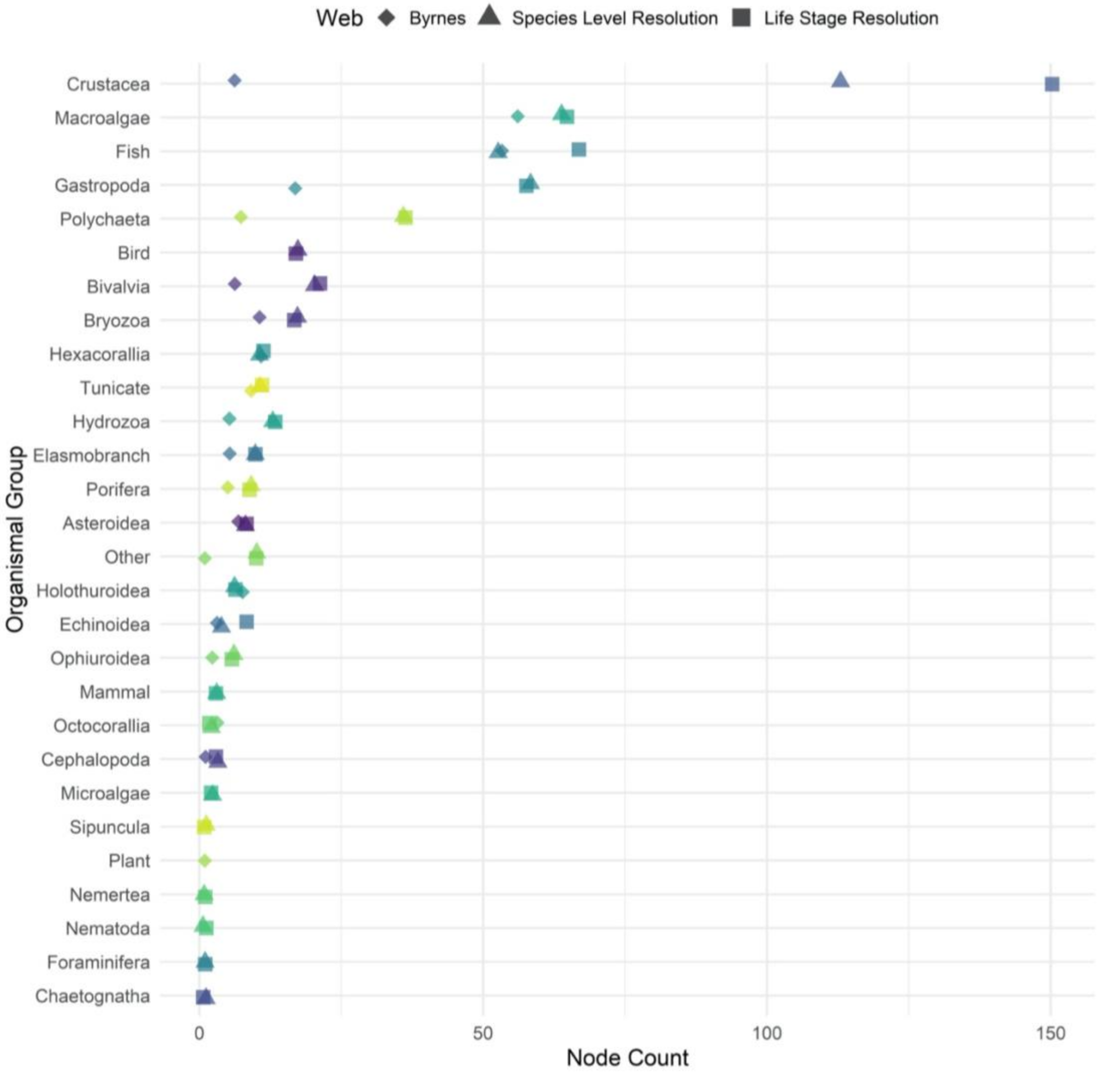
2.9 Summary of food-web enhancements

Resolving the kelp-forest food web for free-living species affected key network metrics, such as network size, link density, connectance, degree distribution, and percentages of top, intermediate, and basal nodes (Table 2.2). Improving resolution of free-living species led to a large increase in food-web richness. Both the species-resolution and life stage-resolution versions of the free-living web were more than twice as large as the Byrnes et al. 2011 web (Table 1). 489 species (546 life stages) were included in the resolved free-living web (217 were included in Byrnes et al. 2011). Improved resolution of small crustaceans and other invertebrate taxa contributed the most to this increase (Figure 2.2). Crustaceans are the richest taxonomic group in the resolved network, with 120 species. Gastropods and polychaetes increased notably as well. In Byrnes et al. 2011 and Graham 2004, macroalgae and fish were richest taxonomic groups. The numbers of species in these groups increased slightly with increased resolution (Figure 2.2), but their relative contributions to overall food-web richness decreased as other taxonomic groups were resolved. Rather than being comprised of mostly fish and macroalgae, the resolved free-living food web shows the kelp forest as a more diverse assemblage of organisms, with crustaceans as the most species-rich group.

Table 2.2 Commonly reported food-web metrics for the fully resolved life-stage web, the resolved web aggregated to taxonomic species, and the Byrnes et al. 2011 food web (data provided by SBC LTER). Trophic level is prey-averaged trophic level. All metrics were calculated in R Version 3.6.2 with packages *igraph* (Csardi and Nepusz 2006), *NetIndices* (Kones et al. 2009), and *cheddar* (Hudson et al. 2013).

Resolution	Byrnes	Species	Life Stages
Assembly	Free-living (FL)	Free-living (FL)	Free-living (FL)
Nodes	217	490	546
Links	1807	8353	8759
Link Density	8.33	17.05	16.04
Connectance	0.038	0.035	0.029
Mean Tropic Level	1.58	2.82	2.79
Max Trophic Level	3.74	4.95	4.97
Mean Shortest Path	2.56	2.86	3.03
Longest Chain	9	9	9
Transitivity	0.12	0.12	0.09
Mean Degree	16.59	34.09	32.08
SD Degree	16.08	29.21	27.24
Mean Generality	8.29	17.05	16.04
SD Generality	15.60	18.88	23.01
Mean Vulnerability	8.29	17.05	16.04
SD Vulnerability	6.56	24.09	17.91
% Top Nodes	0.46	6.12	5.49
% Intermediate Nodes	39.17	78.78	80.77
% Basal Nodes	60.37	15.10	13.74
% Cannibalistic Nodes	5.99	5.51	2.75
% Omnivorous Nodes	24.88	65.71	62.82

Figure 2.2 Numbers of nodes in each organismal group in the life-stage web (squares), the web aggregated to taxonomic species (triangle), and the Byrnes et al. 2011 food web (diamonds, data provided by SBC LTER).



2.10 Limitations and potential enhancements

I restricted my definition of kelp forests to rocky reef habitat, but kelp forests can have sand channels throughout and are often surrounded by sand. For this reason, I included sand-dwelling species that are known to associate with kelp forests specifically, however I did not include the sand community in general, even though this habitat is often interspersed and adjacent to the kelp forest. Once a subtidal sandy food web has been created, it should be easy to connect kelp forest and sand-associated food webs.

Although the food web separates distinct life stages into separate nodes, it does not include multiple sizes classes for each species. Changes in diet associated with size are common across fishes and could alter network structure. Additional resolution could be added to the web by including size classes for species that experience strong ontogenetic shifts in diet.

It might be possible to assign interaction strengths to links with allometric scaling or experimental work, or to model how different interaction strengths would affect the network. The body size information in the nodes makes that possible for others to pursue. Furthermore, site-specific densities are available for > 200 organisms surveyed by CINP KFM and SBC LTER. Adding this information, and perhaps inferring densities for other taxa based on allometric scaling might make it possible to use this food web for dynamic modeling.

Although this food web improves resolution for many groups of organisms (including crustaceans, gastropods, invertebrates, birds, cryptic fishes), it was not able to capture all species or links. This is a commonly cited criticism of food webs, in particular large networks (e.g., Paine 1988, Polis 1991, Hall and Raffaelli 1993, Winemiller and Polis 1996, Goldwasser and Roughgarden 1997). I attempted to minimize this by using information from many sources, inferring links, and constructing a web that was cumulative over space and time. I did not attempt to resolve other potentially important taxa like protozoa (ciliates, flagellates, etc.), diatoms, and other microbes (viruses/bacteria/fungi). Nodes such as small particles of detritus represent their own complex systems that surely deserve future study. Additional sampling would be expected to further increase network size and complexity.

3. Parasitic web

3.1 Introduction

After improving the resolution of free-living species in the kelp-forest food web, I sought to resolve the parasites. Although ubiquitous in food webs (Lafferty et al. 2008), parasites are even less considered in food-web studies than free-living invertebrates, and only a few food webs report parasites (McLaughlin et al. 2020). The process for adding parasites to a food web is distinct from adding free-living taxa. As a starting point, I used the resolved free-living node list as a potential a host list. From that potential host list, I assembled a node list of known parasites, by life stage, from the literature, augmented by extensive field sampling. Parasite information and consumer strategy was recorded for each parasite life stage. From these two node lists, I created a bipartite host-parasite matrix. I assigned host-parasite links in the matrix (0,1) using published records, direct observations, or inference. Many host-parasite links are “forbidden” based on taxonomic mismatches (e.g. shark tapeworms do not infect sponges), and such links were assigned 0 with confidence. Other host-parasite links are inferable. For instance, many parasites are transmitted through feeding interactions of free-living species, so I used feeding links in the free-living web to infer likely hosts of trophically transmitted parasites that were sufficiently generalist that links were likely determined by diets. I used presence in other hosts and species natural history to infer likely hosts of directly transmitted generalist parasites. Many host species had never been dissected for most parasite groups, and if reported, most host species had not been well sampled for parasites. Thus, many likely host-parasite links had not been directly observed (false negatives). I therefore estimated the prior probability of false negative links for fishes, birds, mammals, and elasmobranchs using a generalized logistic regression and, where possible, by generating a posterior estimate using Bayes' theorem. I documented all nodes and links with a justification for inclusion, confidence, reference, and locality of the observation, which enables investigators to filter their own node and link list. Finally, after constructing the bipartite host-parasite network, I created an additional bipartite network of interactions between predators and parasites (Lafferty et al. 2006) to capture links representing concomitant mortality of parasites when ingested by non-host species. This assumed that predators consumed the parasites of their prey. Parasite-parasite links were not observed, and therefore not entered, though there could be as yet unobserved interactions among trematode parthinitae (asexual larval stages) that share the same molluscan host. Adding parasites to the kelp-forest food web makes it the most specious food web to date.

3.2 Research motivation

Giant kelp forests have not traditionally been studied in the context of parasitic interactions. Host diversity begets parasites diversity (Hechinger and Lafferty 2005), and healthy ecosystems support rich parasite species that in turn have unique roles in ecosystems (Hudson et al. 2006). It follows that the diverse free-living species and trophic interactions in kelp forests should support diverse parasites and complex life cycles, and in fact many parasite species are known from kelp-forest fish species (e.g., Love and Moser 1983). Parasites are both diverse and well connected, and therefore can substantially enrich food-web links (Lafferty et al. 2006). Even in a well-studied system like the kelp forest, our understanding of the food web is limited until we incorporate parasites.

As consumers, parasites likely play roles similar to predators in kelp forests. Sea otters are a keystone predator in North-East Pacific kelp forests (Estes and Palmisano 1974) and are showing signs of recovery in southern California (Lafferty and Tinker 2014), impeded by white shark recovery (Tinker et al. 2016). In parallel, heavy parasite loads have caused some cases of sea otter mortality (Mayer et al. 2003, Shanebeck et al. 2020), so parasites in southern California kelp forests may influence reestablishment of this species in the food web. More notably, iconic kelp forest species like abalone have suffered mass mortalities from infectious agents (Lafferty and Kuris 1993, Altstatt et al. 1996). Parasites can also regulate the abundance of important species in food webs. Sea urchins, for instance, experience density-dependent regulation from infectious disease when their predators are fished to low abundance (Lafferty 2004). Furthermore, parasites can alter predator-prey interactions in particular ways. Infection with trophically transmitted parasites can sometimes make prey more likely to be eaten by predators (Bethel et al. 1977, Lafferty and Morris 1996). It seems likely that parasites affect food-web dynamics as well as topology.

Food webs affect parasites by affecting host population dynamics and providing pathways for transmission. Marine food webs are altered by fishing, which reduces parasite abundance and diversity by altering host age structure, host density, and food-web complexity (Lafferty 2004, Wood et al. 2010, Wood et al. 2013, Wood et al. 2014). Biomass of targeted species in the northern Channel Islands has increased with the establishment of an MPA network (Caselle et al. 2015), so parasite densities may have also increased in protected areas (e.g. Wood et al. 2013). For instance, giant sea bass are showing signs of recovery in the SBC (House et al. 2016). These large top predators could alter parasite dynamics by serving as final hosts for parasites of fishes and a dead-end host for parasites of birds, mammals, and elasmobranchs. Putting parasites into food webs can help predict changes in disease dynamics. Food webs provide opportunities for parasites and are in turn affected by those opportunities.

3.3 Objective

Provide a high-resolution bipartite host-parasite and predator-parasite networks for Santa Barbara Channel kelp forests.

3.4 System description

Chapter 2 describes the study habitat and free-living food web. In this chapter, “parasites” are consumers which fit the seven types of parasitism defined by Lafferty and Kuris (2002). Commensal and mutualist organisms were also recorded. To maintain parity with the free-living web, I limited the parasite species list to metazoan species that use kelp-forest species as hosts for at least one stage in their life cycle. Bacterial, viral, fungal, and protozoan pathogens that are important in kelp-forest food webs merit inclusion in further work.

3.5 Data sources

Published literature and host-parasite databases were used to create lists of host-parasite associations. A systematic review was conducted to collect parasite records for each free-living species. I searched the Natural History Museum of London host-parasite database, the FishPest database (Strona and Lafferty 2012), WoRMs, BIOSIS citation index, and Google scholar (Genus + species + parasit*, expanded to Genus + parasit* if no records were found). For each host species, I recorded the number of records found in BIOSIS and NHM as an estimate of study effort. Although parasites are often reported at the host and parasite species level, I was often able to infer parasite and host life stages based on knowledge about life cycles. I added to these lists by sampling local fish and invertebrates, with a focus on hosts that were common in the system and not well-studied. As for any food-web study, I was most interested in including common or important parasites, rather than rarities.

3.6 Host collections

I collected fish and invertebrates and dissected them for parasites, with the goal of identifying the most common parasites in the food web. I targeted host groups that are known to transmit trophically transmitted parasites in other systems. I collected most organisms from mainland sites, and sampled opportunistically at sites on Anacapa, Santa Cruz, and Santa Rosa islands (Figure 2.1, Appendix Table 4). See Appendix Table 5 for a list of all species dissected and sample sizes.

Fish collections

I prioritized collecting the most common and abundant fish species based on survey data from 2000-2014 (SBC LTER), as well as personal observation, expert opinion, and amount of parasite data in the literature. Other species (lower abundance or higher past study effort) were collected opportunistically. Fish were collected primarily by spear on SCUBA. Specific size classes were not targeted and the spear tips used were appropriate for the focal species. Small benthic fish were collected using dip nets. All fish were collected under UCSB IACUC protocol 549.2. Fish were either stored on ice and processed within 24 hours of collection or frozen until processing.

Invertebrate collections

Invertebrates are necessary intermediate hosts in many parasite life cycles, but relatively few parasite life cycles have been described in marine environments. I targeted invertebrate species that were abundant and potentially important as intermediate hosts for parasites. I did not collect sessile colonial taxa, such as hydroids, gorgonians, sponges, and tunicates, as they were not expected to be hosts for trophically transmitted parasites (but they do merit further study). Most sampled invertebrates were gastropods and small crustaceans, as they host trophically transmitted parasites in other food webs. Bivalves, large crustaceans, echinoderms, and polychaetes were also dissected. Large invertebrates were collected by hand or using a rock chisel and scraper when appropriate. Small invertebrates were sampled by collecting benthic substrates in plastic or fine mesh bags and removing organisms in the lab. Invertebrates were held live in flow-through seawater until the time of dissection or frozen until processing.

3.7 Parasitological assessment

For each host dissection, the exterior and all internal soft tissues were examined for parasite life stages. Small crustaceans and soft-bodied invertebrates were squashed whole. For larger species, entire host organs were usually searched by pressing soft tissues thin between two glass plates and examining with a stereomicroscope. However, to increase sample size, bilaterally symmetric organs (e.g. gills) were examined from one randomly determined side, and large organs (e.g. muscle, liver) were subsampled in larger fishes. I identified gut contents where feasible to improve host diet data and inform parasite life cycles. I recorded host mass, length (or other species-appropriate measurement), collection method, and host condition at time of dissection (e.g. frozen, fresh). I counted and identified all parasites to the lowest possible taxonomic level and assigned a morphospecies code when species-level identification was not possible. Only a few putative parasites were excluded from additional analysis because they had no identifying features.

