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The food web for the sand flats at Palmyra Atoll

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution and Marine Biology

by

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September 2018

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September 2018

The food web for the sand flats at Palmyra Atoll

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by

John Peter McLaughlin

Acknowledgements

Dedicated to my parents, John and Sue, and to Emily and Cricket. Thank you for all your love and support.

Vita of John Peter McLaughlin
September 2018

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Abstract

The food web for the sand flats at Palmyra Atoll

by

John Peter McLaughlin

This dissertation describes and analyzes the Palmyra Atoll sand flat food web. This food web is unique in measuring the body sizes, densities, and feeding links for all life stages of free-living and parasitic metazoans. Chapter 1 puts the research in context by reviewing the roles of parasites in marine food webs. Chapter 2 starts by describing the physical attributes (sediment particle size, water depth, temperature) of the 35 random sampling sites. It then lists the 22 sampling methods used to estimate the body size and abundance of 670 life stages comprising 275 species. The resulting free-living community contains represents 195 free-living species across 18 phyla, and 389 separate life stages. Chapter 2 then describes how parasites were measured from >2500 hosts collected and dissected to reveal a parasite community with 80 species across 9 phyla, and 281 separate life stages. Chapter 3 then uses stomach contents, field observations, literature, and natural history to estimate 24,575 trophic interactions, ontogenetic development and parasite transmission pathways among the 670 nodes in Chapter 2. Chapter 4 compares the Palmyra sand flat food web with the only published food web described in similar detail, the west coast estuary food web. In both systems, parasites make contributions to richness, abundance, and biomass comparable to

free-living consumer groups, such as birds. Further, in both systems parasites dominate

network structure in ways that free-living consumers cannot. These results suggest that

parasites make general and important contributions to ecosystem structure. Our

understanding of food webs is incomplete without them.

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1 Parasites in marine food webs

1.1 Introduction

"Marine disease" is often used as an epithet to express disdain about parasites that infect fisheries species, species we cherish, or ourselves. As such, "Marine disease ecology" is often a crisis discipline like conservation and veterinary science (or their offspring, conservation medicine), whose aim is to understand and solve problems created by marine diseases. In contrast, the marine parasitology discipline sits within the scientific tradition that observes species, whether they be whales or whale lice, with a more dispassionate, neutral eye characterizing them as neither good nor bad. This impartial view, taken in this chapter, can provide context to marine disease ecologists, better equipping them to find and solve infectious disease problems by providing a broader perspective on the role parasites play in marine ecosystems. Here, we use food webs as a conceptual lens to focus on the question: What can we learn from parasites in marine ecosystems?

From sperm whales eating giant squid, to abyssal sponges filtering organic debris, marine biology is often about food webs. In 1966, Robert Paine changed marine ecology forever when he applied a food-web perspective to the rocky intertidal (Lafferty and Suchanek 2016; Paine 1966), and ecologists have since assembled food webs for more than 100 marine systems (Fig. 1). By tracing energy flow through ecosystems, food webs function like ecological maps illustrating potential indirect effects, bottom-up processes, trophic cascades and resource competition. One way marine ecologists describe and compare food webs is with network theory (Dunne *et al.* 2004). Networks have two elements: nodes (sometimes called vertices) and links (sometimes called edges). In food webs, nodes are

often species or life-stages (e.g. larvae or adults), whereas the links connect who eats whom. Ecologists analyze food webs to measure ecological complexity and estimate ecological stability. Food web complexity is often defined as species richness and the link distribution among those species (May 1973). Food webs, like any complex system, have additional structure. When plotted, some are short and squat, others are tall and thin, some are dense, and others sparse. Such structure, or topology, can be described with graph theory tools, just as shipping routes have topologies that distinguish busy ports from smaller harbors. One of the best-cited marine food webs describes 203 links between 29 nodes in the Benguela current fishery (Yodzis 1998). On average, the shortest distance between nodes in marine webs is just a few links, suggesting that marine systems are less modular than terrestrial systems and perturbations such as over-fishing could spread rapidly through the entire system (Dunne *et al.* 2004). As for the Benguela web, most marine food webs omit parasites (Fig. 1.1). With parasites absent from a major conceptual framework, it is no wonder that ecologists have often ignored parasites.
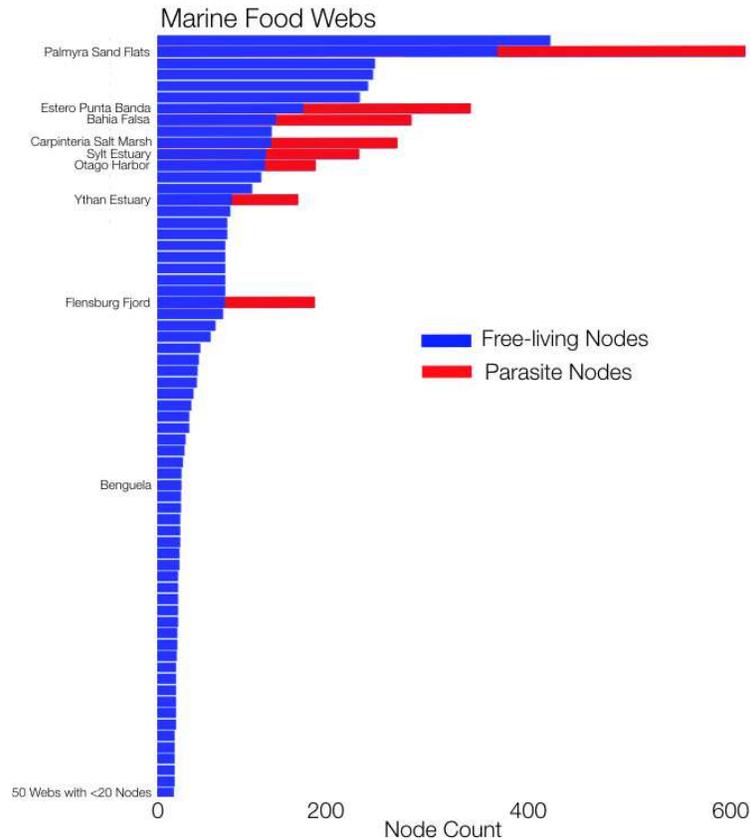
Figure 1. 1 Marine food webs. Most marine food webs do not include parasites.

1.2 Parasites Affect Food Webs

Whether or not ecologists think about them, parasites might be the most abundant organisms in the oceans, and parasitism the most common lifestyle. Viruses, described as "a piece of bad news wrapped up in a protein" (Medawar and Medawar 1985), rule the sea at 10 billion per liter (Fuhrman 1999). Most viruses are bacteriophages, with about 10^{23} viral infections occurring in the ocean every second (Suttle 2007). But all marine species have viruses and other specialist parasites (Dobson *et al.* 2008; Théodoridès 1989), suggesting that there could be more parasitic than free-living species (Windsor 1998). Although we don't know their exact contribution to biodiversity, when researchers have counted them, parasites

increase taxonomic and functional diversity in marine systems. In estuaries, over a third of metazoan species are parasites (Hechinger, Ryan F. *et al.* 2011). This contribution to taxonomic diversity by parasites extends beyond species counts. Some marine taxa are all (e.g. Orthonectida) or mostly (e.g. Platyhelminthes) parasitic, and including parasites adds six new phyla to estuarine webs. In addition to extending taxonomic diversity, parasites bring unique consumer strategies (e.g. parasitoidism, castration) to food webs. Furthermore, parasites balance how consumer-resource body size ratios change with trophic level (Lafferty and Kuris 2002). For instance, even as gray whales ingest tiny benthic amphipods from the muddy seafloor, tiny parasitic amphipods (whale lice) eat the whale's flaking skin. Pervasiveness and uniqueness makes it possible for parasites to affect marine food web structure and dynamics.

Comparing food-web topology with and without parasites helps illustrate how parasites affect food-web structure. Almost all published marine food webs that include parasites are from temperate estuaries (Dunne, J. A. *et al.* 2013). In these food webs, parasites increase complexity (Dunne, J. A. *et al.* 2013), dominating food web structure by participating in 75% of trophic interactions (Lafferty, Dobson*, et al.* 2006), links that would not be accounted for if parasites were omitted. Including parasites increases food web complexity and nestedness, and trophic level resolution, challenging our current ideas about food web structure (Dunne, J. A. *et al.* 2013; Lafferty, Dobson*, et al.* 2006) (Fig. 1.2). Although we now understand that by omitting parasites ecologists have underestimated food web complexity, we are just beginning to investigate the implications of this for energy flow through marine systems.

Palmyra Sand Flats Food Web
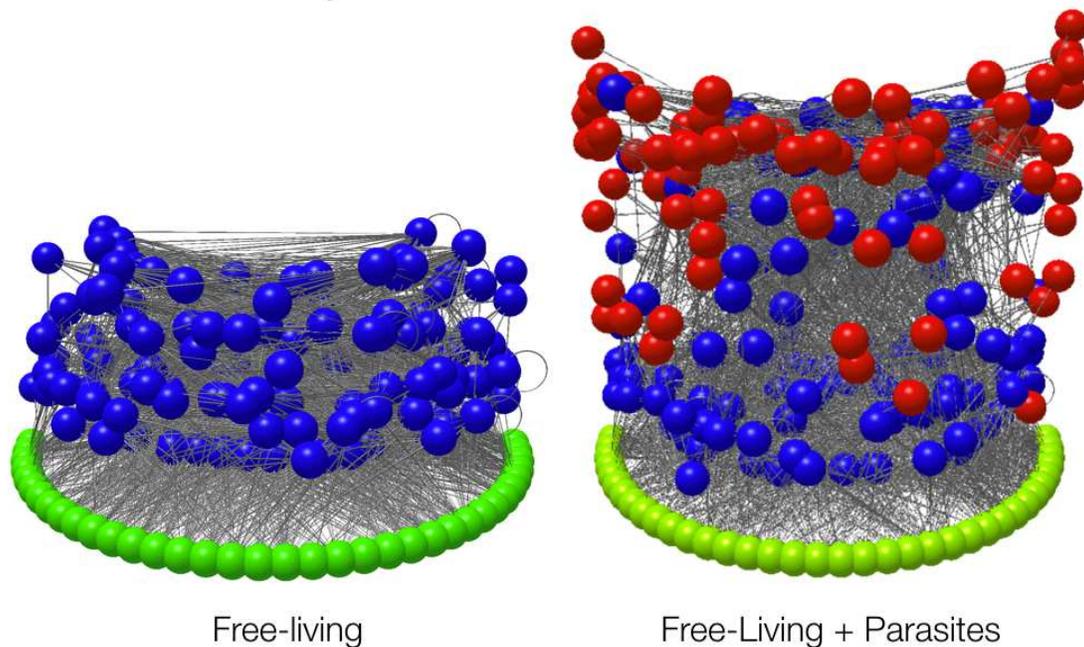
Figure 1. 2 Palmyra food webs. Parasites alter structure and energy flow in the Palmyra marine food web. Spheres indicate species (green, basal; blue, free-living; red, parasites), grey lines indicated feeding links and vertical height indicates trophic level.