3.8 Node list assembly

Parasite life stages were included as separate nodes, and species was the preferred taxonomic unit. Each node was assigned a justification code, a confidence level, a literature reference, and locality for the reference. Additional node metadata includes site on host (ecto-vs. endoparasite), taxonomic information, and life cycle information (see below).

Life stages as nodes

Parasites with complex life cycles infect different host species at each stage. Parasite life stages were either indicated by various data sources (e.g. dissections, published records), or were inferred using trophic interactions in the free-living web. Larval stages were added as nodes if there was no feasible alternative for the focal host to become infected. I assumed that kelp-forest resident hosts became infected through life cycle stages found within the kelp-forest food web, but that transient hosts could have acquired some parasites outside the kelp forest (e.g., if intermediate hosts were not known from the kelp forest). For some parasites, there was insufficient data on host or parasite life history to infer larval stages. Metadata in the node list indicates whether parasites have additional life cycle stages inside the kelp forest, outside, or unknown.

Justification for node inclusion

Parasites are not as well studied as free-living species, so I used parasite-host records from San Luis Obispo, California to Punta San Hipolito, Baja California, Mexico, corresponding to the dominant biotic province of the SBC. I excluded parasites from outside this range or those known to have freshwater life cycles, as well as ectoparasites of birds. I made exceptions for parasites with additional evidence of presence (such as a larval stage found locally, or a local occurrence in another host species), and for those with transient and wide-ranging hosts. For example, if an adult digene was observed in pelicans in Florida, but larval stages of this worm had been observed in the Carpinteria Salt Marsh, the worm was included. I extended the northern range of acceptable parasite records to San Francisco Bay, California for hosts that were known to migrate between northern and southern California regularly (several species of elasmobranchs, birds, and mammals). This also helped account for the relatively low study effort for these hosts in southern California. Appendix Table 6 lists taxa for which geographic records were expanded.

Assignment of node confidence

I assigned confidence in parasitic presence based on justification for inclusion, location of the observation, collection habitat of host species, known parasite range, and when available, parasite prevalence. I rated confidence from 1-4, with 1 being the most confident the parasite is present in the SBC. Parasites that were observed in this study were assigned a confidence value of 1 (43.4 % of parasite nodes). Parasites that were known from kelp forests within the SBC through other sources (e.g. databases, literature) were included with a confidence value of 2 (38.2% of parasite nodes). Parasites not reported from the SBC, but known from the broader Southern CA bight and with reported ranges north to Point Conception were included with a confidence value of 3 (11.1% of parasite nodes). Nodes that were thought to be present through any of the above lines of evidence, but were observed north of Point Conception or outside the greater southern California region were assigned a confidence level of 4 (7.3% of parasite nodes). I also assigned a confidence level of 4 to nodes whose presence in the kelp forest was less certain due to host transience. Inferred life stages were assigned a confidence of 3 or 4, depending on the evidence for the life-stage presence. Parasites are sometimes mis-identified in published records, so, to avoid false positives, I excluded some parasites on the basis of questionable identifications. These were typically parasites that were only known from one host specimen in one local study but were known from an entirely different group of host organisms in a distant locality.

3.9 Link assignment

A subset of free-living species are possible hosts for each life stage and taxonomic group of parasites (e.g. adult tapeworms in the order Trypanorhyncha can only infect elasmobranchs). Parasite-host records in the literature are incomplete lists, so I inferred additional links using species life histories and logic. Parasites can also be killed by free-living species when their hosts are eaten (concomitant predation). I used free-living trophic interactions to infer these feeding links between free-living consumer and parasite. Each link was assigned a justification code, a confidence level, a reference, and locality as a column of metadata.

Justification of links

Links between parasites and hosts were assigned using several data sources, as in the free-living web. Direct observations of parasite-host interactions through our sampling or published studies were assigned. However, direct observation of all possible interactions was unfeasible and sampling effort varied among hosts, so parasite-host interactions are often under-sampled. To account for this, links between parasites and hosts were added in stages using the free-living web, host life history, and parasite life history. First, parasite life cycles were inferred based off of known hosts and host trophic interactions. Trophic interactions among free-living species were then used to infer either transmission of parasites to additional hosts or concomitant predation if parasites were not ingested by suitable hosts. Each link is identified by a code that indicates whether it was observed directly (and the source), or whether it was inferred (and the method of inference, described below). Users of the food web can choose to filter links by link justification to suit their needs.

Life cycle inference

I used several data sources and considered parasite life histories to assign links with likely hosts. If the life cycle was known for the parasite in another system, I inferred links with analogous hosts in the system (a kelp forest species in the same genus or family). For trophically transmitted parasites, I assessed parasite compatibility with potential hosts, and used free-living trophic interactions to determine whether a parasite would encounter a suitable host. For species with unknown life histories, I considered the life history of the next lowest taxonomic grouping and assumed generalism within that level. For example, the digene *Podocotyle californica* has an unknown life cycle, but *Podocotyle enophrysi* is known to infect the snail *Lacuna marmorata* as its first intermediate host (Ching 1991). Digenes are host-specific at this stage, and *Lacuna unifasciata* was the only analogous host species in kelp-forest food web, so it was assigned as the most-likely intermediate host for *Podocotyle californica*. On the other hand, marine acanthocephalans are thought to be generalists at the ordinal level in the first intermediate host (Marcogliese, pers. comm.) and are trophically transmitted. Although a second intermediate host is not necessarily required for development, acanthocephalans of top predators often use fishes as paratenic hosts. In my dissections, fishes were often infected with larval acanthocephalans of birds and mammals, so I assigned amphipod species eaten by infected fish as possible first intermediate hosts. For the 15% of the nodes where a parasite from the dissections could not be identified to family, those without a clear possible host in the kelp forest, or those where nothing was known of the parasite's life history, I did not make any inferences based on life cycle. Such parasites appear as specialists in the data (but see the false-negative assessment below).

Parasite-host inference

The number of parasite species detected is often a function of study effort (Poulin 1997). Because study effort varied among hosts, and was sometimes low, I assigned additional parasite-host links based on expected host compatibility and potential for encounter with infectious stages of parasites. I based compatibility on the host-specificity, known hosts in the system, as well as the life stage of the parasite (e.g. adult tapeworms do not survive if their host is eaten, whereas juvenile tapeworms can infect repeated paratenic hosts and remain viable). Encounter with trophically transmitted parasites occurs through host diet (i.e. are intermediate hosts eaten as prey) and was informed using the free-living food web and life-cycle inferences as described above. Encounter with directly transmitted parasites occurs through shared habitat or contact with other hosts and was informed by other parasite-host records. For example, if a monogene was reported from 15 rockfish species in British Columbia and observed in two species locally, it was assumed to infect other rockfish species present in the SBC kelp-forest food web.

Predator-parasite interactions

Host death is a major source of parasite mortality and may strongly influence parasite-host dynamics. I inferred these predator-parasite interactions using trophic interactions between free-living species. For each free-living consumer interaction, I assessed whether the parasites of the prey host would be killed or transmitted to the predator. If the predator was not a compatible host (see discussion above), I assigned a consumptive link between the free-living consumer and parasite.

Assigning link confidence

Because inferred links could be false positives (reporting a link that does not occur), I treated them as predictions with variable levels of confidence. To indicate confidence in inferred link assignments, I assigned a categorical code from 1-4 based on the strength of evidence for the link (1 being the most confident, 4 being the least). Interactions observed directly in dissections or in literature conducted within the SBC were assigned a confidence value of 1. Interactions known from the literature within the Southern CA Bight were assigned a confidence level of 2. Non-local interactions (but still within the range limits for inclusion) that occurred between species found in our lists were assigned a confidence of 3. Interactions that lacked locality or reference information were assigned a confidence level of 4. When inferred host-parasite links were based on information from inferred predator-prey links, confidence values were set to the lowest confidence value of the information that led to the inference. For example, if an adult trematode infected kelp rockfish with confidence level 3, and leopard sharks ate kelp rockfish with confidence level 2, a concomitant mortality link (predator-parasite) was assigned between the leopard shark and the trematode with confidence level 3.

False negative estimation

Even though many unobserved host-parasite links were inferred to occur based on logic, under-sampling leads to the potential for other false negative links. Such links are particularly likely for generalist parasites that have low prevalence in under-sampled hosts. For instance, if a metacercaria species infects any rockfish species at 5% prevalence, and I sample ten individuals from each of ten rockfish species, I can expect by chance to observe the parasite in only six of the ten species. The remaining four rockfish species might appear to be uninfectable by the parasite, but, assigning 0s in the bipartite host-parasite network would result in false negative links. False negative links make parasites look more like specialists than they actually are, thereby underestimating their importance in food-web measures such as generality, vulnerability, linkage density, and connectance. I estimated false-negative probabilities for unobserved links at the species level and individual host level (I assumed the probability of a false positive observation was low enough to be ignored unless noted). I applied this approach separately to the following bipartite networks: trophically transmitted parasite-fish, directly transmitted parasite-fish, parasite-shark, parasite-bird, and parasite-mammal.

The first step to estimating a false negative probability is to calculate a statistical expectation that a parasite group infects a host group. At the node-level, I used a generalized linear model with observed or inferred link (0,1) as a dependent variable and taxonomic information (host order, host family, parasite order, parasite family, parasite species), host trophic level (calculated from the free-living web), host habitat association, and proportion of the host diet that may contain infective stages as independent variables. Because false negatives arising from under-sampling are common in the parasitological literature (Poulin

1997), I included a square-root transformed sampling effort term (the number of parasite studies on the host in the literature). Model selection was based on AIC, and found that host and parasite taxonomy and traits helped predict links (see Table 3.1) for model results of each network). The interaction between host order and parasite family was important in all bipartite networks, indicating parasite specialization. Study effort was less important in sub networks with higher sampling effort across hosts. From the best-fitting model, I generated predicted probabilities for each link between species *i* and *j*, at existing effort $\hat{\psi}_{ij}$. I then assumed that with increasing effort, the probability that a link was observed $\hat{\psi}_{ij}$ approached the probability that the link exists Ψ_{ij}. Then, by parameterizing the prediction equation with a hypothetical "high" effort (see Table 3.1) for values for each bipartite network), I projected the probability that a link exists $\widehat{\Psi}_{ij}$. According to Baye's Theorem, the probability of a false negative F_{ij}, is:

$$\mathbb{P}(\Psi_{ij} = 1 \;\&\; \psi_{ij} = 0)/\mathbb{P}(\psi_{ij} = 0)$$

Which translates to:

$$F_{ij} = (\widehat{\Psi}_{ij} - \hat{\psi}_{ij})/(1 - \hat{\psi}_{ij})$$

Which is a first approximation for the probability of a false negative link based on species-level data. Namely, the more likely a link occurs based on taxonomy and traits, and the less likely it is to be sampled with existing effort, the more likely an unobserved link is a false negative link due to insufficient sampling effort. I therefore estimated $\widehat{\Psi}_{ij}$ (and its standard error) and $\hat{F}_{ij}$ from data at the species level.

Table 3.1 Generalized linear models used in false negative estimation. Separate models were constructed for each of the following bipartite networks: parasite-mammal, parasite-bird, parasite-shark, trophically transmitted parasite-fish, and directly transmitted parasite-fish.

	Mammals				Birds				Sharks			
	Nparm	*df*	$Wald\ \chi^2$	$p > \chi^2$	*Nparm*	*df*	$Wald\ \chi^2$	$p > \chi^2$	*Nparm*	*df*	$Wald\ \chi^2$	$p > \chi^2$
Host Order x Parasite Family	14	4	39.46	<0.0001	44	27	435.9	<0.0001	210	59	463.98	<0.0001
Host Family [Host Order]												
Host Order	1	1	15.05	0.0001	4	3	37.56	<0.0001	6	2	11.32	0.0035
Parasite Family	14	5	31.89	<0.0001	11	11	176.832	<0.0001	35	13	11.53	0.567
Host Habitat												
Parasite Node [Parasite Family]					14	7	131.3	<0.0001				
Host Trophic Level									1	1	12.99	0.0003
Proportion of diet that could transmit parasite												
√(Study Effort)	1	1	2.21	0.1369	1	1	14.46	0.0001	1	1	5.7	0.017
AICc	106.1				297				538.7			
Generalized R^2	0.516				0.593				0.504			
N rows	87				442				710			
Hypothetical max effort	75				40				10			

	Fish - Trophic Transmission				Fish - Direct Transmission			
	Nparm	*df*	$Wald\ \chi^2$	$p > \chi^2$	*Nparm*	*df*	$Wald\ \chi^2$	$p > \chi^2$
Host Order x Parasite Family	301	74	846.33	<0.0001	252	54	320.85	<0.0001
Host Family [Host Order]	17	14	325.96	<0.0001	18	12	322.91	<0.0001
Host Order	7	3	231.76	<0.0001	6	2	145.09	<0.0001
Parasite Family	43	11	221.6	<0.0001	42	4	93.61	<0.0001
Host Habitat	5	5	165.39	<0.0001	6	5	58.13	<0.0001
Parasite Node [Parasite Family]	105	42	246.15	<0.0001	117	26	213.53	<0.0001
Host Trophic Level	1	1	101.73	<0.0001	1	1	38.31	<0.0001
Proportion of diet that could transmit parasite	1	1	15.86	<0.0001				
√(Study Effort)	1	1	10.45	0.0012	1	1	72.79	<0.0001
AICc	2793				2625			
Generalized R^2	0.346				0.247			
N rows	10132				10720			
Hypothetical max effort	10				10			

I also had individual-level data for many potential links, making it possible to refine the estimate for $\hat{F}_{ij}$ based on dissections. Now, Bayes' Theorem translates to:

$$\hat{F}_{ij} = \hat{\Psi}_{ij}(1 - \hat{d}_{ij})/(1 - \hat{d}_{ij}\,\hat{\Psi}_{ij})$$

Where $\hat{\Psi}_{ij}$ is estimated as above from the species-level data and is $\hat{d}_{ij}$ link detectability (the probability of detecting a link in a sample if that link occurs). $\hat{d}_{ij}$ can be estimated from individual-level data (e.g., several dissected host individuals). In a host species *j* that is known to be infected by a parasite species *i*, the probability d_{ij} of finding an infected individual after dissecting *K* hosts is akin to a series of *K* independent Bernoulli trials, each with a probability of detecting a parasite in a host equal to the parasite's prevalence in the host population, p_{ij}.

$$\hat{d}_{ij} = 1 - (1 - p_{ij})^{\mathrm{K}_j}$$

In the case of a host species where a parasite species *i* has never been detected, the parasite's detectability in dissections is also akin to a series of *K* independent Bernoulli trials, but the parasite's prevalence in the host population must be estimated from infectable hosts. The simplest assumption is that infectable species do not differ in prevalence, so that $\hat{p}_{ij}$ is just the number of individual parasitized hosts $(\sum_{j=1}^{m} i)$ found in combined samples from those host species that are infectable by parasite species i. E.g., $p_{ij}|\Psi_{ij} = 1$,

$$= \frac{\sum_{j=1}^{m} i}{\sum_{j=1}^{m} \Psi_{ij} K_{ij}}$$

Which I estimated as

$$\hat{p}_{ij} = \frac{\sum_{j=1}^{m} i}{\sum_{j=1}^{m} \psi_{ij} K_{ij}}$$

Although there are more complicated ways to estimate prevalence that take into account individual host traits, and biases from excluding infectable hosts where infections have not been detected, the simple method was sufficient to distinguish between likely and unlikely false negatives. Thus, to recap, I estimated $\widehat{\Psi}_{ij}$ using species-level data as above, then further refined the estimate of $\widehat{F}_{ij}$ from dissection data. I used error propagation to report 95% Confidence limits.

With information about $\widehat{F}_{ij}$, I estimated unseen links as probabilities, rather than as 0s (observed links were set to 1, and unobserved links were set to $\widehat{F}_{ij}$). Doing so identified some likely parasite links that were missed. In this case, when the probability of a false negative was > 0.5, I assumed that an unobserved link actually occurred unless clearly contradicted by species life history (but noted the probability of a false positive link = 1 - $\hat{F}_{ij}$). I also identified those host and parasite species that generated substantial error in the network. To keep the overall error rate to < 4%, I therefore removed error-prone species from the network (Table 3.2). These species were typically rare generalists that were easily missed in dissections. I report these removed species and their known links in Appendix Table 6 as potentially useful information for other purposes. Finally, I used the false-negative estimates to correct for biases in network and species-level measures like generality, connectance, and linkage density.

Table 3.2 Parasite species removed from network due to high error in false negative predictions. All species were known from either dissections or published records but tended to be rare generalists or singular observations.

Bipartite network	Phylum	Class	Genus	Species	Stage	Links	Footnotes
Fish - Trophic Transmission	Platyhelminthes	Trematoda	*Derogenes*	*varicus*	adult	3	
Fish - Trophic Transmission	Nematoda	Rhabdita	*Dichelyne*	*kanabus*	adult	7	*1*
Fish - Direct Transmission	Arthropoda	Malacostraca	*Nerocila*	*californica*	adult	8	
Fish - Direct Transmission	Arthropoda	Hexanauplia	*Caligus*	*hobsoni*	adult	12	
Fish - Direct Transmission	Arthropoda	Hexanauplia	*Caligidae.gen*	*spp.*	adult	8	*2*
Fish - Direct Transmission	Platyhelminthes	Monogenea	*Megalocotyle*	*marginata*	adult	6	*3*
Fish - Direct Transmission	Arthropoda	Hexanauplia	*Lernaeopodidae.gen*	sp.A	adult	1	
Fish - Direct Transmission	Arthropoda	Hexanauplia	*Lernaeopodidae.gen*	sp.B	adult	1	
Fish - Direct Transmission	Arthropoda	Ichthyostraca	*Argulus*	*pugettensis*	adult	6	*4*
Fish - Direct Transmission	Arthropoda	Hexanauplia	*Chondracanthus*	*pinguis*	adult	5	*5*
Mammals	Platyhelminthes	Cestoda	*Adenocephalus*	*pacificus*	adult	1	
Birds	Platyhelminthes	Trematoda	*Himasthla*	sp.	adult	3	
Birds	Acanthocephala	Palaeacanthocephala	*Southwellina*	*hispida*	adult	5	
Birds	Platyhelminthes	Trematoda	*Philophthalmus*	*andersoni*	adult	2	
Birds	Platyhelminthes	Trematoda	*Maritrema*	*pacificum*	adult	1	
Birds	Platyhelminthes	Trematoda	*Microphallus*	*nicolli*	adult	1	
Sharks	Arthropoda	Hexanauplia	*Nemesis*	*carchariaeglauci*	adult	1	
Sharks	Nematoda	Rhabdita	*Anisakis*	*simplex sp. complex*	juvenile	1	6
Sharks	Arthropoda	Hexanauplia	*Pandarus*	*cranchii*	adult	1	

1. Different Dichelyne species found very commonly in same host species in our dissections.

2. Links assigned to species node.

3. Most records from North Pacific Rockfish. High number of false negatives. Only known from Olive rockfish in southern CA (Love 1984), found in less than 10% of hosts in that study.

4. Most records from far North (Puget Sound, BC). High false negatives. Only records from S CA were very old (1912-1932) in species that have been regularly sampled since then.

5. Most records from NE Pacific rockfish. 1 instance in southern CA but <1% of individuals (Love 1984).

6. Only removed from shark bipartite network.

Additional link metadata

To allow analysis of the contributions of different types of trophic interactions to the food web, I specified the interaction type for each consumer-resource link following the framework of Lafferty and Kuris 2002 (Table 2.1). The free-living web contained predation and micropredation/grazing links. Some organisms typically referred to as “parasites” fit the definition of micropredation (e.g. gnathiid isopods). Several more types of interactions are possible between symbiotic organisms and their hosts, depending on transmission strategy (trophic transmission or direct transmission), effects on host fitness, and reproduction method (within the host or in the environment). Metadata in the node list (such as site of infection, Appendix Table 1) allows investigators to simplify these link types according to research questions of interest.

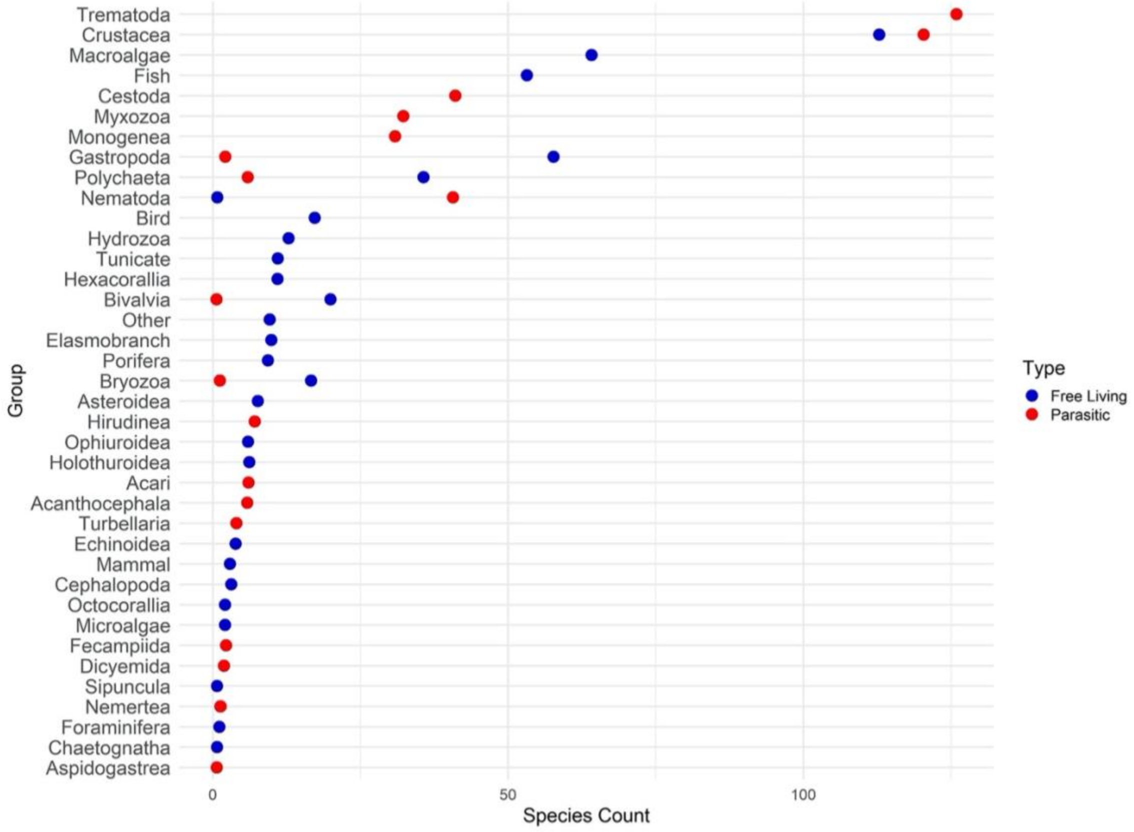
3.10 Summary of web enhancements

Parasitic species contributed substantial taxonomic diversity to the food web and affected commonly reported network metrics (Table 3.3). The resolved predator-prey web had 490 free-living species (546 life stages), and parasites added an additional 422 species (521 life stages), comprising 46.2% of species. Platyhelminthes added the most parasitic species overall, and trematodes were the most diverse group, with 126 species (Figure 3.1). Parasitic crustaceans (mostly copepods) were the second most diverse group, with more parasitic crustaceans than free-living crustaceans (120 vs. 113 respectively), and bringing the total crustacean count up to 233. Nematodes, cestodes, myxozoans, and monogenes were the next most diverse groups, contributing 41, 41, 32, and 31 species respectively. This was on par with free-living polychaetes and bivalves (37 and 20 species, respectively). There were more parasitic (myxozoans) than free-living cnidarians (32 vs. 26, respectively). The kelp-forest taxa became dominated by helminths and crustaceans when parasites were included.

Table 3.3 Commonly reported food-web metrics for the food web with and without parasites, at either species or life-stage resolution. Trophic level is prey averaged trophic level and was calculated without concomitant links. All metrics were calculated in R Version 3.6.2 with packages *igraph* (Csardi and Nepusz 2006), *NetIndices* (Kones et al. 2009), and *cheddar* (Hudson et al. 2013).

Resolution	Species			Life Stages		
Assembly	Free-living (FL)	FL + Parasites, no concomitant	FL + Parasites and concomitant	Free-living (FL)	FL + Parasites, no concomitant	FL + Parasites and concomitant
Nodes	490	912	912	546	1067	1067
Links	8353	10964	19718	8759	11504	21040
Link Density	17.05	12.02	21.62	16.04	10.78	19.72
Connectance	0.035	0.013	0.024	0.03	0.01	0.02
Mean Tropic Level	2.82	3.77	3.77	2.79	3.73	3.73
Max Trophic Level	4.95	5.92	5.92	4.97	5.93	5.93
Mean Shortest Path	2.86	3.11	3.01	3.03	3.27	3.28
Longest Chain	9	10	7	9	10	9
Transitivity	0.12	0.14	0.14	0.09	0.09	0.10
Mean Degree	34.09	24.04	43.24	32.08	21.56	39.50
SD Degree	29.21	32.64	55.79	27.24	29.62	52.32
Mean Generality	17.05	12.02	21.62	16.04	10.78	19.75
SD Generality	18.88	19.73	21.90	23.01	19.03	46.14
Mean Vulnerability	17.05	12.02	21.62	16.04	10.78	19.75
SD Vulnerability	24.09	21.10	47.69	17.91	18.05	18.78
% Top Nodes	6.12	46.93	4.25	5.49	49.30	4.40
% Intermediate Nodes	78.78	45.18	87.35	80.77	43.77	88.66
% Basal Nodes	15.10	7.89	8.40	13.74	6.94	6.94
% Cannibalistic Nodes	5.51	2.96	2.94	2.75	1.41	1.41
% Omnivorous Nodes	65.71	59.65	59.32	62.82	56.51	56.51

Figure 3.1 Species contributions by organismal group in the food web with parasites. Blue circles indicate the number of free-living species in that group, red indicates the number of parasites.



The number of links in the food web more than doubled when parasites were included along with concomitant links (Table 3.3). In the life-stage web, the predator-prey subweb was 41.5% of links, the predator-parasite subweb was 45.3% of links, and parasite-host subweb was 13.0% of links. In the species-level web, the predator-prey subweb was 42.3% of links, the predator-parasite subweb was 44.3% of links, and 13.2% of links were parasite-host links (Figure 3.2).

Figure 3.2 Number of links in each subweb (predator-prey, parasite-host, and predator-parasite) in the species-level food web.

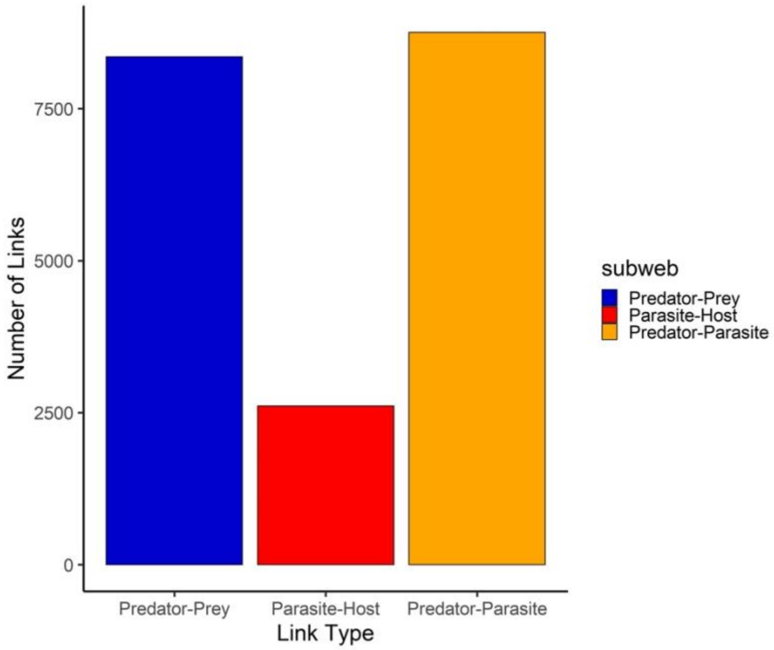
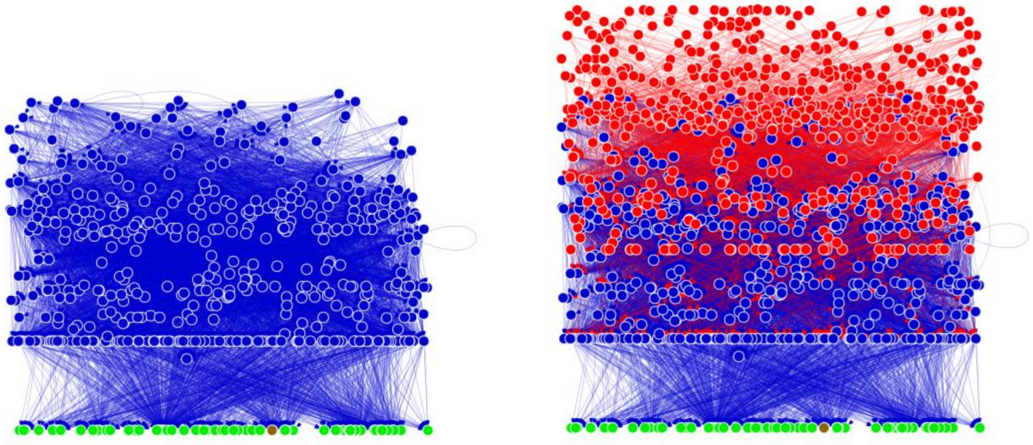


Figure 3.3 Life-stage food web without and with parasites, scaled according to prey-averaged trophic level. Concomitant links not shown. Blue nodes are free-living taxa, red nodes are parasites, green are autotrophs, and brown are detritus. Arrows point from consumers to resources. Created in igraph (Csardi and Nepusz 2006).



3.11 Limitations and potential enhancements

This food web improves resolution of parasite-host interactions, but with over 450 free-living species in the food web, I was not able to observe all parasite species. For instance, I did not attempt to resolve protozoan, bacterial, viral, or fungal pathogens. Many protozoan parasites are known to infect marine organisms, but little is known of their life cycles or effects on host populations. Apicomplexans such as *Aggregata millerorum* from the California Two-spotted octopus (*Octopus bimaculoides*) are prevalent locally (Poynton et al. 1992). Viruses, bacteria, Microspora and other fungi may also have important roles in marine systems, and recent outbreaks of echinoderm infectious diseases have impacted kelp-forest food webs (e.g. Hewson et al. 2014, Behrens and Lafferty 2004,). The food-web construction allows for additional types of organisms, life stages, and interactions to be added, and this is an area for future consideration. Even some metazoan parasites were missed by the sampling program. I aimed to balance coverage of host diversity with sample size, but I was unable to sample all host species in the food web, and sample sizes of some hosts were small. For instance, some unsampled invertebrate taxa are known to host specialist parasites in other regions, ectoparasites may be lost during host collection, and there may be cryptic parasite diversity. It is possible that trematode diversity in particular was underestimated because several studies show multiple genetic species masquerading as just a single morphospecies (Soldánová et al. 2017, Poulin 2011, Miura et al. 2005, Leung et al. 2009). As cryptic species are uncovered, trematode diversity will likely increase along with greater host-specificity (Soldánová et al. 2017). Most samples came from non-protected mainland sites, so it is possible that additional parasites could be detected in MPAs and island locations. Furthermore, rare parasite species were likely not encountered within the moderate per-host samples. Adding rare parasites would further increase diversity, and potentially decrease connectance. Although more sampling would lead to a longer and more complete parasite list, new additions would more likely be rare species that are less important in biomass and energy flow than the parasites described here.

In addition to missing nodes, there are likely many missing (false-negative) links. I have focused on missing links between existing nodes, but missing links also occur between existing and missing nodes, and between missing nodes. I attempted to correct for false negative host-parasite links through inference of parasite life stages, additional host interactions, and false negative estimation, but recognize that additional sampling and resolution of cryptic diversity would improve network accuracy. Although missing links bias food-web properties, by estimating false-negative probabilities, it is possible to correct for much of this bias simply by replacing 0s with false negative probabilities when computing network statistics that count observed links.