As consumers, parasites take energy from hosts for their own maintenance, growth, reproduction and metabolism. Therefore, their direct effects should be proportional to their biomass in marine ecosystems. In estuarine food webs, parasite have the same biomass density as similar-sized free-living species, after accounting for trophic level (Hechinger, R. *et al.* 2011). This suggests that as a group, energetic contributions from parasites are proportional to those from other consumer groups. Indeed, parasite biomass exceeds bird biomass, the top predators in estuaries (Kuris *et al.* 2008). But parasites alter energy flow beyond the host tissue they eat. Hosts can try to avoid infection, often at some cost (Weinstein *et al.* 2018). Infection risk alone forces hosts to invest in immune systems (Moret

and Schmid-Hempel 2000). An important innate immune response was discovered in a marine organism, when in 1882, Ilya Mechnikov observed phagocytes attacking a splinter he had introduced into a sea star larva (Tauber 2003). Furthermore, hosts must repair and replace tissue damaged by parasites (Allen and Wynn 2011), a cost that does not occur in predator-prey interactions. For these reasons, the impact that parasites have on food webs extends far beyond their biomass density, just as some predators affect prey populations as much through the fear they induce as by the individuals they eat.

1.2.1 Parasites as consumers

Most marine ecosystems build on the photosynthesis done by phytoplankton, macroalgae, or algae-coral symbioses (Falkowski *et al.* 2004), and these primary producers are also subject to infection. Viruses, which infect nearly all phytoplankton (Fuhrman 1999), can end phytoplankton blooms (Bratbak *et al.* 1993) and density-dependent dynamics have been demonstrated in the lab (Brussaard 2004). Parasites also infect benthic macrophytes, sometimes with dramatic effect. Between 1931-34 a wasting disease (caused by *Labyrinthula zosterae*) reduced eel grass populations by 90% in the temperate Atlantic (Muehlstein 1989). Caribbean elkhorn coral (*Acropora palmata*) have been decimated by white pox disease caused by an enterobacterium (*Serratia marscens*) associated with the human gut (Patterson *et al.* 2002). Elkhorn coral declines have simplified reef structure, increased algal cover and altered invertebrate communities (Aronson and Precht 2001; Gladfelter 1982). Although parasites can act as herbivores in marine systems, they can also benefit phytoplankton by releasing iron from lysed bacteria (Poorvin *et al.* 2004). Further, viral infection can increase nitrogen uptake and diversify the nitrogen sources an infected cell can use (Monier *et al.*

2017). Finally, viruses can increase phytoplankton diversity by infecting fast growing species, preventing them from displacing slower growing, but more resistant species (Suttle 2007). Thus, frequency-dependent infectious processes can reduce or increase marine primary producers, whereas density-dependent process can and regulate their populations.

Although marine plants can host parasites, parasites can also indirectly affect marine plants through trophic cascades. For instance, sea urchins can increase to densities that defoliate temperate kelp beds, creating urchin barrens. However, urchins can also reach densities that support disease outbreaks, which, in turn decimate urchin populations. Kelp then increases after diseases knock urchin populations back below densities that support disease (Behrens and Lafferty 2004; Scheibling 1986). Although sea urchin epizootics can protect kelp forests, they can harm coral reefs. Perhaps the best example of marine disease altering a food web, was in 1983-84 when an unknown pathogen in the Caribbean reduced urchin (*Diadema antillarium)* densities by 94% (Lessios 1988). This disease-driven urchin die-off led to a phase shift from coral to macroalgae (Dudgeon *et al.* 2010) that has yet to recover. Consumer mass mortalities caused by disease can have destabilizing impacts that extend beyond indirect effects on primary producers.

Marine diseases sometimes cause mass mortalities in other echinoderms, altering the important roles they play in marine systems (Uthicke *et al.* 2009). The latest example occurred between 2013-15, when Sea Star Wasting Disease (hypothesized as a virus) devastated sea star populations along the West coast of North America, from Baja California to Alaska (Montecino-Latorre *et al.* 2016). The dominant sea star in rocky intertidal habitats, *Pisaster ochraecus*, experienced population declines between 59-84% (Menge *et al.* 2016) depressing predation rates on the foundational mussel species, *Mytilus californianus* (Menge

et al. 2016). A similar mass mortality occurred in 1978, when an unknown pathogen devastated *Heliaster kubinji* populations in the Gulf of California (Dungan *et al.* 1982). This keystone predator was the "most common, obvious and widely distributed shore starfish in the Gulf" (Steinbeck and Ricketts 2009), but as late as 2008 the sun star population had not recovered at most sites (Herrero-Pérezrul 2008). What led to these various echinoderm mass mortalities remains a mystery, though warming or pathogen introductions are speculated to be involved (Harvell *et al.* 1999). Other invertebrate mass mortalities are better understood. In 1994, the largest remaining black abalone populations experienced mass mortalities in Southern California (Lafferty and Kuris 1993) due to a novel Rickettsial pathogen that increases in lethality with temperature and in infectivity with temperature variation (Ben-Horin *et al.* 2013). The black abalone population has since failed to recover and the intertidal encrusting community underwent a phase shift (Miner *et al.* 2006). Marine mass mortalities illustrate how parasite-driven trophic cascades (Buck and Ripple 2017) can shift marine ecosystems states in directions that people value or regret.

If sea urchin and sea star diseases can alter food webs, the same might apply to marine mammal parasites. *Toxoplasma gondii* is an apicomplexan parasite that can only reproduce in cats, but can infect and kill marine mammals. For instance, *Toxoplasma gondii* may increase the mortality rate of sea otters (*Enhydra lutris*) which are exposed to this terrestrial parasite by freshwater runoff. About half of all sea otters test positive for T. gondii, and dead sea otters are twice as likely to test positive (Miller *et al.* 2002). Otters are keystone predators (Estes and Palmisano 1974), suggesting otter diseases could destabilize kelp forests. Morbilliviruses infect marine mammals worldwide (Van Bressem *et al.* 2001) and epizootics are triggered when naive populations are exposed to new viruses. Such outbreaks

have caused mass die-offs in pinniped (Härkönen *et al.* 2006) and cetacean populations around the world (Guardo *et al.* 2005). These marine mammal mass mortalities could have indirect effects, because many marine mammals feed at high trophic levels and have high caloric requirements (Hammill and Stenson 2000).

1.2.2 Parasites as resources

Incorporating parasites into food webs leads to an unusual question: What eats parasites? The answer is many things; parasites are prey in over half the interactions in estuarine food webs. Some predators eat parasites on purpose, such as topsmelt that pick lice off gray whales in the whales' estuarine breeding grounds (Swartz 1981), and cleaning symbioses are common in marine ecosystems (Grutter 1999). Many parasites have free-living infective stages that might be food for planktivores (Johnson *et al.* 2010). Indeed, planktonic viruses are important resources for heterotrophic flagellates (González and Suttle 1993), and zoospores produced by fungi that infect algae can be important resources for small grazers and filter feeders in coastal systems (Gleason *et al.* 2011). Trematodes in marine snails produce many free-swimming cercariae (Thieltges *et al.* 2008), with annual biomass production in temperate estuaries exceeding 20 kg per hectare (Kuris *et al.* 2008). These free-swimming cercariae are eaten by filter feeding invertebrates and fishes (Hechinger, Ryan F. *et al.* 2011; Kaplan *et al.* 2009). These and other free-living infective stages could be an abundant energy source for low-trophic level consumers in marine systems.

More often, predators eat parasites by accident. In estuaries, tertiary consumers like crabs (predating snails), fish and birds (predating invertebrates and fish) eat parasites by eating their hosts. When a host is eaten, most parasites (71%) suffer concurrent predation and

are digested, creating a signature triangular link motif between a parasite, its host, and the host's predator. Concurrent predation accounts for 31% of all links in estuary food webs. At Palmyra Atoll, blacktip reef sharks (*Carcharhinidae melanopterus*) eat three mullet (Mugilidae) species, hosting over a dozen parasites that cannot use blacktip sharks as hosts (McLaughlin *et al.* in press). But some parasites can survive their host being eaten by infecting the predator in a process known as trophic transmission (Lafferty and Shaw 2013). These parasites use predation to transmit from a prey host to a predator host. Forty-eight percent of Palmyra Atoll trematodes require their intermediate fish host to be eaten by a Jack (Carangidae) to complete their lifecycle. Including parasites as potential as resources reveals one unexpected way that parasites affect food-web structure (Dunne, J. A. *et al.* 2013).

Although traveling through food webs can be treacherous, some parasites bend food webs to their advantage. The trematode *Euhaplorchis californiensis* encysts on the killifish brain (Shaw *et al.* 2010) and tilts the odds of trophic transmission in its favor. To complete its life cycle, the trematode must navigate the estuarine food web to get from the fish's brain to a bird's gut. Encysted on the fish's brain, the parasite manipulates monoamine neurotransmitters (Shaw *et al.* 2009), causing its fish host to exhibit behaviors that increase bird predation (Lafferty and Morris 1996). This behavior manipulation (Kuris 2003; Lafferty and Shaw 2013) and may be common in marine systems (Poulin 2010), potentially altering the amount and direction of energy flow through marine systems.

Putting parasites in food webs shows how parasite diversity and host use adds to food web complexity. Furthermore, substantial parasite biomass alters energy flows. More relevant to marine biologists might be the extent to which parasites affect free-living species. Parasites infect plants and compete with herbivores. Parasites infect herbivores, releasing

plants from grazing. Parasites infect predators, leading to trophic cascades, and even manipulating prey susceptibility to predators. Parasites even contribute to food webs when they release edible infectious stages. These are all reasons that ecologists should consider parasites in food webs. But to what extent should marine disease ecologists consider food webs when trying to understand marine diseases? Next, we consider how food webs create challenges and opportunities for parasites, and how changes to food webs can increase or decrease infectious diseases.

1.3 Food webs affect parasites

Food webs create opportunities for parasites. The more free-living species in a food web, and the more links among these free-living species, the more parasite species a food web should support (Hechinger and Lafferty 2005). In other words, parasite diversity should respond to food-web complexity (Lafferty 1997). Complexity in marine food webs is related to substrate type (Bellwood and Hughes 2001) structural heterogeneity (Gratwicke and Speight 2005), latitude (Bellwood and Hughes 2001; Roy *et al.* 1998), and physiological stressors (Sanders 1968). Comparing parasites across food webs that differ in integrity can reveal the relationship between food-web complexity and parasite community richness.

Parasites appear to be more sensitive to disturbance than their hosts. Frequent or strong disturbance tends to simplify food webs (Connell 1978), so sites protected from disturbance have more parasites (Lafferty 1997), and parasites are often the last thing to recover after disturbance. In a restored estuary, the full suite of trematode species infecting the California horn snail (*Cerithideopsis californica*) took six years to recover (Huspeni and Lafferty 2004). A similar pattern was observed in the Yucatan Peninsula following a

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hurricane (Aguirre-Macedo *et al.* 2011). Snails returned to a coastal lagoon 6 months after the hurricane, but it took another 8 months for any trematodes to be found in the snails. It took four years for the trematode community to recover (Aguirre-Macedo *et al.* 2011). Similarly, fish parasites in the Gulf of Mexico took over two years to recover from Hurricane Katrina (Overstreet 2007). Parasites are often the first species lost and the to return following perturbations to food webs.

Invasions have less predictable effects on parasites than hurricanes because they don't always simplify food webs. Sometimes invaders can bring their parasites with them. For instance, adding two fish species to a sub-Arctic lake created opportunities for five new parasites to complete their life cycles (Amundsen *et al.* 2013). But when invaders displace native hosts, native parasites can suffer. The invasive Japanese mud snail (*Batillari cumingi*) can exclude native snails (*C. californica)* from California estuaries (Torchin *et al.* 2005). *C. californica* is the only first-intermediate host for about 20 native trematode species, so when the snail is excluded, all its parasites go locally extinct (Torchin *et al.* 2005). Many invaders leave their parasites behind, and in places like San Francisco Bay where most free-living species are exotic, parasites are rare (Foster 2012; Torchin *et al.* 2003). Thus, how parasites respond to species invasions is tied to how invaders affect free-living diversity.