Although false negatives are a concern in ecological networks, false positives are possible due to life cycle inferences, particularly for parasites with assumed low-host specificity. My assumptions about generalism were supported by literature and expert opinion (Marcogliese pers. comm., Marcogliese 2002, Palm and Caira 2008). By assuming generalism at the level indicated by the parasite life history, I ensured that at least one correct host (likely more) was included, with reduced chance of false negatives. Parasite species for which generalism in larval stages was assumed (a few nematodes, some tapeworms, and acanthocephalans) were widespread in many second-intermediate and paratenic host species in dissections, suggesting that there should be more than one infection pathway for such a wide range of hosts to become infected. However, using paratenic hosts makes it more challenging to identify first intermediate hosts by diet alone. I restricted assumptions of generalism to cosmopolitan parasites of wide-ranging hosts that may be less likely to host cryptic species due to increased gene-flow among populations (Goulding and Cohen 2014). By including link justification and confidence levels readers can treat these links as predictions and filter the node and links list to suit their research questions. Despite these limitations, I note that few other studies justify reported food-web links or distinguish between inferred and observed links.

4. Diverse specialist parasites in kelp-forest food webs decrease connectance, in contrast to other systems

4.1 Abstract

Parasites often track food-web linkages through their complex life cycles, but most food webs do not include parasites. Parasites affect food-web properties simply due to increases in species richness, but parasites also tend to increase connectance, in contrast to expectations based on network size alone. Parasites also increase maximum food-chain lengths more than expected due to increasing network size and can alter properties like degree distribution. Most systems examined for parasites so far have been similar (estuaries, salt marshes, sand flats) and contain relatively few species, so there is reason to believe parasites might have different effects on a larger, more complex food web. In addition to being species rich (912 species including parasites in this food web), kelp forests differ from

previously studied systems in having strong trophic interactions, structural complexity, and open nature. I therefore tested whether parasite effects seen in other systems also occurred in kelp forests, and the extent that such changes were driven by network size versus parasite traits. I examined the effects of parasites on the kelp-forest food web by focusing on food-web metrics known to vary with network size in free-living webs. I controlled for network size on degree distribution and longest chain by using the niche model as a reference network. Because parasites eat their hosts but can also be eaten by their hosts' predators (concomitant predation), I distinguished between the effects of these interaction types. I predicted that connectance would decrease when parasites were included due to the increase in network size, but that parasite-parasite interactions might increase connectance, as observed in other systems. The balance of specialists and generalists in a food-web will determine network-level characteristics, so I compared the generality and vulnerability of free-living and parasitic species, as well as the network-level change in these properties when parasites were included. Parasites made up a larger proportion of the kelp-forest food web than any other published food web. Even when potential missing links were accounted for, connectance decreased when parasites were included, in contrast to other systems. Parasites were more specialized than free-living consumers, which amplified scale-dependent effects of network size on connectance. Consistent with other systems, adding parasites increased longest chain length more than predicted based on network size, but this effect was sensitive to whether concomitant links were included. Specialist parasites and concomitant links altered the degree distribution independent of network size. Diverse parasites exploiting specific food chains may be an indicator of important energy flows in kelp-forest food webs. These and other parasites impart unique structure on this iconic system above and beyond adding to its richness.

4.2 Introduction

Researchers listened when Marcogliese and Cone pled to include parasites in food webs (1997). As a result, arctic lake and several soft-sediment intertidal food webs now include parasites (reviewed in McLaughlin et al. 2020). When parasites have been incorporated to the same degree as free-living species, they increase richness (McLaughlin 2018, Lafferty et al. 2006, Dunne et al. 2013, Amundsen et al. 2009, Mouritsen and Poulin 2002, Thompson et al. 2005) and add biomass (Kuris et al. 2008, McLaughlin 2018). Parasites affect food webs in three distinct ways (Lafferty et. al 2008): (1) they add consumer pressure on free-living species, altering vulnerability (Lafferty et al. 2006), which might add stabilizing or destabilizing top-down control on host populations, (2) they can alter overall network properties like degree distribution (Amundsen et al. 2009), robustness (Lafferty 2012), and connectance (Dunne et al. 2013). Third, changes to network properties after adding parasites often result from increasing network size, which alters scale-dependent properties like link density (Dunne et al. 2013). In other cases, parasites have different roles in the food web compared to free-living species. In particular, parasites with complex life cycles may feed on phylogenetically distinct hosts throughout their lives (Parker et al. 2003), so parasite species have discontinuous feeding niches when life stages are aggregated (Dunne et al. 2013). Additionally, because parasites have intimate relationships with their hosts, they can fall prey to their host’s predators (Johnson et al. 2010), so intraguild predation becomes more frequent when parasites are included (Dunne et al. 2013, McLaughlin 2018). To better assess whether parasites affect food webs due to increases in network size, or due to differences between parasites and hosts, I compared several network properties (connectance, link density, species vulnerability, and species generality), before and after adding parasites to a highly resolved kelp-forest food web.

Although there are now several food webs with parasites, there is reason to expect that kelp-forest food webs might be different. Giant kelp (*Macrocystis pyrifera*) forests differ from the salt marsh, lake, and sand flat food webs that have been augmented with parasites. For instance, estuaries, marshes, and sand flats are tidally-influenced and soft-bottomed, whereas giant kelp is subtidal and attaches to rock, which provides habitat for other attached species. Kelp forests experience substantial inputs from surrounding ecosystems so the food-web boundary is less defined (e.g. Zuercher and Galloway 2019). Giant kelp also creates a three-dimensional habitat, akin to terrestrial forests, but that varies spatially by season and year (Ebeling et al. 1985, Dayton and Tegner 1984, Edwards 2004, Rogers-Bennet and Catton 2019). Despite being dynamic, giant kelp forests are productive and support high plant and animal biomass (Graham et al. 2008, Scheil and Foster 2015, Carr and Reed 2016). Although kelp forests in southern California (San Diego to Point Conception) are well-studied (e.g. Davenport and Anderson 2007, Dayton 1985, Foster and Schiel 2010, Kushner et al. 2013, Lamy et al. 2020, Limbaugh 1955, Reed et al. 2011), kelp-forest food webs have not included parasitic interactions. Because parasite diversity derives from host diversity (Hechinger and Lafferty 2005), and healthy ecosystems support rich parasite communities (Hudson et al. 2006), it follows that the diverse free-living species and trophic interactions in kelp forests should support diverse parasites and complex life cycles, and in fact many parasite species are known from kelp-forest fish species (e.g., Love and Moser 1983). The kelp-forest food web has 912 species (Chapter 3, Morton et al. in prep), making it much larger than any other food webs with parasites examined (Dunne et al. 2013, McLaughlin et al. 2018).

Food-web organization is described by metrics that measure complexity and stability. The most basic measures are species richness (S, or more generally, node number) and the number of interactions or links (L). The ratio of links to species can be expressed as link density (L/S), as well as directed connectance (L/S_2, Martinez 1991), which describes the link number realized out of the total possible links. Researchers disagree about whether connectance increases stability (Link 2002, Hayden 1994, McCann et al. 1998, Neutal et al. 2002, Pinnegar et al. 2005). The link distribution among nodes (the degree distribution) may better describe stability, determined by the balance between consumer diet breadth and vulnerability to natural enemies (Schoener 1989). Most food webs have a few generalists and many specialists (Dunne et al. 2002). Dietary specialists are more vulnerable to secondary extinction if their resource is lost (Dunne et al. 2002), so adding a generalist species to a food web will have a different effect on network structure than adding a specialist. Link density tends to increase with network size (Schoener 1989, Martinez 1993, 1994, Hall and Raffaelli 1993, Banašek-Richter et al. 2006), possibly due to increased opportunities for interactions in larger webs (Warren 1990). Further, the relationship between link density and total species determines the effect that increasing network size will have on connectance (reviewed in Banašek-Richter et al. 2006, Dunne et al. 2006). Changes in metrics due directly to network structure should be distinguished from changes in metrics due indirectly to changes in network size.

Parasites increase food web size by adding new species and three new link types (Lafferty et al. 2006), namely: parasites consume hosts, predators consume parasites and sometimes parasites consume other parasites. Through these subwebs, parasites participate in most links, either as consumers feeding on hosts, incidental losses through concomitant predation, or trophically-transmitted stages (Thieltges et al. 2013, Amundsen 2009, Lafferty et al. 2006, Dunne et al. 2013). In the kelp forest, the parasite-host subweb contributes a similar link proportion as other species-level food webs that include parasites (13.2% in the kelp forest, Chapter 3; 17.36% in an arctic lake, Amundsen 2009; 11% in the Palmyra sand flat, 21% average in estuaries, McLaughlin 2018), suggesting parasites should be contributing similarly to link density across systems. Due to their contribution to network size, parasites repeatedly increase food-chain lengths and link density (McLaughlin 2018, Lafferty et al. 2006, Dunne et al. 2013, Amundsen et al. 2009, Thompson et al. 2005). However, webs with >1000 links appear to be scale invariant (Martinez and Lawton 1995), so food-web features might not scale predictably in this large kelp-forest food web. Therefore, past conclusions that parasite effects were mostly size effects (Dunne et al. 2013), might be an artifact of working with relatively small networks.

I first compared species-level differences that describe how species interact within the food web, because the balance between taxon interactions with resources (generality) and enemies (vulnerability) tends to drive many food-web structural aspects (Schoener 1989).

Most parasites tend to be more specialized than predators (Combes 2001), so I hypothesized that parasite generality would differ from predator generality (Lafferty et al. 2008). I predicted that most parasites would be more specialized than predators (e.g. Lafferty and Kuris 2009). However, some marine parasites have many hosts and multiple routes for completing their life cycles in food webs, often using paratenic hosts (intermediate hosts in which little to no development occurs, and that are not strictly necessary for the life cycle) (Marcogliese 2002, Palm and Caira 2002). These parasite types (e.g. shark tapeworms, marine mammal nematodes) are not well-represented in salt marshes, lakes, or mudflats, so in addition to looking at the distribution of generality, I examined the most general species in each food-web version. Specifically, due to the high marine-fish diversity and different top-predator species in kelp forests, I predicted some parasites (such as those using paratenic hosts) might be extreme generalists (e.g. Marcogliese 1996, Køie 1993, Palm and Caira 2002). These species may indicate important trophic pathways in the kelp-forest food web (Marcogliese and Cone 1997).

Predator-prey degree distributions tend to approximate a universal exponential scaling function, indicating that degree distributions in food webs are often skewed (Camacho et al. 2002, Dunne et al. 2002, Stouffer et al. 2005). The stronger the skew, the higher the proportion of specialists relative to generalists. The niche model predicts the exponential degree distribution seen in free-living webs (Camacho et al. 2002, Williams and Martinez 2000). If parasites have different generality and/or vulnerability distributions than predators, the niche model may fail to describe food webs when parasites are included (Lafferty et al. 2008, Warren et al. 2010). However, Dunne et al. (2013) found that increasing degree distribution variability after adding parasites was explainable by increasing species richness, suggesting that parasites and predators affect degree distribution similarly. I reasoned that if parasites had different average generalities and vulnerabilities than free-living species, that they would affect degree distribution variability (generality and vulnerability) in the parasite-rich kelp-forest food web more than would be expected from an increase in species richness alone. I first assessed the assumption that parasite species had different generality and vulnerability distributions compared to free-living species. However, because adding any type of consumer to a network increases the potential prey and enemies a species might be linked with (degree) (Dunne 2006, Warren 1990, Dunne et al. 2013), as well as interaction variability (Dunne et al. 2002), I examined the extent that mean generality, vulnerability, and degree distribution variability increased in the web with parasites due to increasing network size alone.

Even if parasites differ from predators, they will only impact the food web if they are common. Parasites make up 26-38 % of species in estuary, lake, and sand flat food webs (Amundsen 2009, McLaughlin 2018, Lafferty et al. 2006), so I hypothesized adding parasites would affect the kelp-forest even more. Increasing network size tends to increase link density (Reide et al. 2010, Schoener 1989, Martinez 1993, 1994, Hall and Raffaelli 1993, Banašek-Richter et al. 2006, Dunne et a. 2013), and adding parasites tends to increase link density so long as concomitant predation is included (Lafferty et al. 2006, McLaughlin 2018, Amundsen et al. 2009, Dunne et al. 2013), so I hypothesized that the same would occur in the parasite-rich kelp forest. Specifically, I predicted that parasite-host and concomitant links would increase link density, but that adding only parasite-host links may not increase link density if parasites were very host-specific.

In contrast, connectance may decrease with network size in general (Banašek-Richter et al. 2006, Dunne et al. 2006, Reide et al. 2010), but parasites tend to increase connectance when concomitant predation is included (Lafferty et al. 2006, Amundsen et al. 2009, Dunne et al. 2013), so long as connectance is adjusted to account for concomitant links (Lafferty et al. 2006). However, McLaughlin (2018) found that connectance did not change when parasites are included in a tropical sand flats food web. Given that these results conflict, parasite effects on connectance might be system specific, depending on whether most parasites were specialists or generalists, and the extent that parasite species interact with each other. I hypothesized that after adding parasites to the kelp-forest food web, connectance would decline because the network would grow (Banašek-Richter et al. 2006, Dunne et al. 2006, Reide et al. 2010), but this effect might be dampened by parasite generalism and parasite-parasite interactions.

Finally, when parasites are included in food webs without concomitant predation, they increase maximum chain length (Thompson et al. 2005, Lafferty et al. 2006, Huxham et al. 1995, Williams and Martinez 2004), which may decrease food-web stability, in this case because parasites will be more likely to suffer secondary extinction (Lafferty et al. 2008). Parasites are often added to the tops of food chains (Thompson et al. 2005, Lafferty et al. 2006, Huxham et al. 1995), but complex life cycles can alter these chains and concomitant links can add long loops of weak interactions (Lafferty et al. 2008), which may stabilize food webs (Neutet et al. 2002). Lafferty (2008) hypothesized that these outcomes were general, leading to the prediction that adding parasites would increase chain length in the kelp-forest food web above and beyond adding species in general. I examined the effect of parasites on longest chain length in the web both with and without predator-parasite links.

4.3 Methods

The kelp-forest food web I used for these analyses is resolved for free-living species (Chapter 2, Morton et al. in prep) and parasitic species (Chapter 3, Morton et al. in prep). The fully-resolved food web was constructed with life stage (e.g., larva, adult) nested within species (or morpho-species) (excepting benthic diatoms, planktonic diatoms, dinoflagellates, foraminifera, free-living nematodes, bacteria, free-living ciliates, copepod nauplii, filamentous algae, and invertebrate eggs, which are aggregate nodes). Detritus is broken into four categories: carrion, drift macroalgae, small mixed origin (such as would be consumed by a deposit or suspension feeder, with the recognition that this alone is a complex system deserving further resolution) and dissolved organic material. To allow comparison with other published parasite webs, the webs were aggregated to the taxonomic species level before calculating metrics. The free-living web is made up of predator-prey interactions. When parasites were added, this created two additional subwebs: parasite-host, and predator-parasite (concomitant predation). A fourth subweb, parasite-parasite, is possible but was not observed.

I compared three web versions: predator-prey only, predator-prey and parasite-host, and predator-prey + parasite-host + predator-parasite all three subwebs. For each food-web version, I compared the contributions of parasite and free-living species to network size and linkages. I compared free-living vulnerability to enemies in the web with and without parasites (this does not vary between the two versions with parasites). I compared free-living vs. parasitic species vulnerability in the full web that included concomitant predation. Finally, I compared consumer generality of free-living vs. parasitic species (diet breadth, excluding concomitant mortality). I used a Wilcoxon Rank Sum test to determine whether generality and vulnerability distributions differed between free-living consumers and parasites (JMP Pro V14). To better understand how adding parasites affected qualitative differences in consumers, I compared the identities of the top-ten most general consumers with and without parasites.

To compare how parasites affected network structure, I calculated 10 metrics that describe trophic structure and should allow comparison with other published parasite food webs (Table 4.1). To control for increased network size when assessing parasite addition, I measured the deviation between each web version and a similar-sized simulated food web for four of the above metrics that vary within simulations (Williams and Martinez 2008). To create a hypothetical food web, I used the niche model to simulate 1,000 networks with size (S) and connectance (C) matching the empirical food web (Williams and Martinez 2000). For the webs including parasites, I used adjusted connectance (Table 4.1, Lafferty et al. 2006) for niche model simulations. For each version, I calculated the model error (ME) for each metric, (the normalized difference between the simulated model’s median value and the empirical value) (Williams and Martinez 2008). Empirical metrics with |ME|> 1 fall outside the most likely 95% of model values and indicate a statistically significant difference from model values. The ME's sign (negative or positive) indicates whether the model under- or overestimates the empirical metric, respectively. Link density, connectance, mean degree, mean generality, and mean vulnerability do not vary within the niche model, but I compared model predictions of longest chain length and variability of degree, generality, and vulnerability with empirical metrics. If the webs deviated from the niche model in the same way, it suggested they were structurally similar in that trait, whereas if they differed from the niche model in different ways, they likely differed in that trait independent of their size. Because this approach has typically been used with webs < 100 nodes and niche-model fits decline with network size, (e.g., Dunne et al. 2013, Vinagre et al. 2019, Williams and Martinez 2008, Williams & Purves 2011, Wood et al. 2015), the MEs were interpreted with this potential confounding factor in mind. All metrics and niche-model simulations were calculated in R Version 3.6.2 with packages *igraph* (Csardi and Nepusz 2006), *NetworkExtinction* (Corcoran et al. 2019), *NetIndices* (Kones et al. 2009), and *cheddar* (Hudson et al. 2013).

Table 4.1 Summary of web metrics for each web assembly. Adjusted connectance calculated using the method of Lafferty et al. 2006. Denominator for FL+Parasite-Host web was Free-living *(Free-living +Parasites). Denominator for FL + Parasites-Host + Predator-Parasite web was total possible (total species * total species) minus missing parasite-parasite interactions (Parasites* Parasites). False Negative estimation described in Chapter 3.

Assembly	Free-living (FL)	FL + Parasite-Host	FL + Parasite-Host (w/ False Negatives)	FL + Parasites-Host, Predator-Parasite	FL + Parasites-Host, Predator-Parasite (w/ False Negatives)
Nodes	490	912	912	912	912
Links	8353	10964	11614	19718	20368
Link Density	17.05	12.02	12.73	21.62	22.33
Connectance	0.035	0.013	0.014	0.024	0.024
Adjusted Connectance*	-	0.025	0.026	0.030	0.031
Longest Chain	9	10	-	7	-
Mean Degree	34.09	24.04	-	43.24	-
SD Degree	29.21	32.64	-	55.79	-
Mean Generality	17.05	12.02	-	21.62	-
SD Generality	18.88	19.73	-	21.90	-
Mean Vulnerability	17.05	12.02	-	21.62	-
SD Vulnerability	24.09	21.10	-	47.69	-

4.4 Results

Species-level differences

Parasites had lower overall diet breadth than free-living species (Figure 4.1, Z = -9.724, p <0.0001). The median diet breadth was seven for free-living predators (IQR 4-29), and two for parasites (IQR 1- 4). However, the generality distributions overlapped: the most generalist parasite had 114 hosts, and the most generalist predator had 129 prey. Of free-living species, anemones (Hexacorallia), fishes, elasmobranches, and birds had the broadest diets (Figure 4.2). Sponges, bivalves, and other filter feeders had the lowest diet breadth, but this undercounted phytoplankton species that were often aggregated to higher taxonomic levels. The most general parasitic groups (at the species level) were acanthocephalans, nematodes, and cestodes, which are all trophically transmitted parasites that use paratenic hosts in their life cycles. As a result, the top ten most generalist taxa changed when parasites were included (Table 4.2). In the free-living web, the most general consumers were fishes and anemones. Three fish parasites joined the generalist ranking. The fourth and sixth most general species were seal parasites (*Pseudoterranova decipiens* and *Corynosoma strumosum)* that use fishes as intermediate hosts, and the tenth spot was *Hysterothylacium aduncum*, a nematode that uses fishes as its final host. Therefore, the parasite community comprises many specialists and a few extreme generalists. In line with this observation, mean generality was lower in the predator-prey + parasite-host web (Table 4.1). The network-level generality variability was nominally larger in this web than the predator-prey web, but significantly less than expected based on network size alone (Table 4.3). This may be attributed to the wide distribution of parasite host breadth, which almost entirely overlapped with free-living consumer diet breadth distribution. When parasites were included with concomitant links, generality variability was even lower than expected based on network size (Table 4.3), likely because concomitant links make predators appear more general in the overall network and make the generality distribution more uniform. Overall, parasites were more specialized than free-living taxa, although some highly general taxa were present.

Figure 4.1 Diet breadth of free-living vs. parasitic species in food web containing predator-prey and parasite-host links.

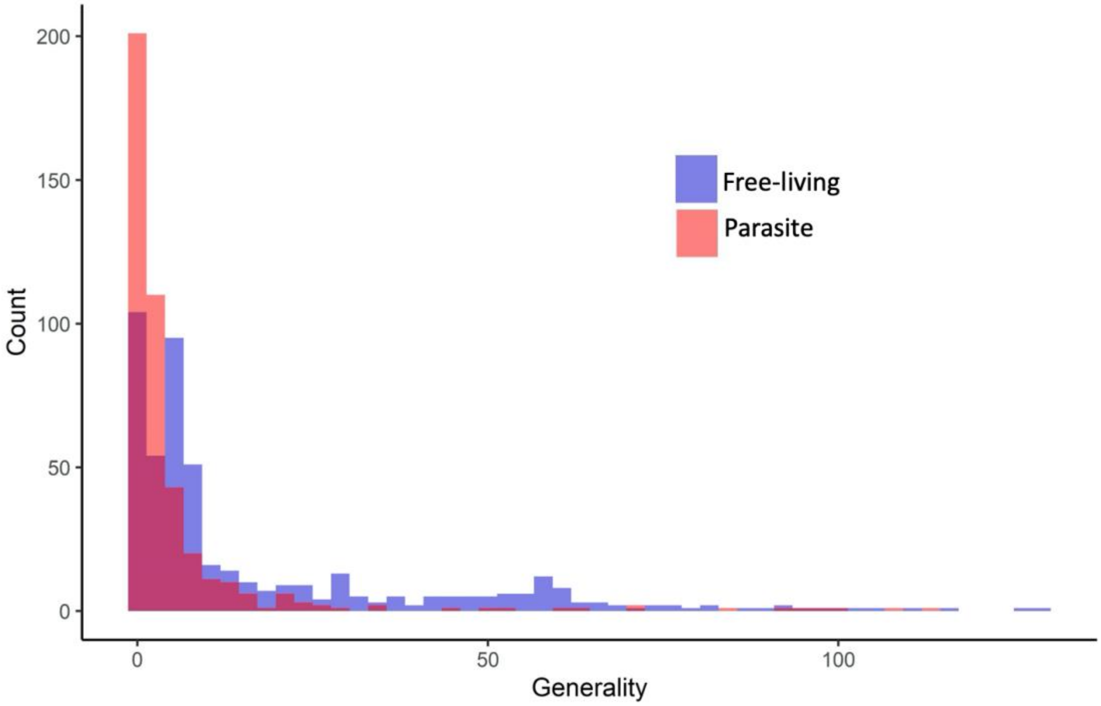


Table 4.2 Top ten most general species (diet breadth) in the free-living food web and the web including parasite-host interactions. Parasitic species are bolded. A: Anemone, F: fish, P: parasite.

Assembly	Free-living (FL)		FL + Parasite-host	
Rank	Taxon	Gen	Taxon	Gen
1	*Semicossyphus pulcher (F)*	129	*Semicossyphus pulcher (F)*	129
2	*Embiotoca jacksoni (F)*	127	*Embiotoca jacksoni (F)*	127
3	*Anisotremus davidsonii (F)*	116	*Anisotremus davidsonii (F)*	116
4	*Halichoeres semicinctus (F)*	111	***Pseudoterranova decipiens (P)***	114
5	*Paralabrax clathratus (F)*	106	*Halichoeres semicinctus (F)*	111
6	*Urticina lofotensis (A)*	102	***Corynosoma strumosum (P)***	107
7	*Phanerodon furcatus (F)*	101	*Paralabrax clathratus (F)*	106
8	*Anthopleura sola (A)*	98	*Urticina lofotensis (A)*	102
9	*Hypsypops rubicundus (F)*	95	*Phanerodon furcatus (F)*	101
10	*Caulolatilus princeps (F)*	92	***Hysterothylacium aduncum (P)***	101

Figure 4.2 Diet breadth of free-living vs. parasitic species by organismal group in food web containing predator-prey and parasite-host links.

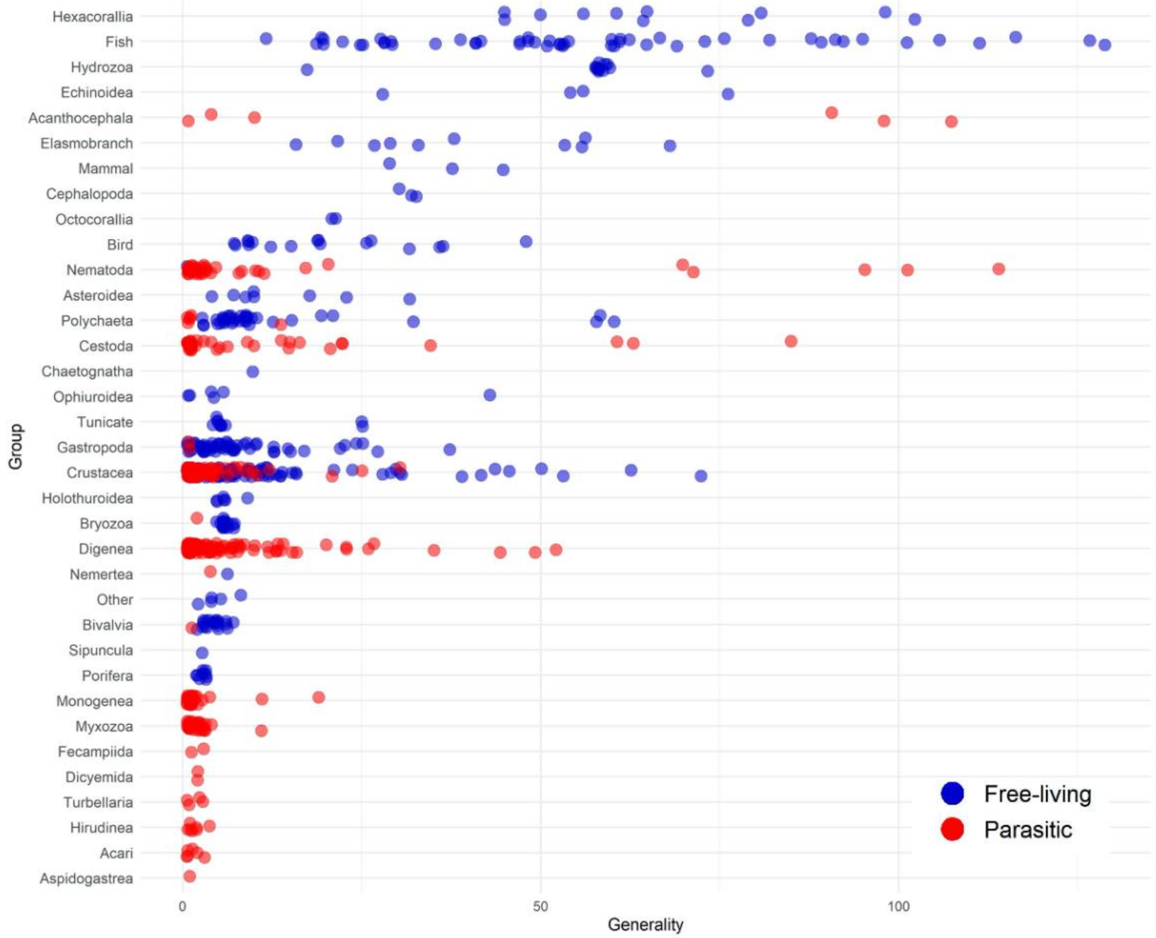
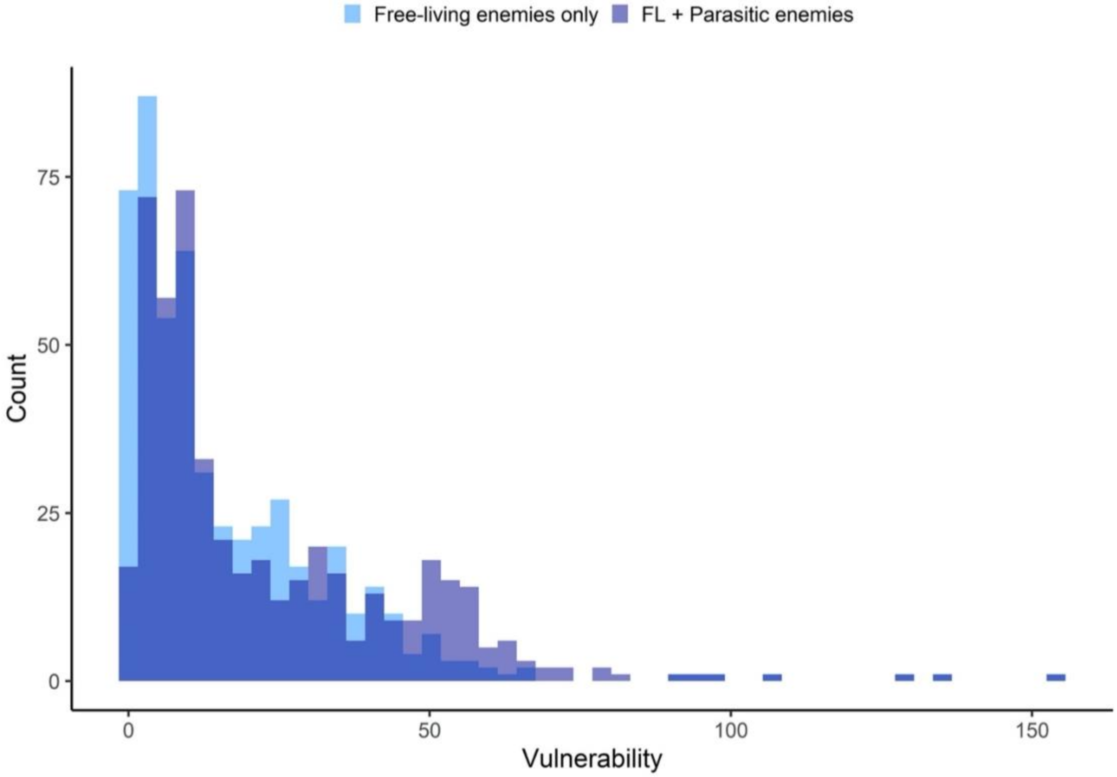


Figure 4.3 Vulnerability of free-living species to natural enemies in webs with and without parasites.



Adding parasites increased free-living vulnerability (Figure 4.3, Z = 5.329, p <0.0001), whereas parasites were less vulnerable overall than free-living species (Figure 4.4, Z = -2.499, p <0.0125), possibly because when a parasite's host is eaten, this sometimes transmits the parasite to another host. Moreover, top predators tend to have more parasites than very low trophic levels, and be subject to less predation risk themselves, so their parasites would be less vulnerable to concomitant predation. Even though parasites were less vulnerable to enemies than free-living consumers, parasites increased network mean vulnerability (all consumptive links, including concomitant) relative to the free-living web (Table 4.1). Changes to the vulnerability distribution in the food web with parasites led to greater degree variability than predicted by network size (Table 4.3). Variability in vulnerability tends to be underestimated by the niche model (e.g., Vinagre et al. 2019), so this could explain the relatively high |ME|s for this metric.

Figure 4.4. Vulnerability of free-living vs. parasitic species in the food web including predator-prey, parasite-host, and predator-parasite interactions.

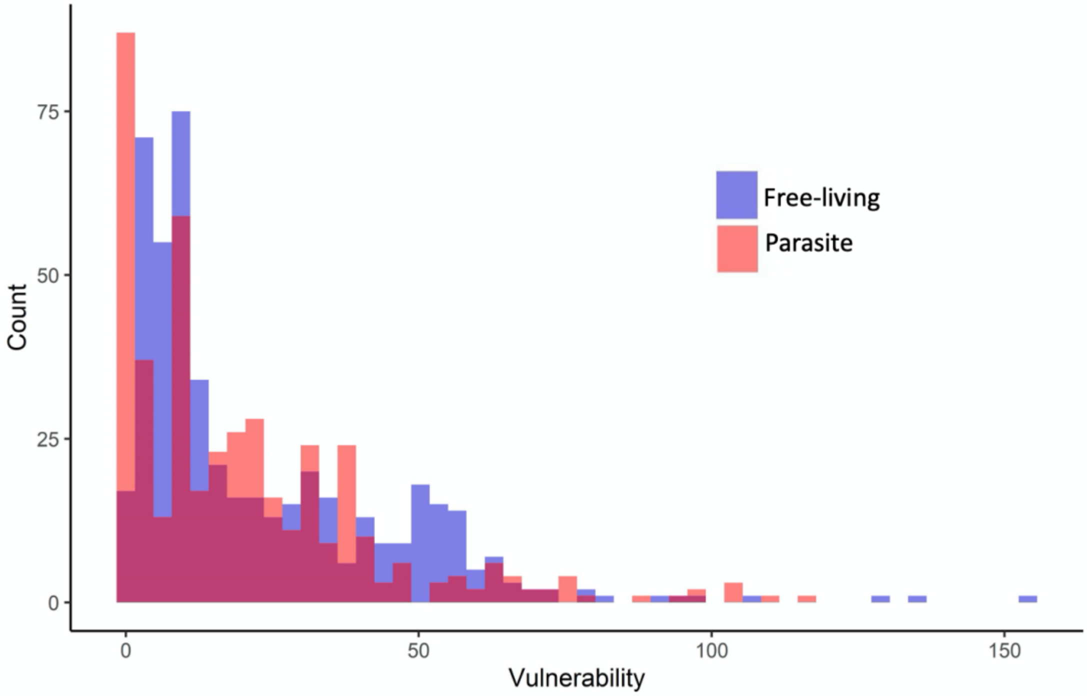


Table 4.3 Model errors for the metrics that vary within the niche model (Williams and Martinez 2008). Bold values (|ME|> 1) indicate that empirical values were significantly different from model predictions.