Parasites don't all respond the same to food web changes (Strona and Lafferty 2016; Wood and Lafferty 2015). Generalist parasites are more "robust" to changes in food web structure, whereas specialists and parasites with complex life cycles that function as serial specialists are sensitive to host extinctions (Lafferty and Kuris 2009; Rudolf and Lafferty 2011; Strona and Lafferty 2016; Wood and Lafferty 2015). Because natural disturbances can be common, parasites evolve to specialize on dependable hosts (Strona and Lafferty 2016).

Although parasite diversity declines with free-living species loss and food web simplification, the details are important. If some hosts benefit from food web simplification, their parasites will have increased opportunities for transmission. Furthermore, it remains difficult to predict how parasite prevalence and intensity will respond to food-web complexity. On balance, complex marine food webs with intact trophic structure (such as protected reefs) should promote diverse parasite faunas, whereas simplified or diffuse webs (such as disturbed or over-fished environments) should be dominated by generalist parasites, or by parasites that infect weedy species (with lower parasite diversity overall).

1.3.1 Fishing affects parasites

One way to observe how food webs affect marine disease is to contrast parasites in fished and unfished areas. Fishing removes larger, older, higher trophic level species first, so the system becomes dominated by smaller, younger, lower trophic level organisms, with a trend toward food-web simplification (Pauly *et al.* 1998). So, we expect fishing to reduce some parasite populations. Within marine protected areas in Chile, parasites are more ecologically abundant (per square meter) than in fished areas, but only one parasite species was more abundant per host, suggesting that fishing can reduce parasite populations by reducing host populations (habitat and resources for parasites) (Wood *et al.* 2013). This process was supported by a meta-analysis that found parasite abundance in fished species was lower in fished areas than unfished areas (Wood and Lafferty 2015). Fishing effects might percolate through complex life cycles. Differences in top predator abundance probably explain why parasite diversity was higher in reef fish at unfished Palmyra Atoll than at fished Kiritimati Atoll (Lafferty, K. *et al.* 2008). Wood *et al.* (2014) investigated this idea further by

contrasting parasite abundance at fished vs. unfished sites spanning six Line Islands, finding that trophically transmitted parasites decreased with increased fishing pressure, whereas parasites with direct life cycles increased. Thus, parasite responses to changes in food-web structure can vary with parasite life cycle, host specificity, and transmission strategy (Wood *et al.* 2014). Although fishing can decrease parasitism in direct response to host loss, other parasites might increase in abundance due to compensatory increases in host abundance.

Cascading indirect effects between fishing and parasites are also possible, especially when fishing predators increases prey abundance. We might expect increased directly transmitted parasites in prey at fished populations, and this has been reported in urchin populations released from predation by the spiny lobster fishery in Southern California (Behrens and Lafferty 2004). By the same mechanism, fishing grazers might increase disease in plants. Sea turtle declines are a hypothesized factor contributing to sea grass wasting disease. Low water flow and accumulated detritus facilitate infection in dense sea-grass beds, conditions that occur when sea grasses are not cropped short by grazing sea turtles (Jackson *et al.* 2001). Indirect effects are easier to predict for simple food chains. In more complex food webs, predictions are harder to make. For instance, fishing removes sea urchin predators from Galapagos reefs, so it was predicted that the denser urchin populations in fished areas would be infected with more parasitic snails. However, sea urchin predators also eat mutualistic crabs, which eat the parasitic snails. Parasitic snails were therefore less abundant at fished sites because fishing indirectly increased crab predation pressure on parasitic snails (Sonnenholzner *et al.* 2011). Greater knowledge of food-web complexity and parasite life-cycle complexity are necessary to predict how particular parasites will respond to food-web changes. With change, there will be winners and losers.

1.3.2 Host quality affects parasites

In terms of host selection, a parasite's success can depend on whether one considers it as a parasite species or an individual. An individual parasite's growth and fecundity depends on host quality. Well-fed hosts may have surplus energetic stores that parasites can tap, especially when parasites have high energetic demands or strong within host competition (Mideo 2009). Trematodes in starved snails produce fewer and poorer quality transmission stages (Seppälä *et al.* 2008), acanthocephalans in amphipods grow to smaller size when hosts are food deprived (Labaude *et al.* 2015), and parasitic mussel larvae grow larger in fish hosts that are better in condition (Österling and Larsen 2013). Well-fed hosts grow more and can attain a larger size, which leads to more habitat for parasites (Lo *et al.* 1998). Resource quality can also influence host behavior and alter parasite transmission rates. Zooplankton fed low-quality food grow to smaller sizes, have lower size-corrected feeding rates, and thus encounter fewer parasite spores (Penczykowski *et al.* 2014). Large zooplankton offered low quality food also reduce their feeding rate, so they encounter fewer parasite spores as well (Penczykowski *et al.* 2014). Well-fed hosts also live longer, which increases parasite life spans and lifetime reproduction (Penczykowski *et al.* 2014). Infected snails survive better when they are well fed, so their trematode parasites also live longer (Krist *et al.* 2004). Although host quality should benefit individual parasite success, food-web dynamics might lead to tradeoffs between host quality and abundance. Predators, for instance, might keep prey at low densities, thereby preventing crowding, and improving prey as hosts for parasites, while also making these hosts harder to contact. Further, it is not clear that a well-fed host is a better host if malnourished hosts have weakened immune response (Cohen, Beaver*, et al.*

1993). However, crowded phytoplankton (Tillmann *et al.* 1999) and snails (Krist *et al.* 2004) are not necessarily better hosts, perhaps because benefits gained from weakened immune defenses are outweighed by consequent limited resources for parasites and decreased host life span (Tillmann *et al.* 1999). The relative importance of host density and host quality for parasite fitness remains understudied and is likely to be context-dependent. The host is both habitat and food for its parasites, so having a well-fed host is like living in a house with a well-stocked refrigerator and a good landlord (or maybe living with your parents). When it's time to move, it might be easier to find a vacant run-down property, but would you want to live there?

Putting parasites into food webs helps us to better understand marine diseases. Changes to food webs alter host diversity, abundance and quality, and this has corresponding effects on parasite diversity, transmission success, and fitness. As food webs change, whether from fishing, climate disruption, or species invasions, we can expect parasite communities to change as well. Such changes might not be welcome. They could introduce new parasite species to which native hosts have little evolutionary history, or they could lead to parasite extinctions that add to biodiversity loss, and change the relative abundance of hosts. A theory for how food webs affect parasites will help us better understand why a particular infectious disease has become problematic, give insight into how restoration might reduce a costly marine disease, or let us use parasites as indicators to follow changes to food web complexity. Combining dispassionate parasitology with food webs can help marine disease ecologists identify how parasites may threaten or contribute to marine biodiversity.

1.4 Summary

1. Complex life histories enmesh parasites into marine food webs differently than free-living consumers.

2. Parasites make substantial and unique contributions to marine food web structure and dynamics.

3. Parasites make contributions to energy flow in marine systems (both as consumers and resources) that are on par with their free-living counterparts.

4. Infectious processes can directly or indirectly structure marine communities.

5. Parasites can be impacted by perturbations to food webs (such as overfishing).

6. Understanding parasites in marine food webs will help us better conserve and manage marine ecosystems.

2 Body size, density, biomass, and life stages of organisms from the intertidal sand flats at Palmyra Atoll

2.1. Introduction

We measured the diversity, body sizes and densities for the unicellular and multicellular eukaryotic organisms living in and on the 3.14 ha of intertidal sand flats at Palmyra Atoll. The survey has several noteworthy inclusions: (1) parasites (infectious agents) on the same empirical footing as their free-living hosts, (2) biomass-density information, (3) ontogenetic stages for each species, and (4) body-size estimates for each of these stages. The dataset contains 670 life stages, comprising 275 species from 51 orders and 22 phyla. The data set also includes descriptive information on the habitat affiliations, consumer strategy, life style and taxonomy of all individual life stages. Most estimates of species life stages were collected using consistent sampling methods scaled to abundance and body size. We also include quantitative descriptions of the physical habitat at each of 35 focal sampling sites. We provide detailed metadata for all of our species and habitat data. We plan to use these data to address several general questions about ecological communities, and encourage potential collaborators to contact us. In particular, we will combine these data with a partner dataset on feeding interactions to create a detailed food web for the Palmyra Atoll sand flat community.

2.2 Research Motivation

Quantitative information on species abundances and body sizes has advanced our understanding of community structure and dynamics, but few systems have been comprehensively surveyed (e.g. see Berlow *et al.* 2009; Brose, U *et al.* 2006; Cohen *et al.* 2003; Cohen *et al.* 2009; Woodward *et al.* 2005). The biotic survey data are part of a broader effort to build a detailed food web for Palmyra Atoll. Food webs are ecological maps that describe feeding links between consumers and resources. We focused our efforts on the intertidal sand flats because they contain a trophically intact community (with large biomass of top-predators) in a tropical system that is qualitatively different from most published food webs that include parasites (i.e. Amundsen *et al.* 2009; Hechinger, Ryan F. *et al.* 2011; Mouritsen *et al.* 2011; Preston *et al.* 2012; Thieltges *et al.* 2011; Zander *et al.* 2011). We included parasites as nodes because they can affect food web structure (Dunne, J. A. *et al.* 2013; Lafferty, Dobson*, et al.* 2006). We separated species by life stage because ontogenetic diet shifts and growth are common between stages (Rudolf and Lafferty 2011). We measured body size because this can give information about energetics and inform predator-prey relationships (Woodward *et al.* 2005). We include descriptions of the physical habitat, as these can affect food web structure (Gibert and DeLong 2014; Rezende *et al.* 2009). In addition to using these data to build and analyze a food web, we plan to investigate hypotheses about community structure that require body-size abundance information. Collected between, Aug-2009 and Dec-2015, these data also contribute a biological and physical inventory of a large habitat within the Palmyra Atoll National Wildlife Refuge and throughout the tropical Pacific. We are making these data public to foster additional analyses and seek collaborations.

2.3 System description

We completed a biotic survey for the intertidal sand flats of Palmyra Atoll. Located 1680 km south of Hawai'i, Palmyra is a remote and relatively pristine coral atoll. Palmyra was designated as US National Wildlife Refuge in 2001 and incorporated into the Pacific Remote Islands Marine National Monument in 2014. During WWII, several thousand servicemen were stationed at Palmyra, but the atoll was abandoned after the war (Collen *et al.* 2009). Palmyra has never supported permanent human habitation or a commercial or subsistence fishery. As a result, the marine food web is intact, with a high apex-predator biomass (DeMartini *et al.* 2008; Sandin *et al.* 2008; Stevenson *et al.* 2007). Previous studies indicate the prevalence, intensity of infection and richness of parasites of reef-fish is higher at Palmyra compared to an inhabited island in the same island chain (Lafferty, K. *et al.* 2008; Wood *et al.* 2015).

Comprising 3.14 hectares, the intertidal sand flats of Palmyra Atoll are habitat for a rich species assemblage and provide a diverse set of ecosystem services. At Palmyra, 275 species comprising 51 orders from 22 phyla call the sand flats home. Globally, intertidal flats provide shoreline protection, nursery habitat for fish, foraging habitat for migratory birds, and support subsistence and recreational fisheries (Beaumont *et al.* 2007). For example, recreational fishing on intertidal sand flats habitats generates more than $140 million dollars in annual revenue for the Bahamas, alone (Fedler 2010). Like coastal zones around the world, intertidal sand flats face a number of anthropogenic threats, including nutrient pollution, increasing turbidity, overfishing, rising sea-levels, habitat loss through development, erosion and invasive species (Brown and McLachlan 2002; Davenport and

Davenport 2006; Defeo *et al.* 2009; Lafferty and Kuris 2009; Murray *et al.* 2015). Intertidal sand flats are an important and understudied system, both at Palmyra Atoll and globally.