Assembly	Free-living (FL)	FL + Parasite-Host	FL + Parasites-Host + Predator-Parasite
Longest Chain	**-1.50**	**-3.00**	0.00
SD Degree	**-3.33**	**-2.65**	**-8.86**
SD Generality	0.75	**2.75**	**3.50**
SD Vulnerability	**-7.65**	**-4.25**	**-14.69**

Network-level differences

Parasites contributed more richness to the kelp forest (absolutely and proportionally) than to any other food web (Figure 4.5a). The predator-prey web had 490 free-living species (compared with 22-140 species in past parasite food webs), and parasites added an additional 422 species (46.2% of species) (Table 4.1, Figure 4.5). The rich parasite assemblage changed network characteristics related to the number of links per species and network size. The total link count in the food web increased with parasite inclusion, particularly due to concomitant links. The predator-prey subweb contained 44.3% of links, 13.2% of links were parasite-host links, and 42.3% of links were between predators and parasites (Chapter 3, Morton et al. in prep). Link density (*L/S*) increased when parasites were included with concomitant links, but only slightly (Table 4.1). Even though parasites increased network size by 86.1%, link density decreased from 17.1 links per species to 12.0 links per species when only the host-parasite subweb was added. When concomitant links were included, link density increased by 26.8% relative to the free-living web. Parasites were overall more specialized than free-living species, and their high richness reduced mean link density when concomitant links were not accounted for. Even though generality, vulnerability, and overall link density increased when parasites were included with concomitant links, the increases in link density were not enough to increase connectance, as was observed in other food webs (Figure 4.6).

At 3.5%, connectance in the free-living kelp-forest food web was already lower than in most food webs (Fig 4.7, Reide et al. 2010, Dunne et al. 2004, Dunne et a. 2013, McLaughlin 2018), likely due to its large size and high resolution (Dunne et al. 2004). The further decrease in connectance to 2.4% after parasite addition was explainable, in part, by the lack of parasite-parasite interactions in the kelp-forest food web. Specifically, although there were potentially many parasite-parasite interactions in the network (178,084), none were seen (unlike in estuarine networks, where such links are common). Excluding parasite-parasite interactions from consideration as possible links would mean that adding parasites reduced network connectance from 3.5% to 3% (as opposed to 2.4%) (Table 4.1). Similarly, the predator-prey + parasite-host web connectance can be adjusted to account for the missing potential predator-parasite and parasite-parasites links, which means that adding only host-parasite interactions reduced connectance from 3.5% to 2.5% (as opposed to 1.3% unadjusted) (Lafferty et al. 2006). These differences underscore how parasite effects on connectance are highly sensitive to what potential links are included (Lafferty et al. 2006). Regardless, adding parasites decreased connectance, independent of how it was calculated.

Figure 4.5 Parasite and free-living richness in the kelp-forest food web relative to other published food webs with parasites (Amundsen 2009, Thompson et al. 2005 Dunne et al. 2013, Lafferty et al. 2006, McLaughlin 2018). Panel a shows total number of species, panel b shows proportions of parasites vs. free-living species.

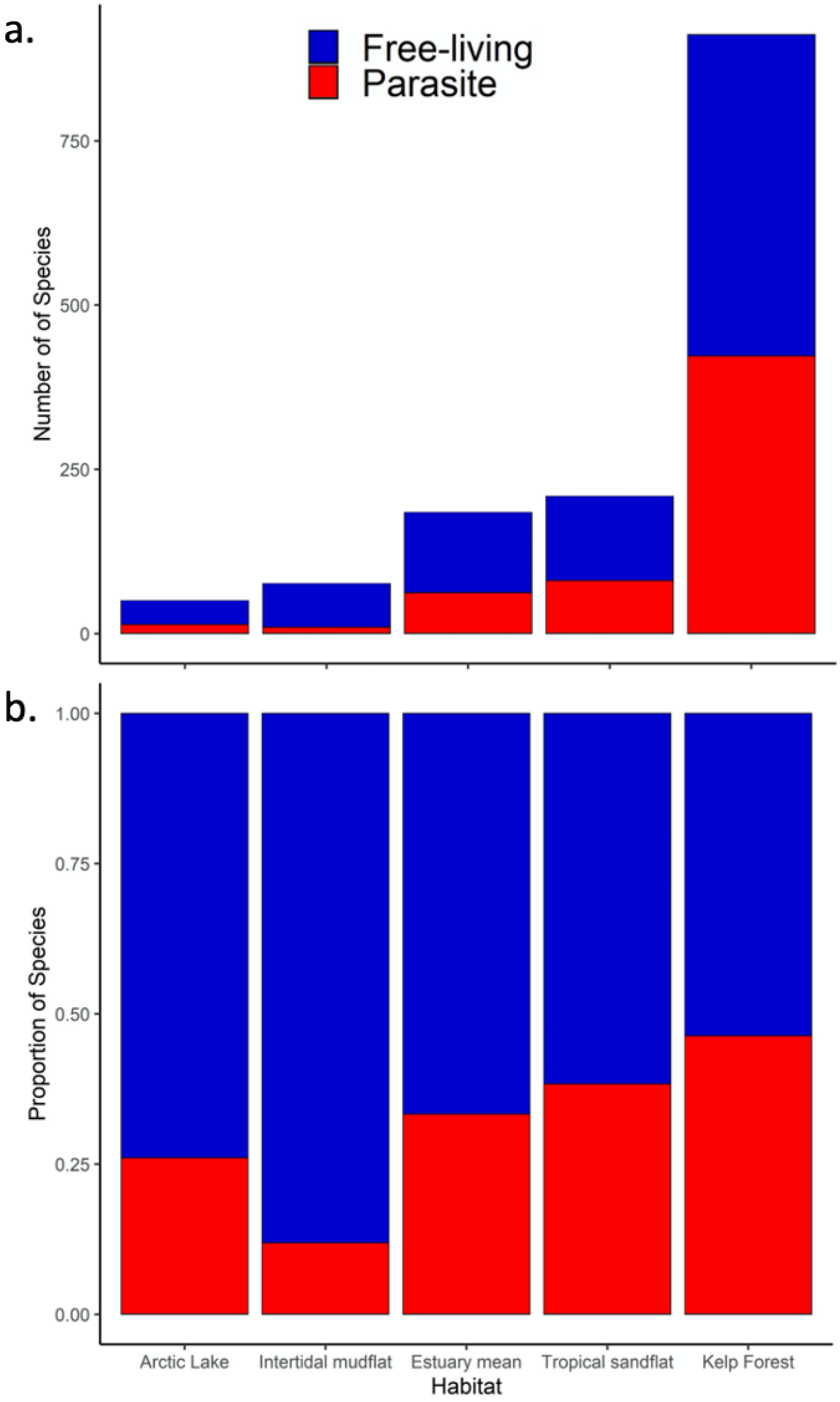
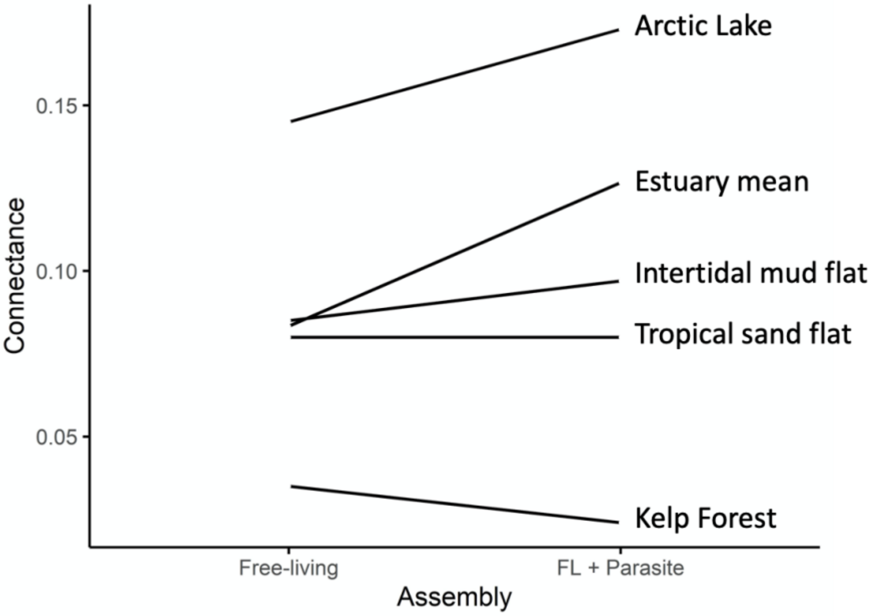


Figure 4.6 Trends in connectance with inclusion of parasites the food webs (Amundsen 2009, Thompson et al. 2005 Dunne et al. 2013, Lafferty et al. 2006, McLaughlin 2018). FL + Parasite includes concomitant links. Unadjusted connectance is shown for the kelp forest.



Longest chain length was also sensitive to what links were included in the food web. I predicted that parasites would increase longest chain length more than expected with increasing web size. The longest chain was one link longer in the web with parasites without concomitant links, and this difference was greater than expected based on network size (Table 4.1, 4.3). Both of these web versions had somewhat longer chains than predicted by network size, but the web with parasites deviated from the niche model by twice as much (Table 4.3). Surprisingly, longest chain length was significantly lower in the web with parasites and concomitant links than in predator-prey web and was similar to expectations based on network size (Table 4.1, 4.3). Aggregating life stages to species meant that predators of individual life stages became predators of the entire species, which shortened some food chains. This reinforces that the effects of parasites on network-level structures depend on the types of parasite links considered.

4.5 Discussion

Adding parasites to the kelp-forest food web increased network size and complexity through both parasite-host links and concomitant links. The change in connectance seemed mostly due to an increase in network size, rather than a distinctive role for parasites. On the other hand, specialist parasites and concomitant links altered the degree distribution independent of network size. Adding parasites reduced overall generality, increased variation in generality much less than expected based on network size, and increased the length of the longest chain, which appears to be an effect of parasites acting as top consumers (Lafferty et al. 2006). Parasites also increased vulnerability of free-living consumers, and the network overall when concomitant links were included. Variability in vulnerability was greater than expected based on network size, so this also seems to be an effect of parasites. Parasites are specialized themselves, but increase vulnerability of their prey, and are vulnerable to many of their hosts' predators. Some outcomes depended on whether or not concomitant links were included (longest chain, link density), or whether parasite-parasite links were included (connectance decreasing substantially) or not (connectance decreasing slightly). Although I did not investigate how parasites increased discontinuous feeding niches or intraguild predation, these effects are inevitable outcomes of adding parasites to food webs (McLaughlin 2018). Unlike in past studies, adding parasites decreased connectance, largely due the combination of parasite specificity, larger network size, and a lack of parasite-parasite interactions.

Parasites affected network structure because parasitic taxa in the kelp-forest food web were more specialized than free-living species. This was driven by the most species-rich groups: trematodes and copepods. Most parasitic copepods did not exhibit a broad host-range throughout their life cycle. Trematodes have complex life cycles, but are fairly host-specific at each stage and do not use paratenic hosts, so total host range is somewhat constrained. Furthermore, not all parasite species had all life stages in the kelp-forest food web (e.g. adult trematodes found in transient hosts), so their host breadth within the kelp forest was narrower than it could have been (and narrower than seen in other food webs that usually contain all trematode life stages). Although there were many specialist parasite species, the most generalist parasites were common in fish dissections (Chapter 3, Morton et al. in prep). An acanthocephalan of seals and two nematodes (one of fish, one of seals) were among the most general consumers, along-side iconic kelp-forest fishes such as the California sheephead and kelp bass (and in-fact parasitizing them as well). These parasites were common in dissections (Morton et al. in prep), have low host-specificity as larvae, and used repeated paratenic hosts. Larvae of shark tapeworms and seabird acanthocephalans were also abundant, but were not quite as generalist. To my knowledge, this is the first food web with parasites that features paratenic host use as a prominent food-web feature. However, these extreme generalists were outnumbered by specialists.

As with other food webs, including concomitant links increased vulnerability and variation in vulnerability more than expected with increasing network size. This was, in part, because concomitant predation links make parasites vulnerable to free-living predators, and because parasites increase free-living consumer vulnerability. In addition, vulnerability and degree variability may have been affected by decreasing niche model fit with web size (e.g., Dunne et al. 2013, 2014, Vinagre et al. 2019, Williams & Martinez 2008, Williams & Purves 2011, Wood et al. 2015), so it is difficult to assess whether these effects were parasite-specific or due to network size. I did not observe parasite-parasite links, but these would be expected to further increase parasite vulnerability.

Adding parasites to the food web reduced connectance, consistent with scale-dependence, and this effect may have been more pronounced due to the low diet breadth of the parasites in the food web. As networks grow, the proportion of specialists tends to increase (Dunne et al. 2002), so the fact that specialization increased after adding parasites does not necessarily indicate a unique effect of parasites. However, link density also tends to increase with size, even as the proportion of specialists increases, and I observed that link density decreased when parasites were added without concomitant links. Even when concomitant links were included, the proportional increase in link density was small. This suggests that scale-dependent effects of increasing web size on connectance were amplified by adding species that were more specialized than free-living species.

The reduced connectance with parasites in the kelp-forest food web contrasted with other food webs containing parasites (Figure 4.6, Dunne et al. 2013, Amundsen 2009, McLaughlin 2018, Thompson et al. 2005). It is possible that this difference relates to differences in food-web construction, including errors in how links were estimated. For instance, low connectance could be partly explained because I did not observe parasite-parasite interactions in the kelp forest, or predation on parasite free-living stages, whereas these were common and well-connected in other food webs with parasites (e.g., Lafferty et al. 2006). Complete removal of these potential interactions from the web reduced the difference in connectance between the free-living web and the webs with parasites, but it did not completely remove it. However, if these interactions are present but rare (e.g. a few trematode species that share a host), inclusion of those links would have minimal impact on connectance. Some network attributes that appeared to change with network size might actually be due to changes in sampling effort (particularly connectance and diet breadth). As networks grow, it becomes harder to sample all interactions (Paine 1988, Polis 1991, Hall and Raffaelli 1993, Winemiller and Polis 1996, Goldwasser and Roughgarden 1997). Given the size of this network, it is possible that decreasing connectance and increasing specialization with web size were at least in part due to variation in sampling effort. I attempted to minimize this by building a cumulative metaweb that used records from various literature sources, multiple forms of inference, as well as estimating false negative links (Chapters 2 and 3, Morton et al. in prep). With additional sampling, additional links would surely be detected, so connectance would increase and specialists may have broader diets than realized. Correcting for estimated false negative links increases the number of host-parasite links by 650, however link density would increase by only 0.7, and connectance would increase by only 0.1%, indicating the overall results were robust to undersampling. It is possible that resolving cryptic species would increase species richness along with host-specificity, but additional feeding observations for specialists may also be observed with more sampling, as would increases in diet breadth for generalists, which would have opposing effects on degree distribution. In fact, the food web is large enough that even a 20% increase in the number of links would only slightly change connectance (a 20%

increase in links would change directed connectance from 2.4% to 2.8% in the web with parasites). A more likely explanation for why adding parasites decreased connectance in the kelp-forest web is that it contained more specialist parasites. In particular, the kelp forest had many parasitic copepods, which were relatively host-specific and therefore reduced mean link density.

Network size and parasite addition increased chain length in the kelp-forest food web, consistent with other systems (e.g., Thompson et al. 2005, Lafferty et al. 2006, Huxham et al. 1995, Williams and Martinez 2004, McLaughlin 2018). Longest chain length increased more than predicted based on web size when parasites were added. The longest chain in the free-living web was also longer than predicted based on web size, but to a lesser degree. Counter to predictions, when concomitant links were included, the longest chain shortened. The chain in question shortened due to concomitant predation on parasite life stages that were aggregated to species, but when life stages were considered separately, parasites did increase chain lengths (Chapter 2, Morton et al. in prep). Other food webs have examined these effects at species level resolution (as done here), so it is unclear whether this effect is unique to the kelp-forest food web or a consequence of web size. The chain lengths in the kelp-forest food web were longer than observed in other systems (Lafferty et al. 2006, McLaughlin 2018), which may have provided more opportunities for these types of species interactions.

With nearly equivalent free-living and parasitic diversity, it follows that concomitant predation was the most common link type in this and other food webs (Lafferty et al. 2006).

Although parasite consumption does not likely affect the predator energetically, it certainly affects the parasite, as indicated through vulnerability. The proportion of predators in the system that can serve as hosts vs. those that will lead to the death of the parasite will determine parasite dynamics in the system. For example, larval acanthocephalans, tapeworms, and trematodes have been shown to modify host behavior to increase predation risk, and thus parasite transmission to the next host (Bethel and Holmes 1977, Ness and Foster 1999, Lafferty and Morris 1996, respectively), but this may also enhance concomitant predation risk. Parasite-induced behavior can increase transfer of energy to upper trophic levels (Lafferty and Morris 1996), thus the contribution of parasites to energy flow in kelp forests is an area for future work. Concomitant links are key to understanding the interactions between predator and parasite populations in food webs (Johnson et al. 2010).

Differences between these results and other food webs that include parasites, are likely, in part, because the kelp-forest food web had relatively more parasite species (Figure 4.5, Dunne et al. 2013, Amundsen 2009, McLaughlin 2018, Thompson et al. 2005) and more species altogether. It would be worthwhile to further explore connectivity of parasites in food webs as food webs become more diverse. The kelp-forest food web had a large proportion of ectoparasites, which were fairly specialized and not trophically transmitted, and so may be very weakly connected to the food web. Although kelp forests are biodiverse ecosystems, the high diversity was also due to this food web being a time-integrated metaweb for the entire Santa Barbara Channel Region, whereas the other webs have focused on a specific bounded habitat (such as a single estuary) during a specific time frame. The kelp-forest food web encompasses more species overall due to its spatial and temporal range, but it is unclear why this would affect the parasite proportion. The kelp-forest web also includes parasite-host and predator-prey records from the literature, whereas other parasite webs were constructed solely from field sampling and inference. There is an extensive knowledge base on kelp-forest trophic ecology in the Santa Barbara Channel Region, and I used all available sources to inform both free-living and parasite species, so it is unlikely that parasites were overrepresented by this method. Parasites are under-sampled in many hosts, heavily parasitized top-predators are often challenging to collect (birds, sharks, etc.), and cryptic species are discovered regularly (Soldánová et al. 2017, Poulin 2011, Miura et al. 2005, Leung et al. 2009), so the true parasite richness is likely higher. I was conservative in my decisions to included parasite-host records, especially for transient hosts (see Chapter 3, Morton et al. in prep). For example, sea bird feather lice were excluded, which would have added an additional 24 parasites. The methods used in the web construction should not have biased the ratio of parasites to free-living species in a systematic way, but cryptic diversity may be present in both parasitic and free-living invertebrates. It seems likely that additional efforts to detect free-living species would also detect additional parasites.

Changes to network properties can, in theory, affect ecosystem dynamics. Increased specialization allows for stronger top-down effects on hosts, and also strengthens the dependency of parasite diversity on host diversity. Although not addressed here, this dependency is even stronger when one considers parasite life stages (Rudolf and Lafferty 2011, Lafferty 2012). Kelp forests have traditionally been considered in the context of how trophic interactions (e.g. “keystone” predation) (e.g. Estes and Palmisano 1974) affect dynamics (Steneck et al. 2003, Dayton et al. 1992), and large food webs made up of strong interactions were once thought to be unstable, particularly when connectance is low (May 1990). The inclusion of parasites as well as the many weakly interacting free-living species may aid our understanding of food-web stability as webs may be stabilized by many weak interactions (McCann et al. 1998). Most parasites will have relatively weak effects on their hosts, and additional loops of weak interactions created by concomitant links could have a further stabilizing effect on food webs (Neutal et al. 2002, Lafferty et al. 2008), so adding parasites may improve our understanding kelp-forest food-web stability.

Host diversity begets parasite diversity (Hechinger and Lafferty 2005) and kelp-forest food webs are no exception. The kelp-forest ecosystem provides diverse food sources and diverse predators for both free living and parasitic species, and a complex food web that can be used to further develop food-web theory concerning relationships between connectance and food-web stability. Parasites that can navigate the complex kelp-forest trophic network via their life cycles are able to exploit the diverse host species that congregate in kelp forests, and many others may be along for the ride with their transient hosts. Future work could address potential relationships between host specificity and vulnerability to predation in this system, and opportunities that food webs provide to predators and parasites (Benesh et al. in review). Diverse parasites exploiting specific food chains may be an indicator of important energy flows in the ecosystem. These and other parasites impart unique structure on this iconic system above and beyond adding to its richness. The completed kelp-forest web makes it possible to understand how parasites affect and are affected by stability, energy flow, and ecosystem dynamics.

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Appendix

Table 1. Metadata for node-list columns.

Column Name	Description
Node.ID	Unique code for Life stage nodes
Name.Sp.stage	Genus.species.sp.ID.stage.ID
Sp.stage	SpeciesID.stageID
sp.ID	Unique code for species
stageID	Numerical code for life stage category, values 1-6. (1) adult, spore; egg; (2) 1st stage larvae: L1-L3 nematode in crustacean; (3) parthenitae, copepodid, acanthella or cystacanth in arthropod, juvenile isopod; cysticercoid/ procercoid; (4) 2nd stage larvae: cystacanth in non-arthropor, cercaria, metacestode in non-arthropod, chalimus; (5) metacercaria, L3+ or paratenic nematode (not in crustacean); (6) multiple stages (as in dicyemids)
Stage	Node life-cycle stage, specific to type of organism. Possible values: Adult, spore, egg, acanthella, Adult, copepodid, Juvenile, larvae, nymph, parthenitae, procercoid, chalimus, cystacanth, Juvenile, metacestode, juvenile/paratenic, Juvenile, L3, metacercaria, multiple, or dead (for detritus)
Presence.code	Letter code indicating node presence. Allows filtering of extinct species, etc. Published web analysis includes local and inferred nodes. (L) local and extant, (I) inferred life cycle link, (E) extinct, (P) protozoa, (N) not local, (R) remove
Type	Indicates whether species has intimate relationship with resources: symbiont or free.living
Organismal.Group	Taxonomic grouping corresponding to most commonly used groupings (e.g. Polychaete). Common names used if appropriate (e.g. Birds)
Working.Group	Common name for functional group (e.g. cucumbers)
WorkingName	Common name for the species if available. Not a unique identifier.
Phylum	Taxonomic Phylum according to World Register of Marine Species as of March 2020.
Class	Taxonomic Class according to World Register of Marine Species as of March 2020.
Order	Taxonomic Order according to World Register of Marine Species as of March 2020.
Family	Taxonomic Family according to World Register of Marine Species as of March 2020.
Genus	Taxonomic Genus according to World Register of Marine Species as of March 2020.
Specific.epithet	Taxonomic species according to World Register of Marine Species as of March 2020.
Sp.name	Genus.species
Resolution	Taxonomic resolution of node (e.g. Species, Genus, Family, etc.)
Habitat_Site	Habitat association within kelp forest or infection site on host if parasitic. Values include: benthic substrate, External.Host, Holdfast, Internal.Host, kelp-fronds, Kelp-water column, non-specific, rock, sand, Transient, water column
Consumer.Strategy	Organism feeding method. Values include: Autotroph, Castrator, Commensal, Detritivore, EctoCommensal, Ectoparasite, EggPredator, Endoparasite, Filter, Herbivore, MicroPredator, non-feeding, Omnivore, Pathogen, planktivore, Predator, Scavenger, Suspension
Consumer.Type	Consumer strategy according to Lafferty and Kuris 2002. Values include: Castrator, Micropredator, non-feeding, Parasite, Pathogen, Predator, Trophically Transmitted Parasite
Mobility	Organism mobility. Values include: Mobile, Sessile, Host-dependent, Passive

Table 1. (continued)

Column Name	Description
Life.Cycle	For parasitic species, code (1-7) indicating whether life cycle occurs in food web. NA for free-living species. (1) Occurs outside system, known; (2)Plausibly occurs outside system but could be in or out (transient hosts); (3)Full life cycle in kelp forest, known or inferred; (4)Life cycle occurs at least partially inside kelp forest (presence of larval stages) but unknown full cycle; (5) unknown life cycle, or known compatible hosts in web (importance of kelp forest unknown); (6) Not examined; (7) not applicable due to parasite life history
size	organism size (numerical value)
size.unit	unit of size measurement
size.metric	Description of what organism size refers to, and whether it is an average, maximum, etc.
Size.reference	Reference for size measurements
Confidence.in.Node	Numerical code identifying certainty category: (1) very certain, (2) certain, (3) somewhat certain, (4) uncertain but plausible
justification	Description of sources used to justify node presence.
thermal.province	Thermal association based on known species range (NA for parasitic species): warm (for species ranging from Point Conception, CA, USA to at least Baja California, Mexico; cold (species whose southern range limit is Point Conception, CA, USA), and both (species which ranged from at least North of San Francisco Bay to at least Baja California, Mexico), or unknown
locality	Locations associated with references of species observation. Does not encompass all known localities of species.
reference	References indicating species presence
Range	Known geographical range
Synonomy	Species synonomies according to World Register of Marine Species (marinespecies.org), FishBase (fishbase.org), or Integrated Taxonomic Information System (ITIS.gov)
Fishbase.OR.WoRM	Search terms used to locate synonomies
biosis.diet.search.ter	Search terms used in Biosis citation index search for diet items
NHM.Search.Terms	Search terms used in Natural History Museum of London parasite-host database
Google.Scholar.PS.	Search terms used in Google Scholar search for parasite-host records
biosis.SearchTerms	Search terms used in Biosis citation index search for host-parasite records
BIOSIS.PS.records	Number of parasite-host records returned in Biosis parasite-host search
NHM.records	Number of parasite-host records returned in NHM parasite-host search
FishPest	Search terms used in FishPest search (http://panic.alwaysdata.net/hpph/). Only searched for fish hosts.
Biosis.host.only.ter	Search terms used in Biosis citation index search for free-living species records
Biosis.host.only.rec	Number of records returned in Biosis search for free-living species
NHM.host.count	Number of host-species returned for each parasite species in NHM database (https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/search.jsp), accessed using R package "HelminthR", version 1.0.7 (Gibson et al. 2005).

Table 2. Zooplankton sampling sites and dates. While vessel was at anchor within a kelp forest, a 30 cm diameter, 200 micron plankton ring net was dropped to the bottom and pulled to the surface at a rate of 0.33 m per second. Multiple tows at the same site on the same day were pooled to give n = 8 tows.

Location	Latitude	Longitude	Sample Date	Sample time (24:00)	Depth (m)
Arroyo Burro, Mainland	-34.239	-119.444	7/13/2015	9:44	8.2
Arroyo Burro, Mainland	-34.239	-119.444	7/13/2015	10:33	8.4
Arroyo Burro, Mainland	-34.239	-119.444	7/13/2015	10:36	8.4
Arroyo Burro, Mainland	-34.239	-119.444	7/13/2015	10:40	8.5
Arroyo Burro, Mainland	-34.239	-119.444	9/28/2015	20:04	8.2
Arroyo Burro, Mainland	-34.239	-119.444	11/11/2015	8:33	7.6
Mohawk Reef, Mainland	-34.236	-119.437	7/13/2015	11:54	7.1
Mohawk Reef, Mainland	-34.236	-119.437	7/13/2015	12:10	7.1
Mohawk Reef, Mainland	-34.236	-119.437	7/13/2015	12:18	7.1
Mohawk Reef, Mainland	-34.236	-119.437	9/28/2015	20:20	7.6
Mohawk Reef, Mainland	-34.236	-119.437	9/28/2015	20:22	7.6
Mohawk Reef, Mainland	-34.236	-119.437	11/11/2015	8:53	7.6
Anacapa Island	-34.012	-119.362	7/28/2015	11:55	6.1
Anacapa Island	-34.012	-119.362	7/28/2015	12:02	6.1
Anacapa Island	-34.012	-119.362	7/28/2015	12:10	6.1
Santa Cruz Island	-34.030	-119.435	7/28/2015	9:20	8.1

Table 3. Metadata for links-list columns.

Column Name	Description
consumers	Node.ID of consumer
consumerName	Name.Sp.stage of consumer
Consumer.Sp.stage	Sp.ID.stage.ID of consumer
consumerSP	Sp.ID of consumer
consumerStage	Stage.ID of consumer
resources	Node.ID of resource
resourceName	Name.Sp.stage of resource
Resource.Sp.stage	Sp.ID.stage.ID of resource
resourceSP	Sp.ID of resource
resourceStage	Stage.ID of resource
Consumer.Interaction.Code	Code indicating consumer interaction type, after framework of Lafferty and Kuris 2002. (1) predation, (3) micropredation/grazing, (4) parasitic castration,(5) pathogen, (6) Typical parasite, (8) Parasitoid, (12) trophically transmitted parasite, (14) concomittant predation, (16) predation on free-living non-feeding stage, (19) parasite intraguild antagonism , (20) intimate habitat association (non-trophic)
Site	Code indicating type of association between interacting species. (1) Internal parasitic interaciton, (2) Ectoparasitic Interaction, (3) Free-living species interaction, (NA) Concomitant predation
confidence	Numerical code identifying certainty category: (1) very certain, (2) certain, (3) somewhat certain, (4) uncertain but plausible
justification	Code indicating best justification for inclusion. (1) personal observation; (2) in LTER or CNIP surveys; (3) in literature (incl. books); (4) inferred via shared habitat and general diet cateory; (5) grey literature; (6) more broadly in literature (e.g. group listed but not that species); (7) expert opinion; (9) related species observed directly; (10) inferred based on closely related species in literature; (11) inferred based on host trophic links and known hosts from literature; (12) inferred based on parasite presence and known life cycle; (13) inferred based on False Negative likelihood (supported by life history information)
Localities	Locations where observations occurred (or where associated references took place). For inferred links, these are the locations of studies that provided natural history information supporting the inference.

Table 4. Sites where sampling for parasites occurred.

Program	Location	Site Name	Latitude	Longitide
LTER	Mainland	Arroyo Quemado	34.468	-120.119
LTER	Mainland	Naples	34.422	-119.952
na	Mainland	UCSB seawater intake	34.404	-119.836
LTER	Mainland	Goleta Bay/ Pier	34.414	-119.822
na	Mainland	Rich's IV	34.400	-119.780
na	Mainland	Unnamed, Near Arroyo Burro	34.413	-119.746
LTER	Mainland	Arroyo Burro	34.400	-119.745
LTER	Mainland	Mohawk	34.394	-119.730
LTER	Mainland	Carpinteria	34.392	-119.542
PISCO	Anacapa Island	WIN	34.009	-119.396
CINP KFM	Anacapa Island	East Fish Camp	34.004	-119.376
na	Anacapa Island	Unnamed, Back Side	34.010	-119.375
PISCO	Anacapa Island	South	34.011	-119.368
PISCO	Santa Cruz Island	Haz	34.061	-119.829
LTER	Santa Cruz Island	Diablo	34.059	-119.757
LTER	Santa Cruz Island	Twin Harbors West	34.044	-119.715
CINP KFM	Santa Cruz Island	Pelican Bay	34.035	-119.703
PISCO	Santa Cruz Island	Valley	34.983	-119.663
CINP KFM	Santa Cruz Island	Yellow Banks	33.990	-119.563
CINP KFM	Santa Cruz Island	Pedro Reef	34.038	-119.525
CINP KFM	Santa Rosa Island	Rhodes Reef	34.033	-120.107
CINP KFM	Santa Rosa Island	East Point	33.940	-119.965

Table 5. Species dissected and sample sizes. Some species dissected were not included in the food web if they did not meet abundance criteria but are included here as they may be useful for other parasitological studies.