2.3.1 Habitat information

To estimate species abundances at Palmyra Atoll we multiplied density estimates by total available habitat. To delineate the habitat area available, we used Google Earth to create polygons around the intertidal soft-bottom habitats of the flats, whereas we mapped rocky intertidal habitat during on-the ground surveys before creating polygons in Google Earth. To calculate their area, all polygons were exported as a KMZ file to http://www.zonums.com/online/kmlArea/. The rocky intertidal is 0.005 percent of the total habitat area, while the sand flats comprise the remaining 0.995 percent. Some of our sampling methods were restricted to one habitat or the other. To accommodate this difference we present both corrected and uncorrected estimates of density and biomass density. Uncorrected estimates reflect the density of organisms in a habitat. Corrected estimates reflect density or organisms in the system. Corrected estimates were generated by multiplying uncorrected estimates by the fraction of total system area that habitat comprises.

2.3.2 Site characterization

We focused our sampling effort at 35 randomly selected sites on the intertidal sand flats. To select these sites, we mapped potential sampling areas by placing a grid of points, set 100 m apart, across the entire Atoll. We then retained only those points that fell within the sand flat habitat designated above. We then randomly selected 35 of those points as sampling sites (Figure 2.1). At each site, we sampled the density and sizes of organisms. Sampling

within each site was restricted to the soft-sediment sand flats. At each focal site, we performed the following sampling: walking transects (high and low tide), snorkel transects, quadrats and cores (Figure 2.2 details the sampling orientation at focal sites). To minimize disturbance, cores and quadrats were collected after the other sampling methods had been completed at a site. Samples were pooled by method at each site so variance in our density estimates uses sites as replicates. We supplemented our sampling at these focal sites with additional sites or methods as necessary (e.g., when a taxon was not adequately measured by the methods above).
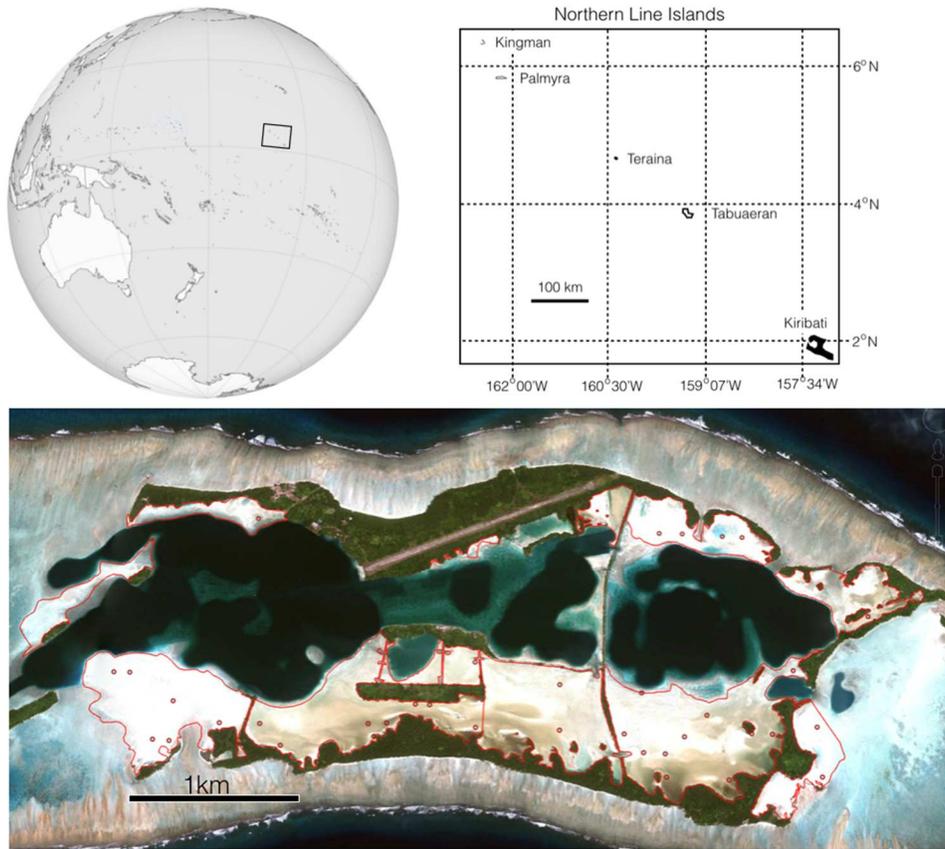
Figure 2. 1 A map of Palmyra, the intertidal sand flats and a locations of the 35 focal sampling sites.
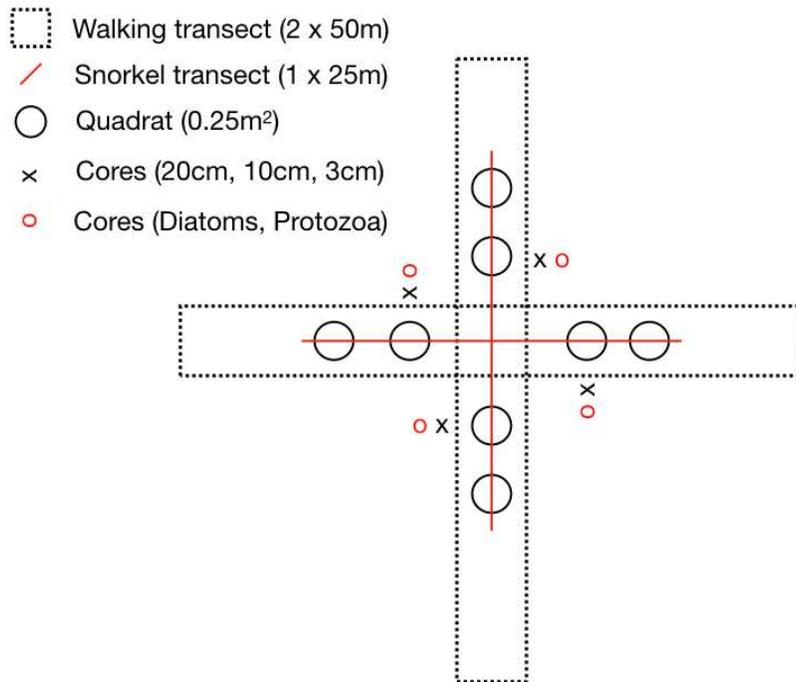
Figure 2. 2 An illustration of the sampling protocol undertaken at each focal sampling site.

For intertidal species, solar irradiation increases primary productivity and temperature. Environmental temperature can affect consumer-resource interactions because ectotherm metabolism (most species on the sand flats) increase with temperature. To characterize temperature and light intensity, we placed loggers (Onset HOBO Pendant® Temperature/Light 64K Data Logger) which measure temperature and lux at the 35 focal sites between 19 October 2009 to 10 November 2009. We assumed this time window would be sufficient to characterize the sites due to minor seasonality in light and temperature at Palmyra Atoll. Each logger took light and temperature measurements every 12 minutes,

(except for the logger at site Banjoes.1, which recorded every 17 minutes), resulting in 2613 measurements for all sites with the following exceptions:

- Banjoes.1 had 1845 measurements due to the measurement interval

- Cookies.2 logger was bitten and destroyed

- Sixes.4 and Down.East.2 were partially buried and excluded from light intensity estimates

Some loggers recorded unrealistically high temperatures and light intensities, so we capped the highest temperature at 43 °C and lux at 120,000. To match the water depth at each site to each temperature/light record, we fit a spline to the times and heights of the high and low Palmyra Atoll tides for that time period. From this spline, we estimated the site- water level for each time point associated with a temperature/light record. We then subtracted the site elevation from the tidal height to estimate water depth for each light/intensity measurement.

Temperature and light intensity varied over the day, less so from day to day, and even less so from site to site. The mean temperature across sites was 31.2 °C (variance across site means = .036 °C). The lower a site's elevation (e.g., sites that tended to be deep), the higher was its mean and variance in temperature. Temporal variation in temperature within a site was higher than among sites (average within site variance = 8.8 °C), and mostly increased with hourly light intensity and depth. At a particular depth, temperature decreased with the incoming tide at night and increased with the incoming tide during the day. To characterize the light environment at a site with a metric meaningful for primary productivity, we converted lux values over time to the average Daily Light Integral (DLI) (or integrated PPFD). Average DLI was 13.79 moles of photons per m^2 per day (S.D. = 6.0) and tended to

increase with site elevation due to light attenuation during submergence. These readings

show that most of our sample sites were both warmer and brighter relative to the conditions

experienced by most marine species.

To estimate the densities of phytoplankton, zooplankton and fishes, we needed

accurate estimates of average water volume present on the sand flats as well as the fraction of

time that water was above certain minimum depths required for animals of different body

sizes. To do this, we compared changes in water depth at 35 focal sites to tidal changes

predicted at the Honolulu Reference Station (1612340) over one year. Tides in Hawaii are

reported in Imperial units, which we report here for convenience, but convert to metric when

estimating biomass densities. The offsets for Palmyra Atoll relative to the Honolulu

Reference Station are (A) Time: (high tide: 79 minutes, low tide: 73 minutes), (B) Height:

(high tide: +0.60 feet, low tide: -0.20 feet). There is no offset recommended for mean sea

level. The observed difference at 25 inches on the reference tide stick at Palmyra Station (9-

Sep-2009) and sea level height in Honolulu was 0.95 inches, which was due to coarse

measurement and about 0.5 inches of wind chop. We calculated the site elevation by

comparing depth at the site with the depth at the Palmyra Station reference tide stick. One

observer measured depth at a site while a second observer simultaneously noted tidal height

at the station tide stick (elevation is tidal height minus depth). Measured depths were

standardized to 25 inches on tide stick and corrected relative to this baseline. We then

calculated the water depth (presented in cm) at each site for every high and low tide over the

course of a year. Any negative water depths were set to zero. The height and time estimates

for the high and low tides over the course of one year (2009) were generated from 1334

estimates of water depth at each of 35 sites. From these, we estimated average water volume

on the flats by multiplying the average depth across sites by the area of the sand flats. We were also able to estimate the fraction of time that there was sufficient water to meet the various fish species minimum depth requirements or to exclude various shorebird species.

2.4 Species quantification

Biotic surveys usually organize species as irreducible units. Here, we disaggregate species into their component life stages. Broken into broad groups based on their trophic level and lifestyle, species are presented in the following order: (i) detrital, (ii) autotroph (iii) mixotroph (iv), free-living consumer, (v) commensal consumers and (vi) infectious consumers. Body size is the most common axis along which food web matrices are organized (Brose, Ulrich, Williams, Richard J*., et al.* 2006; Loeuille and Loreau 2005; Otto *et al.* 2007; Rezende *et al.* 2009; Zook *et al.* 2011), and within these broad groups species are ordered according to the mass of their adult stage. Below, we provide additional background information on the species.

We sought to create a comprehensive list, from viruses to vertebrates, of the species and life stages that occur on the intertidal sand flats at Palmyra Atoll. Below, we describe the methods used to quantify the density, body size and biomass density of these organisms. In some instances, we also sought to augment our direct observations (species life stages) with logical inference. For example, we had direct observations of the prevalence of bucephalid trematode parthenitae in clams, but could not identify them to species because of their larval status. But, we were able identify bucephalid trematode metacercariae in fish to species. These metacercariae in fish must have come from the parthenitae in clams. So to match the stages we partitioned the prevalence of bucephalid trematode parthenitae in clams according

to the relative abundance of bucephalid trematode metacercariae species in fish. This approach to assembly creates a more accurate and realistic species list, as opposed to the other options: creating unreal life cycle gaps or artificially inflating species richness. Some organisms have life stages that we know occur on the flats but we were not able to identify to species because quantification would have been impractical, our sampling methods did not capture them, or because larvae could not be identified to species. To fill these gaps, we quantified life stages indirectly when possible (e.g. trematode cercaria). We apportioned the observed biomass of trochophore larva, crab megalopae, crab zoeae, shrimp zoeae, copepod nauplii and fish larvae to separate species according to the relative abundance or biomass of adult species. This results in the larvae of species within these groups having identical body sizes but different densities, this prior to being used in any abundance to body size comparisons, these larvae should be reaggregated (e.g. all trochophore larvae). When we could not quantify a life stage (e.g. helminth eggs, oncomiracidia, miracidia) we omitted it from density and biomass estimates, but assigned it a body-size estimate. While, these life stages may not be major contributors to species' biomasses, they may be important contributors to food web structure and population dynamics. Including species for which we have no abundance information is helpful because it permits including those species in topological analyses of network structure. Our methods for estimating the species properties are described below.

Most entries in the species list for the Palmyra Atoll intertidal sand flats represent life stages. This level and evenness of resolution is higher than most biotic surveys. We identified organisms to the lowest taxon possible, although we sometimes used a morphospecies designation for difficult to ID organisms in the "Common.Name" column. Although, these

species are not identified to the lowest possible taxonomic category, they do represent distinct species life stages, and are accompanied by all the taxonomic information we could provide.

We have provided several different classification schemes for species in order to facilitate analyses and interpretation. For example, each species has a unique code that can be used to aggregate life stages. We have also provided an "Organismal.Group" designation for each node to make interpretation easier. The columns: "Feeding type" (i.e. feeding, non-feeding, autotrophic), "Lifestyle" (e.g., free-living, infectious, commensal), "Consumer Strategy" (e.g., predator, macroparasite, pathogen, detritivore), and "Native" or "Non-native" status all provide additional information. The "Residence" column describes the general vagility of individual life stages on seasonal time scales; the "Mobility" column does this at a daily time scale. These columns allow us to consider the expected proportion of a species' interactions that are captured in the system. For example, several shorebirds undergo seasonal migrations between Palmyra and breeding grounds in Alaska.

2.5 General sampling methods: Free-living

Our general sampling methods were designed to survey free-living organisms based on their habitat (e.g., planktonic, benthic) and body size, regardless of taxonomic affiliation. These general methods are detailed directly below. Some free-living Taxa required special treatment.

2.5.1 Bird surveys

To estimate shorebird density on the flats, we conducted nine bird surveys between June 2012 and December 2015. During each bird survey, all flats habitat was exhaustively surveyed at low tide by 2-3 experienced birders (using binoculars and spotting scopes), each of whom followed different prescribed routes and observation points chosen to allow observation of the entire flat while minimizing double counting. Each observer carried aerial photographs of the flats. If a bird was observed interacting with the habitat (e.g., roosting, feeding, but not high-altitude flyovers), its position was marked on the photograph in the field. Bird locations were transferred from paper photos, to Google Earth, from which we derived a latitude and longitude for each observation. These georeferenced observations could then be analyzed in a GIS program, allowing us to estimate, for example, average bird densities in each flat or within a radius from a sampling site.

2.5.2 Fish transects

We used walking transects to estimate the densities and body sizes of non-gobioid fishes and large benthic invertebrates (e.g. sea cucumbers and mitre snails). Walking transects were conducted by a single trained observer at medium to high tide. To better sample fish we supplemented our 35 focal sites, with 36 randomly chosen sites for walking transects only (71 total). Two 50 m x 2 m band transects were conducted at all 71 sites during the day and the 35 focal sites at night. We identified and counted all fish and large benthic invertebrates in a moving window, estimating their total length to the nearest centimeter (we also estimated sea cucumber body width). The size of the moving observation window was determined by local visibility. Counts were pooled across transects at each site, giving us a

sample area of 100 m^2 at each site. The section on "Taxon-specific methods: Free-living"

below has more information on the density, body size and biomass density estimation of non-

gobioid fish. By combining density and body size estimates from walking transects with our

estimates of water depth (above) we were able to estimate the biomass density of non-

gobioid fish species present on the Palmyra sand flats.

2.5.3 Shrimp transects

We used specialized methods to estimate the densities of large burrowing shrimp.

Ghost shrimp were difficult to sample because their burrows can extend several meters into

the substrate, and adult ghost shrimp consistently evaded our sample cores. There is typically

one adult per burrow (Kinoshita 2002) and previous surveys have used burrow counts to

estimate ghost shrimp density (Ohshima 1967; Tamaki 1988). The ghost shrimp on Palmyra

produce burrows with several incurrent openings, visible as depressions surrounding a central

excurrent opening, a volcano-shaped mound. To estimate adult ghost shrimp density at the 35

focal sites, we used transects to count the volcano-shaped excurrent mounds. The shrimp

transects were identical to our walking transects (100 m^2 sampled per site) except that they

were performed at low tide. Adult ghost shrimp body size was estimated from specimens

collected for parasitological analysis. We estimated ghost shrimp biomass density by

combining density estimates from shrimp transects with body size estimates from our

parasitological collections.

The zebra mantis shrimp (*Lysiosquillina maculata*), which is the largest mantis shrimp in

the world, is present on the Palmyra sand flats. These shrimp create U-shaped burrows,

whose openings are uniformly circular and flush with the surrounding substrate. We

confirmed that breeding pairs occupy a single burrow with collections for parasitological analysis. We estimated zebra mantis shrimp density along shrimp transects, estimating one shrimp per burrow opening. We estimated adult zebra mantis shrimp body size separately, with specimens collected for parasitological analysis. We estimated zebra mantis shrimp biomass density by combining density estimates from walking transects with body size estimates from our parasitological collections.

2.5.4 Snorkel transects

We estimated the density and body size of goby species on snorkel transects. During daytime medium to high tides, we conducted two 25 m x 1 m snorkel transects at the 35 focal sites. As a single observer moved along the transect, all gobies within a moving window ahead of the observer were identified, counted and had their total lengths estimated to the nearest centimeter. Goby counts were pooled across both transects at a site, giving an effective sample area of 50 m^2 at each site. We used length-weight relationships derived from our parasitological dissections and from the literature to estimate the mass of each individual observed in the field. We combined our estimates of mass and density to estimate goby biomass density on the flats.

2.5.5 Quadrats

We estimated the density and body size of medium-sized, near-surface benthic organisms (e.g. common snails, acorn worms and small stomatopods) using circular quadrats that were 0.25 m^2 in area. Eight quadrats were placed at the 35 focal sites during medium to high tides. While snorkeling, an observer carefully flushed away the top 3 cm of sediment by

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slowly waving their hand above the substrate, which revealed soft-bodied organisms, such

acorn worms, without damaging them. All organisms in a quadrat were identified and

counted. Counts were pooled across quadrats within a site, giving a pooled sample effort of 2

m^2 per site. At each site, for each species, we measured the length and width of the first ten

individuals encountered. We used length-weight relationships derived from our dissections to

estimate the mass of each individual measured. Species biomass density estimates for each

site were based on the average individual mass estimates multiplied by our density estimates.

2.5.6 20cm Substrate cores

To estimate the density and body size of large benthic infauna (e.g. fiddler crabs and

clams), we sank four 20 cm diameter (314.2 cm^2) cores at each site. Cores were sunk quickly

to 50 cm or until the coral matrix prevented further penetration. All sediment from the cores

was passed through nested sieves (5 mm followed by 1 mm pore size) and all organisms

collected were counted and identified. Organism counts were pooled across cores within

sites, giving a sample area of 1256.6 cm^2 at each site. We also measured the body size (e.g.

usually total length or carapace width for crabs) of the first ten individuals encountered of

each species encountered at a site. We used length-weight relationships derived from our

dissections to estimate the mass of each individual measured. Species biomass density

estimates for each site were based on the mean mass estimates multiplied by our density

estimates.

2.5.7 10 cm Substrate cores

To estimate the density and body size of medium-sized benthic infauna (e.g. polychaete worms, phoronids, sand anemones), we sank four 10 cm diameter cores (79 cm^2) at each site, alongside our larger 20 cm cores. Cores were sunk quickly to 50 cm or until the coral matrix prevented further penetration. All sediment was passed through nested sieves (5 mm followed by 1 mm pore size) and all organisms collected were counted and identified. Organism counts were pooled across cores within a site, for a total sample area of 314 cm^2 per site. For each species, we also measured the body size (length and width) of the first ten individuals encountered at each site. We used length-weight relationships derived from our dissections to estimate the mass of each individual measured. Species biomass density estimates for each site were based on mean mass estimates multiplied our density estimates.

2.5.8 3 cm Substrate cores

To estimate the density and body size of small benthic infauna (e.g. parchment tube worms, and small sea cucumbers), we sank four 3 cm diameter cores (7.07 cm^2) to a depth of 5 cm at each site. All the sediment from each site was aggregated (total sample area of 28.28 cm^2 at each site) and passed through nested sieves: 1 mm, 0.5 mm, 0.125 mm and 0.063 mm. We then weighed each sediment size class and removed a sample for processing, which we also weighed. The ratio between these sediment weights was used to estimate the density of organisms identified and counted in the subsample. Samples were processed under a confocal microscope. Because no organisms were recovered from sediment 0.063 mm - 0.125 mm in size we stopped processing this sediment size class after 15 sites. We measured the body size (total length, width and height) of each individual encountered. Organisms were assigned to a

shape, which was used to estimate their biovolume. An individual organism's mass was estimated by multiplying its biovolume by a tissue density of 1.1 g/mL (Peters 1986). These mass estimates were then multiplied by morphospecies density estimates to generate biomass density estimates for each site.

2.5.9 Diatom cores

To estimate the body size and density of substrate surface-dwelling diatoms, we collected and processed samples after (Byers 2000). We used modified 3 cc syringes to take sediment cores with an area of 64 mm^2 and a depth of 4 mm giving a total volume of 151 mm^3 (accounting for the displacement of the plunger) in each sample. At the 35 focal sites we took 4 samples totaling an area of 256 mm^2. We immediately preserved the aggregated samples in 6% Lugol's solution and packed them on ice for transport back to the lab. We diluted samples with 1 mL filtered water and stirred samples for 1 min to uniformly suspend all sediment particles. After this, we pipetted off 350 µL of solution and placed it on an 18 mm cover slip. We estimated the shape and body size (length, width, and height) of all diatoms counted along two haphazardly selected transects at 100x magnification, which gave us a field of view of 2 mm on each transect and a combined transect area of 72 mm^2. To estimate diatom density at each site, we summed our counts across transects and multiplied them by the ratio of total transect area to coverslip area (4.5). We then multiplied this by the ratio of the volume examined (350 µL) to the volume of the entire sample (1.604 mL), which was 4.58. Diatoms were separated into 17 volume based logarithmic size classes or morphospecies. The shape (ellipsoid, disc, etc.) of each morphospecies was used to estimate the biovolume (Sun and Liu 2003) of each of its individual members. The mass of each

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individual was estimated by multiplying its biovolume by a tissue density of 1.1 g/mL (Peters 1986). These individual mass estimates were then multiplied by morphospecies density estimates to generate biomass density estimates for each site.