Phylum	Host Group	Host Genus	Host Sp.	N
Annelida	Polychaeta	*Diopatra*	*ornata*	3
Annelida	Polychaeta	*Pherusa*	*papillata*	1
Annelida	Polychaeta	*Phragmatopoma*	*californica*	61
Annelida	Polychaeta	*Spirorbinae*	*spp.*	25
Arthropoda	Amphipoda	*Acanthinuella*	*spirata*	2
Arthropoda	Amphipoda	*Caprella*	*spp.*	102
Arthropoda	Amphipoda	*Caprella*	*verrucosa*	1
Arthropoda	Amphipoda	*Unk. Gammaridea*	*sp.*	11
Arthropoda	Decapoda	*Cancer*	*antennarius*	6
Arthropoda	Decapoda	*Cancer*	*sp.*	10
Arthropoda	Decapoda	*Hemigrapsus*	*spp.*	4
Arthropoda	Decapoda	*Heptacarpus*	*spp.*	327
Arthropoda	Decapoda	*Hippolyte*	*clarki*	32
Arthropoda	Decapoda	*Hippolyte*	*sp.*	83
Arthropoda	Decapoda	*Isocheles*	*pilosus*	7
Arthropoda	Decapoda	*Loxorhynchus*	*crispatus*	6
Arthropoda	Decapoda	*Loxorhynchus*	*grandis*	14
Arthropoda	Decapoda	*Pachygrapsus*	*sp.*	1
Arthropoda	Decapoda	*Pagurus*	*hemphilli*	1
Arthropoda	Decapoda	*Pagurus*	*samuelis*	4
Arthropoda	Decapoda	*Panulirus*	*interruptus*	6
Arthropoda	Decapoda	*Pugettia*	*producta*	8
Arthropoda	Isopoda	*Idotea*	*sp.*	10
Arthropoda	Isopoda	*Penidotea*	*resecata*	6
Arthropoda	Isopoda	*Sphaeromatidae*	*sp.*	3
Arthropoda	Isopoda	*Unk Isopoda*	*sp.*	1
Chordata	Elasmobranch	*Cephaloscyllium*	*ventriosum*	6
Chordata	Elasmobranch	*Heterodontus*	*francisci*	5
Chordata	Elasmobranch	*Mustelus*	*henlei*	1
Chordata	Elasmobranch	*Rhinobatos*	*productus*	1
Chordata	Elasmobranch	*Torpedo*	*californica*	1
Chordata	Fish	*Alloclinus*	*holderi*	1
Chordata	Fish	*Anisotremus*	*davidsonii*	4
Chordata	Fish	*Brachyistus*	*frenatus*	15
Chordata	Fish	*Caulolatilus*	*princeps*	2
Chordata	Fish	*Chromis*	*punctipinnis*	14
Chordata	Fish	*Embiotoca*	*jacksoni*	20
Chordata	Fish	*Embiotoca*	*lateralis*	3
Chordata	Fish	*Gibbonsia*	*montereyensis*	2
Chordata	Fish	*Girella*	*nigricans*	8
Chordata	Fish	*Haliochoeres*	*semicinctus*	13
Chordata	Fish	*Heterostichus*	*rostratus*	6
Chordata	Fish	*Hyperprosopon*	*argenteum*	2
Chordata	Fish	*Hyperprosopon*	*ellipticum*	4
Chordata	Fish	*Hypsoblennius*	*jenkinsi*	3
Chordata	Fish	*Hypsurus*	*caryi*	8
Chordata	Fish	*Hypsypops*	*rubicundus*	2
Chordata	Fish	*Lythrypnus*	*dalli*	1
Chordata	Fish	*Medialuna*	*californiensis*	19
Chordata	Fish	*Micrometrus*	*aurora*	2
Chordata	Fish	*Neoclinus*	*stephensae*	2
Chordata	Fish	*Ophiodon*	*elongatus*	4
Chordata	Fish	*Oxyjulis*	*californica*	23
Chordata	Fish	*Oxylebius*	*pictus*	15
Chordata	Fish	*Paralabrax*	*clathratus*	18
Chordata	Fish	*Phanerodon*	*furcatus*	1
Chordata	Fish	*Pleuronicthys*	*verticalis*	1
Chordata	Fish	*Rhacochilus*	*toxotes*	15
Chordata	Fish	*Rhacochilus*	*vacca*	16
Chordata	Fish	*Rhinogobiops*	*nicholsii*	2
Chordata	Fish	*Scorpaena*	*guttata*	7
Chordata	Fish	*Sebastes*	*atrovirens*	15
Chordata	Fish	*Sebastes*	*auriculatus*	2
Chordata	Fish	*Sebastes*	*carnatus*	1
Chordata	Fish	*Sebastes*	*caurinus*	1
Chordata	Fish	*Sebastes*	*goodei*	1
Chordata	Fish	*Sebastes*	*mystinus*	12
Chordata	Fish	*Sebastes*	*paucispinus*	1
Chordata	Fish	*Sebastes*	*rastrelliger*	2
Chordata	Fish	*Sebastes*	*serranoides*	17
Chordata	Fish	*Semicossyphus*	*pulcher*	16
Cnidaria	Anemone	*Epiactis*	*prolifera*	3
Echinodermata	Echinoderm	*Mesocentrotus*	*franciscanus*	19
Echinodermata	Echinoderm	*Patiria*	*miniata*	9
Echinodermata	Echinoderm	*Strongylocentrotus*	*purpuratus*	24
Echinodermata	Holothuroidea	*Eupentacta*	*quinquesemita*	2
Echinodermata	Ophiuroidea	*Ophioplocus*	*esmarki*	22
Mollusca	Bivalvia	*Chaceia*	*ovoidea*	1
Mollusca	Bivalvia	*Crassedoma*	*giganteum*	9
Mollusca	Bivalvia	*Lithophaga*	*plumula*	1
Mollusca	Bivalvia	*Mytilus*	*californianus*	30
Mollusca	Bivalvia	*Parapholas*	*californica*	18
Mollusca	Cephalopoda	*Octopus*	*bimaculoides*	32
Mollusca	Gastropoda	*Acanthodons*	*luten*	1
Mollusca	Gastropoda	*Acteocina*	*harpa*	3
Mollusca	Gastropoda	*Aegires*	*albopunctatus*	2
Mollusca	Gastropoda	*Aeolid*	*sp.*	3
Mollusca	Gastropoda	*Alia*	*carinata*	204
Mollusca	Gastropoda	*Amphissa*	*columbiana*	21
Mollusca	Gastropoda	*Aplysia*	*californica*	5
Mollusca	Gastropoda	*Barleeia*	*californica*	5
Mollusca	Gastropoda	*Barleeia*	*haliotiphila*	243
Mollusca	Gastropoda	*Bulla*	*gouldiana*	2
Mollusca	Gastropoda	*Caecum*	*californicum*	8
Mollusca	Gastropoda	*Ceratostoma*	*nuttalli*	29
Mollusca	Gastropoda	*Ceratostoma*	*sp.*	5
Mollusca	Gastropoda	*Clathurella*	*canfieldi*	3
Mollusca	Gastropoda	*Conus*	*californicus*	83
Mollusca	Gastropoda	*Corambe*	*pacifica*	21
Mollusca	Gastropoda	*Crepidula*	*adunca*	8
Mollusca	Gastropoda	*Crepipatella*	*lingulata*	197
Mollusca	Gastropoda	*Cuthona*	*lagunae*	5
Mollusca	Gastropoda	*Cuthona*	*sp.*	8
Mollusca	Gastropoda	*Cypraea*	*spadicea*	50
Mollusca	Gastropoda	*Dendronotus*	*sp.*	20
Mollusca	Gastropoda	*Diodora*	*arnoldi*	2
Mollusca	Gastropoda	*Dirona*	*picta*	3
Mollusca	Gastropoda	*Doriopsilla*	*albopuntata*	5
Mollusca	Gastropoda	*Doto*	*amyra*	32
Mollusca	Gastropoda	*Erato*	*columbella*	1
Mollusca	Gastropoda	*Eulithidium*	*pulloides*	90
Mollusca	Gastropoda	*Flabellina*	*Iodinea*	28
Mollusca	Gastropoda	*Gnorimosphaeroma*	*sp.*	1
Mollusca	Gastropoda	*Hermissenda*	*crassicornis*	1
Mollusca	Gastropoda	*Homalopoma*	*baculum*	1
Mollusca	Gastropoda	*Iselica*	*ovoidea*	1
Mollusca	Gastropoda	*Kelletia*	*kelleti*	51
Mollusca	Gastropoda	*Lacuna*	*unifasciata*	94
Mollusca	Gastropoda	*Lirularia*	*sp.*	2
Mollusca	Gastropoda	*Maxwellia*	*gemma*	29
Mollusca	Gastropoda	*Megastraea*	*undosa*	23
Mollusca	Gastropoda	*Megathura*	*crenulata*	39
Mollusca	Gastropoda	*Metaxia*	*convexa*	2
Mollusca	Gastropoda	*Mitra*	*idae*	10
Mollusca	Gastropoda	*Navanax*	*inermis*	9
Mollusca	Gastropoda	*Neobernaya*	*spadicea*	2
Mollusca	Gastropoda	*Norrisia*	*norrisii*	25
Mollusca	Gastropoda	*Ocinebrina*	*circumtexta*	1
Mollusca	Gastropoda	*Ocinebrina*	*interfossa*	1
Mollusca	Gastropoda	*Ocinebrina*	*sp.*	3
Mollusca	Gastropoda	*Ocinebrium*	*Subangulato*	2
Mollusca	Gastropoda	*Ophiodermella*	*inermis*	2
Mollusca	Gastropoda	*Polycera*	*atra*	2
Mollusca	Gastropoda	*Pseudomelatoma*	*torosa*	6
Mollusca	Gastropoda	*Pteropurpura*	*festiva*	49
Mollusca	Gastropoda	*Pteropurpura*	*trialata*	5
Mollusca	Gastropoda	*Pupillaria*	*salmonea*	2
Mollusca	Gastropoda	*Serpulorbis*	*squamigerus*	9
Mollusca	Gastropoda	*Tegula*	*aureotincta*	12
Mollusca	Gastropoda	*Triopha*	*catalinae*	4
Mollusca	Gastropoda	*Triphora*	*sp.*	1
Mollusca	Gastropoda	*Trivia*	*californiana*	1
Mollusca	Gastropoda	*Unk Nudibranch*	*sp.*	7
Mollusca	Gastropoda	*Urosalpinx*	*subangulata*	10

Table 6. For these host species, parasite records were included from San Francisco Bay, CA, USA to Punta San Hipolito, Baja California, Mexico.

Common name	Genus	species
Leopard shark	*Triakis*	*semifasciata*
Brown Smooth-hound shark	*Mustelus*	*henlei*
Seven-gill shark	*Notorynchus*	*cepedianus*
California sea lion	*Zalophus*	*californianus*
Pacific bottlenose dolphin	*Tursiops*	*truncatus*
Giant sea bass	*Stereolepis*	*gigas*
Western/Clark's Grebe	*Aechmophorus*	*occidentalis*
Great Egret	*Ardea*	*alba*
Great blue heron	*Ardea*	*herodias*
Snowy Egret	*Egretta*	*thula*
Common Loon	*Gavia*	*immer*
California Gull	*Larus*	*californicus*
Mew Gull	*Larus*	*canus*
Heermann's Gull	*Larus*	*heermanni*
Western Gull	*Larus*	*occidentalis*
Surf Scoter	*Melanitta*	*perspicillata*
Black crowned night heron	*Nycticorax*	*nycticorax*
Brown Pelican	*Pelecanus*	*occidentalis*
Double crested cormorant	*Phalacrocorax*	*auritus*
Pelagic cormorant	*Phalacrocorax*	*pelagicus*
Brandt's cormorant	*Phalacrocorax*	*penicillatus*
Caspian tern	*Sterna*	*caspia*
Elegant tern	*Sterna*	*elegans*
Royal tern	*Thalasseus*	*maximus*

Table 7. Links removed due to high false negative errors.

Parasite Class	Parasite Genus	Parasite species	Host Class	Host Genus	Host species	Link evidence
Cestoda	*Adenocephalus*	*pacificus*	Mammalia	*Zalophus*	*californianus*	3
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Embiotoca*	*jacksoni*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Hypsurus*	*caryi*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Paralabrax*	*clathratus*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Rhacochilus*	*toxotes*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Rhacochilus*	*vacca*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Scorpaena*	*guttata*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Sebastes*	*serranoides*	1
Hexanauplia	*Caligidae.gen*	spp.	Actinopterygii	*Semicossyphus*	*pulcher*	1
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Chromis*	*punctipinnis*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Hypsypops*	*rubicundus*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Medialuna*	*californiensis*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Oxyjulis*	*californica*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Rhacochilus*	*toxotes*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Scorpaenichthys*	*marmoratus*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Sebastes*	*atrovirens*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Sebastes*	*carnatus*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Sebastes*	*mystinus*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Sebastes*	*serranoides*	3
Hexanauplia	*Caligus*	*hobsoni*	Actinopterygii	*Semicossyphus*	*pulcher*	3
Hexanauplia	*Chondracanthus*	*pinguis*	Actinopterygii	*Hexagrammos*	*decagrammus*	3
Hexanauplia	*Chondracanthus*	*pinguis*	Actinopterygii	*Scorpaenichthys*	*marmoratus*	3
Hexanauplia	*Chondracanthus*	*pinguis*	Actinopterygii	*Sebastes*	*auriculatus*	3
Hexanauplia	*Chondracanthus*	*pinguis*	Actinopterygii	*Sebastes*	*caurinus*	3
Hexanauplia	*Chondracanthus*	*pinguis*	Actinopterygii	*Sebastes*	*serranoides*	3
Hexanauplia	*Lernaeopodidae.gen*	sp.A	Actinopterygii	*Sebastes*	*atrovirens*	1
Hexanauplia	*Lernaeopodidae.gen*	sp.B	Actinopterygii	*Chromis*	*punctipinnis*	1
Hexanauplia	*Nemesis*	*carchariaeglauci*	Elasmobranchii	*Triakis*	*semifasciata*	3
Hexanauplia	*Pandarus*	*cranchii*	Elasmobranchii	*Triakis*	*semifasciata*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Cymatogaster*	*aggregata*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Embiotoca*	*lateralis*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Hyperprosopon*	*argenteum*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Phanerodon*	*furcatus*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Rhacochilus*	*vacca*	3
Ichthyostraca	*Argulus*	*pugettensis*	Actinopterygii	*Sebastes*	*caurinus*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Atherinops*	*affinis*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Cymatogaster*	*aggregata*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Embiotoca*	*jacksoni*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Paralabrax*	*clathratus*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Phanerodon*	*furcatus*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Rhacochilus*	*vacca*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Scorpaena*	*guttata*	3
Malacostraca	*Nerocila*	*californica*	Actinopterygii	*Stereolepis*	*gigas*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*atrovirens*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*auriculatus*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*carnatus*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*caurinus*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*serranoides*	3
Monogenea	*Megalocotyle*	*marginata*	Actinopterygii	*Sebastes*	*serriceps*	3
Palaeacanthocephala	*Southwellina*	*hispida*	Aves	*Ardea*	*herodias*	3
Palaeacanthocephala	*Southwellina*	*hispida*	Aves	*Gavia*	*immer*	3
Palaeacanthocephala	*Southwellina*	*hispida*	Aves	*Nycticorax*	*nycticorax*	3
Palaeacanthocephala	*Southwellina*	*hispida*	Aves	*Pelecanus*	*occidentalis*	3
Palaeacanthocephala	*Southwellina*	*hispida*	Aves	*Phalacrocorax*	*auritus*	3
Rhabdita	*Anisakis*	*simplex sp. complex*	Elasmobranchii	*Notorynchus*	*cepedianus*	3
Rhabdita	*Dichelyne*	*kanabus*	Actinopterygii	*Cymatogaster*	*aggregata*	3
Rhabdita	*Dichelyne*	*kanabus*	Actinopterygii	*Embiotoca*	*jacksoni*	3
Rhabdita	*Dichelyne*	*kanabus*	Actinopterygii	*Embiotoca*	*lateralis*	3
Rhabdita	*Dichelyne*	*kanabus*	Actinopterygii	*Rhacochilus*	*vacca*	3
Trematoda	*Derogenes*	*varicus*	Actinopterygii	*Ophiodon*	*elongatus*	1
Trematoda	*Derogenes*	*varicus*	Actinopterygii	*Sebastes*	*caurinus*	3
Trematoda	*Derogenes*	*varicus*	Actinopterygii	*Sebastes*	*paucispinis*	3
Trematoda	*Himasthla*	sp.	Aves	*Gavia*	*immer*	3
Trematoda	*Himasthla*	sp.	Aves	*Larus*	*californicus*	3
Trematoda	*Himasthla*	sp.	Aves	*Larus*	*canus*	3
Trematoda	*Maritrema*	*pacificum*	Aves	*Larus*	*californicus*	3
Trematoda	*Microphallus*	*nicolli*	Aves	*Gavia*	*immer*	3
Trematoda	*Philophthalmus*	*andersoni*	Aves	*Sterna*	*caspia*	3
Trematoda	*Philophthalmus*	*andersoni*	Aves	*Thalasseus*	*maximus*	3