2.5.10 Protozoan cores

We estimated the size and density of individual benthic protozoa in the same manner as diatoms, using identical but separate syringes and a different container. We collected four samples at 34 focal sites (one site was lost). We did not add Lugol's solution to the protozoan samples after collection. With these exceptions, Protozoa cores were processed in the same manner as diatom cores. We estimated individual protozoan mass by multiplying their biovolume by a tissue density of 1.1 g/mL (Peters 1986). Protozoans were separated into volume based logarithmic size classes or morphospecies. Multiplying individual mass estimates by observed densities observed allowed us to generate biomass density estimates for 21 protozoan morphospecies at each site.

2.5.11 Zooplankton

To estimate zooplankton density and body size, we collected zooplankton in a 63 μm mesh net with a 30cm diameter mouth. Using this net, we sampled 2.85 m^3 of water in each sample. Zooplankton samples were collected at each site, one during the day (35 sites) and one at night (33 sites). We estimated planar (m^2) zooplankton densities by multiplying mean volumetric zooplankton densities (stratified by sample time) by the average water volume on the flats (see "Water Volume Estimates" above) and then dividing by the total area of the flats. We calculated degrees of freedom using the Satterthwaite approximation (Satterthwaite

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1946; Thompson 1992) for stratified samples, which can generate fractional degrees of freedom. Zooplankton samples were fixed in buffered 10% formalin. All zooplankton samples were sorted to morphospecies (e.g. large harpacticoid copepod, chaetognath) or stage (e.g. nauplius, zoea, megalops, trochophore, etc.) and counted. A subset of individuals from each morphospecies was measured (length, width, height) and converted to a biovolume. Each individual's mass was estimated by multiplying its biovolume by a tissue density of 1.1 g/mL (Peters 1986). We multiplied mean mass of zooplankton morphospecies by their density to estimate biomass density at each site.

2.5.12 Phytoplankton

To estimate phytoplankton biomass density, at each of the 35 focal sites, on two different occasions we collected 1 L of seawater from three depths: surface, mid-water, bottom. All 70 samples were collected during the day at high tide and placed in the dark, on ice and transported back to the lab for processing. While total water depth was often less than a meter (samples generally separated by less than 0.5 m) to account for the variation in chlorophyll a concentrations with depth, we amalgamated all samples for each site. Prior to analysis, samples were gently shaken to uniformity, and 120mL of water was extracted and passed through each Type A/E glass fiber filter (Whatman). Filters were put in the dark and frozen. Samples were processed and analyzed for chlorophylls a, b, $c_1 + c_2$ and phaeopigments according to Arar and Collins (1997) on a Thermo Scientific GENESYS 20 spectrophotometer. We were able to successfully extract chlorophyll a from 39 of the 70 samples. Both chlorophyll b and phaeopigments were also present in the samples so we used Lorenzen's monochromatic equation to correct our estimates of chlorophyll a concentration

(Arar and Collins 1997). We estimated the biomass density for two size classes of phytoplankton: microphytoplankton and nanophytoplankton. Relationships between chlorophyll *a* concentrations and phytoplankton density and biovolume were estimated using equations from Jiménez *et al.* (1987). Biomass density was estimated by converting multiplying biovolume by a tissue density of 1.1 g/mL (Peters 1986).

2.5.13 Rocky intertidal zone

To estimate the density of organisms associated with rocky intertidal zone that was sometimes adjacent to the sand flats, we conducted transects at 28 randomly chosen locations in the rocky intertidal habitat. Transects extended the length (height) of the habitat and transect width ranged between 10 cm and 50 cm, depending on gastropod density (narrower transects where snails were denser). All organisms within the transect boundaries were collected and brought back to lab for identification and counting. The first 20 individuals of each species on each transect were measured and weighed. We derived biomass density estimates for each transect from transect specific mean body-size measurements multiplied by our density estimates. The biomass density for the habitat was the mean of these transect biomass densities.

2.6 Taxon-specific methods: Free-living

Our general methods were designed to survey organisms based on their habitat (e.g. planktonic, benthic) and body size regardless of taxonomic affiliation. However, density estimates for some Taxa required either the development of additional, specific sampling methods or special statistical treatment. We detail those cases for free-living taxa below.

2.6.1 Birds

Our density estimates for birds reflect the mean bird counts across our surveys, adjusted by habitat availability. We only included bird species that interact with the habitat, and not birds that simply overfly the habitat (e.g. boobies and frigatebirds). At Palmyra, shorebirds forage on the flats during the daytime low tides. For each bird species we estimated the maximum water depth in which they will forage (Helmers 1992). We then used tidal information to determine the fraction of daylight hours during which water levels were shallower than these depths. This estimate of habitat availability was then used to correct the observed bird densities. In other words, to estimate average bird densities we discounted the densities observed at low tide by the fraction of daylight hours when the flats were sufficiently shallow for birds to feed. Body size information for birds was obtained from the literature or from birds measured at Palmyra. Multiplying these corrected densities by our body-size estimates allowed us to estimate the mean biomass density on the flats at Palmyra.

2.6.2 Non-gobioid fish

We estimated the individual mass of each non-gobioid fish observed by developing length-weight relationships. First, non-gobioid fish species were broken into size classes based on age at maturity, ontogenetic diet shifts, shared consumers and field observations of population structure and spatial distributions at Palmyra Atoll. We estimated the length (total length or fork length) of each of the 6926 individual fish observed on our walking transects. We converted length estimates into mass estimates using slopes (*a*) and intercepts (*b*) derived from species-specific linear regressions of log length and log weight from 648 individual fish

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collected from the intertidal sand flats. For some species, the number of individuals collected at Palmyra was inadequate for regression and length-weight relationships for these species were collected from FishBase (Froese and Pauly 2012) and other sources.

Most fish leave the flats when they are exposed at low tide. To estimate average fish densities at Palmyra, we determined the minimum depth requirements of each fish species size class and then adjusted our observations by the fraction of time during which the habitat met those requirements. We used walking transects to estimate the densities of fish species by size classes. We estimated the minimum water depth required for each species size class based on the shallowest water level at which it was observed on a fish transect. Transects that did not meet the minimum depth required for a fish species size class were removed from the density estimates for that fish size class. For example, if the water level was too shallow for an adult surgeonfish in two of seven transects, only the five transects with sufficient water were used to estimate fish density. Next, we integrated fish densities at each site across the tidal series by calculating the fraction of time water depth exceeded the minimum requirements for a species size class at each site over the course of a year (see "Water Volume Estimates"). We corrected site-specific density estimates by multiplying them by the fraction of time with suitable water depth. For instance, if the water level was suitable for an adult surgeonfish 70% of the time, we multiplied fish density (accounting for water depth as described above) by 0.7. Density estimates were computed using the "survey" package in R (Lumley 2016) and stratified across sample time (Night & Day). Degrees of freedom were calculated using the Satterthwaite approximation (Satterthwaite 1946; Thompson 1992) for stratified samples, which can generate fractional degrees of freedom. A few species size classes were estimated in a different manner due to lack of data. We used these density and

mass estimates to generate biomass density estimates for each non-gobioid fish species size class.

2.7 General sampling methods: Parasite

Our general methods were designed to survey parasitic organisms based on their host's lifestyle and their abundance in those hosts. Those general parasitological methods are detailed immediately below. The density estimates for some parasite taxa required additional treatments, which are explained in the "Taxon-specific methods: Parasite" section

2.7.1 Fish parasitology

For parasitological analyses, we captured a subset of fishes from various flats, using IACUC approved methods. Fish were processed so that every tissue type was examined for parasites as described in Kuris *et al.* (2008); Shaw *et al.* (2005); Vidal-Martínez *et al.* (2012); and Vidal-Martínez *et al.* (2017). All eukaryote parasites were identified to species and counted. A subset of parasites from each species were measured (total length, maximum width, maximum height), assigned a shape and converted to a biovolume. A parasite's mass was estimated by multiplying its biovolume by a tissue density of 1.1 g/mL (Peters 1986).

To estimate parasite abundances in non-gobioid fish, we applied a host-length to parasite-count regression from the dissected fish to the size-frequency abundance data described above. This allowed us to estimate the number of parasites in each non-gobioid fish that we counted but did not dissect. We evaluated the six models below by regressing each against fish total length and then fish weight (12 total models of parasite distribution), for each of the 413 individual parasites interactions (Zuur *et al.* 2009):

- Generalized linear model with Poisson distribution

- Generalized linear model with negative binomial distribution

- Zero-adjusted model with Poisson distribution

- Zero-adjusted model with negative binomial distribution

- Zero-inflated model with Poisson distribution

- Zero-inflated model with negative binomial distribution

We ordered models by AIC and selected the one that best fit the observed data, not necessarily the model with the lowest AIC. For some fish-parasite interactions there was insufficient data for any models to converge. In these cases, we combined host-parasite records by fish family, parasite group (e.g. nematode, trematode) and parasite stage (e.g. larval, adult) and evaluated the same 12 models. To estimate parasite biomass density, we summed modeled projections of parasite abundances in each fish at each site and then multiplied these by the mean mass of each parasite species stage.

To estimate parasite abundances in gobies, we first separated each goby species into adult and juvenile size classes. We then multiplied the size-frequency abundance data for each goby species-size class by the prevalence and mean intensity of each parasite species in that goby species-size class.

2.7.2 Invertebrate parasitology

To estimate parasite abundances in invertebrates we collected, euthanized and processed invertebrate hosts for parasites, then modeled their abundances. Each parasite encountered was identified and counted. A subset of parasites from each species was measured (total length, maximum width, maximum height), assigned a shape and converted

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to a biovolume. The parasite mass was estimated by multiplying their biovolume by a tissue density of 1.1 g/mL (Peters 1986). Biomass estimates were derived from the mean species mass. Unless noted otherwise, parasite abundances in invertebrate hosts were estimated using prevalence and mean intensity. To estimate parasite biomass density we summed modeled projections of parasite abundances in each invertebrate, at each site and then multiplied these by the mean mass of each parasite species stage.

2.7.3 Bird parasitology

We were not able to collect birds for parasitological analyses, so we had to infer the identity of their parasites and model their abundances. Our efforts focused on endohelminths, which are important for trophic structure (Hechinger and Lafferty 2005). While ectoparasites (e.g. lice and mites) are likely present on the birds, we did not include them because we not able to infer their identities and we were not able to find any literature for ectoparasites on Palmyra bird species. We inferred the identities of endohelminthes in birds from trophic interactions and personal observations. For example, USFWS provided us some estimates of *Philophthalmus* sp.1 on Bristle-thighed Curlews (*Numenius tahitiensis*). With the exception of *Philophthalmus* sp.1, bird parasite body sizes were obtained from the literature. To estimate parasite intensities and prevalences we compared Palmyra birds to ecologically analogous birds (Table: Bird.Parasitology), for which we were able to obtain records of parasite body size and intensity (K. Sheehan, pers. comm.). We estimated the average biomass for each parasite group differentiated by within-host habitat (e.g. gut trematodes, blood trematodes) of each bird analog. The biomass of each group was then converted into a fraction of host biomass, which we applied to our Palmyra bird analogs. When multiple

species of trematodes occurred in a host species and shared the same habitat within that host species (e.g. gut) we partitioned the total trematode biomass within that host according to the relative biomass of the trematode species in their molluscan first-intermediate hosts at Palmyra. Parasite abundances in birds were estimated as the difference between average estimated biomass of a parasite species and its average body size. Thus, we were able to infer endohelminth biomass density in birds at Palmyra.

2.8 Taxon-specific methods: Parasite

Our general methods were designed to survey organisms based on their habitat (e.g. planktonic, benthic) and body size regardless of taxonomic affiliation. However, density estimates for some Taxa required either the implementation of additional, specific sampling methods or special statistical treatment. We detail those cases for parasitic taxa below.

2.8.1 Clonal trematodes in molluscs

Infections by philophthalmid and schistosomatid trematodes were easily identified and their prevalences calculated. We pooled all unidentified trematode infections by molluscan host and partitioned the prevalence according to the relative density (g/ha) of the metacercarial stage of each unaccounted for trematode species. Trematodes exhibit clonal growth in their molluscan first-intermediate hosts. We estimated the mass of individual infections of these clonal parasite colonies by estimating the fraction of host tissue they had replaced and multiplying this fraction by the total mass of the molluscan host's soft tissue. Single species infections by clonal trematodes are generally the rule (Kuris 1990; Kuris and Lafferty 1994; Lafferty *et al.* 1994), and the lack of observed double infections at Palmyra

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Atoll confirm this. Hence, we estimated total clonal trematode biomass densities as a product of host densities, infection prevalence, and mean individual mass.

2.8.2 Free-swimming trematode cercaria

Cercariae are free-living trematode infectious stages that are shed into the water column. Cercariae were not preserved well in our sampling methods, and thus we were not able to estimate their densities from our zooplankton samples. We obtained the body size and mean daily cercariae shed rate from Thieltges *et al.* (2008). Assuming they live for 24 hours, cercariae density estimates were obtained by multiplying mean daily shed rates by the density of the clonal trematodes that give rise to them. We estimated cercarial biomass density by multiplying these mean densities by body size estimates for individual cercaria obtained from the literature.

2.8.3 Adult flatworms in elasmobranchs

Cestode parasites are important in the sand flats habitat, but we were not permitted to sample two of their elasmobranch hosts: the sicklefin lemon shark, *Negaprion acutidens* and the spotted eagle ray, *Aetobatus ocellatus*. The most common elasmobranch is the black tip reef shark, *Carcharhinus melanopterus*, which we collected and dissected as per the fish parasite protocol described above. The sicklefin lemon shark was too rare to sample, so we based its cestodes on the intensities observed in *C. melanopterus*, (we assumed these species had sufficient diet overlap to share trophically transmitted prey). We were also not able to collect the spotted eagle ray for parasitological analysis so we used published records to infer the identity and intensities of cestodes that we assume they acquired by eating benthic

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invertebrate hosts. For example, the most important second intermediate host at Palmyra is the conch *Conomurex luhuanus*, which is infected with larval cestodes similar to those found in eagle rays elsewhere. Monogenean parasites have been reported from eagle rays elsewhere (White *et al.* 2010), but we did not include them because there are few monogeneans present in other fishes at Palmyra (Vidal-Martínez *et al.* 2017). We estimated adult cestode biomass density in these two elasmobranch hosts as the product of their host's density, parasite abundance and parasite body size. The contribution of these adult cestodes to total parasite biomass is relatively inconsequential but they are important components of network structure.

2.8.4 Parasites in zooplankton

We did not perform systematic parasitological analyses on zooplanktonic organisms. However, some of the observed parasite species (particularly nematode and cestodes) belong to taxa known to use zooplanktonic organisms as their first intermediate hosts (Marcogliese 1995). Parasite host identity and prevalence estimates were gathered from the literature for various parasite groups (i.e. nematodes and cestodes) (Marcogliese 1995). If the prevalence of a parasite group described more than one parasite species (e.g. cestodes in calanoid copepods) that prevalence was apportioned according to the relative biomass of the succeeding stages of the parasites it described. Parasite density estimates were obtained by multiplying host density by parasite prevalence and mean parasite intensity. Parasite biomass density estimates were obtained by multiplying parasite density by mean parasite body mass.

2.9 Limitations and potential enhancements

Although the biotic survey for the intertidal sand flats at Palmyra Atoll is well resolved, we welcome input from colleagues allowing its improvement and will update the dataset if we acquire substantial new data. We also recommend contacting the authors to make sure no updates are pending. Below, we outline data limitations, as well as some prospects for their improvement.

2.9.1 Species inclusion

The data's primary limitation is the under-representation and omission of some groups. Ectoparasites of birds are omitted, as are symbiotic bacteria for all species. Meiofauna, which includes the smallest free-living metazoans (e.g. nematodes, turbellarians and loraciferans) are underrepresented. We plan to systematically incorporate meiofauna in the near future. The parasites of meiofauna organisms are also poorly known. The taxonomic diversity of unicellular organisms (both free-living and symbiotic) is also underrepresented, with most aggregated by size classes. The free-living copepod fauna is divided into six morphospecies that might represent species aggregations. The parasites of zooplankton are also not well known and none were directly observed in our samples. Because of this, we only included parasite life stages in the zooplankton that were necessary to complete the lifecycles of parasites that were directly observed in other hosts. We also did not quantify the parasites of the phytoplankton (e.g. parasitic dinoflagellates, chytrids or perkinsids). Users of this data base should be aware of these limitations when drawing conclusions about certain groups or subwebs.

2.9.2 Body size

Body size is a common descriptive measure in ecology and organizing metric food web analyses (Brose, Ulrich, Jonsson, Tomas, *et al.* 2006; Cohen *et al.* 2003; Woodward *et al.* 2005). Our body size estimates span 9 (total length) and 22 (mass) orders of magnitude. The magnitude of this variation should diminish the influence of sampling error on the approximation for any node in most analyses. There are two kinds of body size estimates that can be improved. First, any organism for which we used a proxy could benefit from direct measurement. Second, we used size classes to distinguish morphospecies for some unicellular organisms (e.g. benthic diatoms, ciliates, phytoplankton). It would be beneficial to confirm that these size-based (total length) groups accurately describe discrete morphospecies.

2.9.3 Density

There are two broad groups whose density estimates can be improved. The first group consists of organisms whose density we estimated indirectly. This group includes adult organisms for which we used proxies and the larval stages of many free-living organisms and trematode cercariae. Density estimates for larval stages could be obtained empirically (Kuris *et al.* 2008; Thieltges *et al.* 2008). The second broad group consists of organisms whose densities we did not quantify. These organisms can be broken into two types: (1) life stages that we know are present, (2) life stages for species that are likely present but which we did not adequately describe. The first type includes helminth-associated life stages like eggs, miracidia and oncomiracida. Helminth egg production and survivability of other infective stages can vary and will need to be quantified on a specific basis (Kearn 1986; Llewellyn

1963; Poulin 1997). The second unquantified group includes species that may have been aggregated into morphospecies types: mostly unicellular groups like phytoplankton, diatoms and ciliates. These groups must be disaggregated and described before the densities of their constituent species can be estimated. All the groups mentioned above require more attention to elevate them to the same empirical footing as more consistently well-documented groups like birds and commercially important fishes and invertebrates.

3 A food web including infectious agents and life stages for the intertidal sand flats at Palmyra Atoll

3.1 Introduction

We assembled an interaction network for the unicellular and multicellular eukaryotic organisms living in and on the 3.14 ha of intertidal sand flats at Palmyra Atoll. The food web has several noteworthy inclusions: (1) parasites (infectious agents) on the same empirical

footing as their free-living hosts, (2) life stage information for both free-living and infectious organisms, (3) 22 types of interactions. The nodes in the network are 670 life stages, comprising 275 species from 51 orders and 22 phyla. There are 24,575 individual links describing the interactions between these nodes. The data set compliments a partner data set describing a quantitative survey of these same organisms, together they create a detailed description the Palmyra Atoll sand flat community. We plan to use these data to address several general questions about ecological communities, and encourage potential collaborators to contact us.

Although most food webs only include consumer-resource interactions between free-living organisms, such as predator-prey and herbivore-plant interactions (Lafferty, Dobson, *et al.* 2006), we recognize 22 possible interaction types (described here and below), that are differentiated by consumer strategy (Lafferty *et al.* 2015; Lafferty and Kuris 2002). Non-trophic interactions, such as commensalism and transmission, that are informative about system structure and dynamics are also included. Due to ontogenetic shifts in diet or host, trophic interactions must be delineated by life-history stages, in addition to species. The number of possible interactions in a network is the square of the number of nodes in the network being evaluated. There are 448,900 possible interactions in the Palmyra sand flats network, which makes the direct observation of all interactions unfeasible. To subsidize our directly observations (i.e. field observation, gut content analysis, parasitological analysis) we also included interactions in the literature, expert opinion and the known interactions of similar species (Hechinger, Ryan F. *et al.* 2011; Polis 1991).

The network is organized along two niche axes. First, the network is ordered according to broad consumer strategy. Species are separated into broad groups based on their trophic level

and lifestyle, and in the following order: (i) detrital, (ii) autotroph (iii) mixotroph (iv), free-living consumer, (v) commensal consumers and (vi) infectious consumers. Body size is the most common axis along which food web matrices are organized (Brose, Ulrich, Williams, Richard J*., et al.* 2006; Loeuille and Loreau 2005; Otto *et al.* 2007; Rezende *et al.* 2009; Zook *et al.* 2011), and within these broad groups species are ordered according to the mass of their adult stage (or next largest stage if the adult stage is not present in the habitat).

For explanatory purposes, below we have broken our network into four subwebs (quadrants). Quadrants are organized around organism lifestyle (free-living or parasitic) and trophic role (consumer or resource) (Lafferty, Dobson*, et al.* 2006). This representation of consumers is symmetrical, all organisms have the potential to consume one another. Free-living organisms are consumers and resources in the first quadrant, while parasites are consumers and resources in the fourth quadrant. Parasites are consumers and hosts are resources in the second quadrant, and predators are consumers while parasites are resources in the third quadrant. Thus, including information about link type provides an additional framework for organizing food web structure.

3.2 Predator-prey interactions

The predator-prey quadrant is comprised of interactions between free-living organisms. In this quadrant, the link types we recognize are predation, social predation, micropredation, facultative micropredation, detritivory, scavenging, decomposition, predation on free-living non-feeding stage, and acquisition of dissolved nutrients. Predator-prey interactions that were directly observed were based on gut content analyses, field observations and inference from parasitological information (i.e., if a host had a parasite that

it could only get from eating a particular prey item, we concluded it fed on that prey item). The trophic links in this quadrant are the same as those represented in almost all published food webs.

3.3 Parasite-host interactions

Infectious agents, such as parasites and pathogens, are often omitted from food webs (Cohen, Beaver, *et al.* 1993; Marcogliese and Cone 1997). In the host-parasite quadrant, we integrate parasites into the food web as consumers. Interaction types found in this quadrant include: parasitic castration, pathogen infection, macroparasitism, parasitoidism, trophically transmitted parasitic castration, trophically transmitted pathogenism, trophically transmitted macroparasitism and trophically transmitted commensalism. With the few exceptions all parasite-host interactions were based on direct observations. Recognizing and differentiating between these different interaction types is critical to the precise inclusion of parasites in food webs.

3.4 Predator-parasite interactions

Including parasites in food webs requires us to consider them as potential resources. Including interactions that recognize parasites as resources has important impacts on network structure (Dunne, J. A. *et al.* 2013; Johnson *et al.* 2010; Lafferty, Dobson*, et al.* 2006). Parasites are resources in the predator-parasite quadrant, which includes the interaction types: concurrent predation on symbionts (safely eating parasites hosted by a prey species), trophic transmission denotes an infection pathway (eating parasites in prey that can infect the predator), predation on free-living non-feeding stages, and transmission (when eating a free-

living infectious stage leads to transmission). Trophic transmission and transmission indicate the process of infection and should not be included in analysis of trophic structure. Concurrent predation on symbionts might not represent energetically significant resources for a predator and therefore are not relevant for estimating node trophic level or food web robustness (Lafferty, Hechinger, *et al.* 2006; Lafferty and Kuris 2009). However, these mortality sources for transmission stages could be important for control of parasite abundance in subsequent hosts – a bottom up effect. Including these link types in trophic level estimates will elevate predator trophic levels and lower parasite trophic levels, and including them in robustness analyses will lead to erroneous outcomes. We can infer the presence of trophic transmission interactions, transmission and concurrent predation on symbionts from the predator-prey and host-parasite quadrant. Predation on free-living non-feeding stages and Predation on commensal non-feeding stages, are based on our observations in other systems (Hechinger, Ryan F. *et al.* 2011; Kaplan *et al.* 2009; Mouritsen *et al.* 2011; Thieltges *et al.* 2011; Zander *et al.* 2011).

3.5 Parasite-parasite interactions

Antagonistic interactions between parasite species (Parasite Intraguild Antagonism) can be important (Graham 2008; Kuris *et al.* 1979; Telfer *et al.* 2010) and may be common (Pedersen and Fenton 2007). They are also difficult to observe. We restrict our examination of antagonistic interactions between parasites to interactions among larval trematodes in their molluscan first intermediate hosts. Intraguild predation appears to be the primary force structuring larval trematode communities in their molluscan first intermediate hosts (Kuris 1990; Kuris and Lafferty 1994). Dominance hierarchies dictate the outcome of intraguild

predation between trematodes in their first intermediate hosts. More dominant trematodes can completely replace infections by subordinate species. We used relevant sources (Rohde 1981), and principles for a putative dominance hierarchy outlined in Kuris (1990), based on indirect evidence of dominance, and recent experimental evidence (Garcia-Vedrenne *et al.* 2016; Hechinger, Ryan F *et al.* 2011) to assemble dominance hierarchies for these larval trematode communities (to indicate which species were predators or prey). Interactions between parasites in hosts can be important determinants of their distribution, prevalence and abundance (Esch *et al.* 1990; Lafferty *et al.* 1994).

3.6 Limitations and potential enhancements

The primary limitation of the network is the under-representation and non-representation of some groups. These limitations are outlined explicitly in the partner data set providing a quantitative survey of the organisms on the intertidal sand flats at Palmyra Atoll.

Of the 24,575 links in the Palmyra Atoll intertidal flats food web, only 1456 were directly observed. The remaining 94% of links are inferred. The method used to infer each link is included in the Links_List data table and defined in the Variable_Description metadata table (Table 2B). The fraction of inferred links in food webs is not well documented, but the ratio reported here is similar those reported in the few webs for which this information has been published (Kuris *et al.* 2008; Preston *et al.* 2012; Warren 1989). Inferring the presence of links is necessary because, even significant investment in direct observation of trophic interactions often only captures a fraction of organism's actual diet (Polis 1991). Thus, limiting webs to directly observed interactions ensures the omission of consumer-resource interactions, especially in speciose systems like Palmyra. However, while

modeling should improve overall network quality, it will not capture all unobserved links and some modeled links will not actually occur. Link information could be improved by including experimental information. For example, consumer-resource interactions in mesocosms are particularly useful for excluding interactions that do not occur. Direct observations could also be improved by applying new molecular techniques to gut content analyses.

4 Parasites make important and general contributions to ecosystem structure

4.1 Introduction

If all parasites disappeared, what would we lose? At the biosphere scale, we would lose many species (Dobson *et al.* 2008). Even though parasitism is the most common lifestyle on Earth (Price 1980), we know less about the role parasites play in local communities (Lafferty, K. D. *et al.* 2008; Marcogliese 2003; Marcogliese and Cone 1997) than we do about species from other groups (e.g. megaherbivores, predators, pollinators, mycorrhizal fungi). Although,

some ecological studies have incorporated parasites on the same empirical footing as their

free-living counterparts (Amundsen *et al.* 2009; Preston *et al.* 2012), most are restricted to

estuarine systems (Hechinger, Ryan F. *et al.* 2011; Huxham *et al.* 1995; Mouritsen *et al.*

2011; Thieltges *et al.* 2011; Zander *et al.* 2011). Temperate estuaries on the Pacific coast of

North America represent the only three places where all parasites in a system have been

systematically counted and measured (Hechinger, Ryan F. *et al.* 2011). In these temperate

estuaries, parasites make significant contributions to diversity (Lafferty, Hechinger*, et al.*

2006), abundance (Hechinger, R. *et al.* 2011), biomass (Kuris *et al.* 2008), trophic structure

(Lafferty, Dobson*, et al.* 2006) and network topology (Dunne, J. A. *et al.* 2013). They

comprise one third of estuarine diversity (Lafferty, Hechinger*, et al.* 2006), and after

accounting for their high trophic level, estuarine parasites are as abundant as free-living

consumers (Hechinger, R. *et al.* 2011). With their biomass exceeding that of birds, parasites

make important contributions to estuary energetics (Kuris *et al.* 2008). Parasites also modify

energy-flow by participating in 70% of trophic interactions (Lafferty, Dobson*, et al.* 2006),

and altering food-web topology in unique ways (Dunne, Jennifer A *et al.* 2013). Removing

parasites would strongly alter temperate estuaries.

Some estuary attributes suggest that these contributions by parasites may not extend to

other systems. First, in west coast estuaries, California horn snails (*Cerithidiopsis*

(*Cerithidia*) *californica*) are the most abundant free-living species and are obligate first

intermediate hosts for >20 parasite species (Kuris *et al.* 2008). Second, birds are the most

diverse free-living group and serve as definitive hosts for the majority of estuarine parasites

(Hechinger, Ryan F. *et al.* 2011). Third, the estuaries studied are temperate systems with

relatively few species and high productivity (Correll 1978; Nixon 1980), conditions that

might favor parasitism. This leads to the question we address here: Are parasites important in any other systems?

To test whether parasites alter community structure beyond Pacific coast estuaries, we assembled a quantitative food web for the intertidal sand-flats habitat of Palmyra Atoll, a low-lying coral atoll, located in the central Pacific, 1600 km south of Hawaii. The Palmyra dataset incorporates parasites on the same empirical footing as the estuarine datasets, making the two comparable (McLaughlin, In Review). Other physical and biological similarities between the systems facilitate comparison. Both Palmyra and the estuarine systems are soft-sediment, intertidal systems protected from wave-energy. They are also similar in size. The area encompassed by the Palmyra sand flats (314 ha) is close to the mean area of the three estuaries (304 ha, SD = 351 ha) (Hechinger, Ryan F. *et al.* 2011). The systems are similar in diversity. Palmyra has more total species than any estuary, but falls within the range of species per unit area (0.88 species ha^{-1}) found in the estuaries (mean = 1.4 species ha^{-1}, SD = 1.2 species ha^{-1}). Thus, we can compare systems with similar habitats, areas and complexity.

There are several important physical differences in the systems. The systems differ in their physical heterogeneity. The estuaries incorporate four habitats (vegetated marsh, unvegetated pans, mudflats and channels), whereas the Palmyra sand-flats are relatively homogenous planes, intermittently bordered by narrow rocky-intertidal zones. The mobile vertebrate consumers in these systems also have access to different adjacent habitats. Kelp forests and sandy beaches are adjacent to estuaries. Estuarine birds, especially sandpipers and plovers forage on the sandy beaches, whereas, Palmyra birds forage almost entirely on the sand flats at low tide. In Palmyra, large fishes, like blacktip sharks and giant trevally, move between the sand flats and the adjacent lagoons, reef flats and the fore reef. The systems also

differ in latitude; Palmyra is tropical while the estuaries are temperate. As a result, Palmyra experiences little seasonal variation and higher ambient temperatures. The average temperature on the flats at Palmyra (31.2 C) is outside the range experienced in the estuaries (mean 20.2 C, SD = 1.3 C). Finally, the systems differ in their proximity to similar ecosystems. The sand flats at Palmyra are much farther (375.5 km) from other sand flats, than estuaries are from other estuaries (mean = 38.5 km, SD = 23.1 km). These physical differences could alter ecological communities, including parasitism.

Although the systems are similar in overall diversity they do differ in species and community composition across trophic levels, the sanderling (*Calidris alba*) is only shared species. Estuaries are some of the most productive ecosystems on Earth, and include flowering (terrestrial) plants with nutrient inputs derived from terrestrial runoff. Palmyra, like many low-lying coral atolls is a nutrient poor system, with nutrients derived from pelagic inputs. As for primary consumers, although similar snails are present in Palmyra, no single species dominates biomass as does *Cerithideopsis* (*Certihidia*) *californica* in the estuaries. Birds dominate higher trophic level diversity in estuaries, where as fish dominate in Palmyra. An outcome of this role reversal is that the dominant consumers at Palmyra (fish) eat each other, whereas in estuaries the dominant consumers (birds) do not. Intraguild predation (or lack thereof) among definitive hosts may have implications for parasite diversity and their ability to navigate the trophic network. Thus, Palmyra and estuarine systems are different enough in their species composition and ecosystem attributes that any similarities between them are informative about the general role of parasites in ecosystems. If parasites have similar roles across systems, then we would expect to see similar patterns in their

contributions to diversity, biomass, abundance, trophic structure and network topology would be similar in estuaries and Palmyra.

If parasites make similar contributions to diversity across systems, then after accounting for free-living consumer richness, there should be little difference in parasite richness between Palmyra and the estuaries. To make this comparison valid, parasitological surveys in both systems incorporate all infectious agents they encountered, but focus on eukaryotic organisms generally omitting viruses and bacteria. Comparing parasite richness in these systems informs our understanding of parasites diversity at different latitudes, trophic levels and host groups.

In estuaries, parasites are as abundant as similar free-living consumers, after controlling for trophic level. To evaluate if this pattern applies to Palmyra, we test whether parasites and free-living organisms share the same abundance-body size scaling after controlling for trophic level. We also evaluate the consistency of this relationship across systems. If these scaling relationships are maintained, is suggests that metabolic ecology applies to all consumers.

Parasite biomass is substantial in estuaries. If parasites make consistent contributions across systems, we expect parasite biomass density to be similarly high in Palmyra. We can further evaluate whether the distribution of biomass is further conserved among parasitic and free-living species. By comparing biomass distributions across systems, we gain insight into energy flow between compartments and how such compartments differ from system to system.

Parasites dominate trophic interactions in estuaries (Lafferty, Dobson*, et al.* 2006). To evaluate if parasites make similar contributions to trophic structure at Palmyra, we can

examine the fraction of food-web interactions in which parasites participate. Body size is correlated with many ecological traits (Peters 1986), and serves as useful metric for organizing food webs (Woodward *et al.* 2005; Zook *et al.* 2011). As a result, many food web models assume that resource body size range is correlated with consumer body size (Williams and Martinez 2000; Yodzis and Innes 1992). Being smaller than their hosts, parasites in estuaries extend the body-size range over which consumer-resource interactions occur (Lafferty and Kuris 2002). We can determine if these effects are general by comparing the frequency distributions of consumer-resource biomass ratios across systems.

If parasites have similar effects on network topology across systems, we expect Palmyra and estuary food webs will have similar topological metrics (e.g. directed connectance, nestedness) and motif proportions. In food webs there are two types of three-node motifs: motifs without mutual predation (single) and motifs with mutual predation (double) (Fig. 4.1). In estuarine food webs, parasites increase double motifs due to concurrent predation (parasites are consumed when a predator eats their host)(Dunne, Jennifer A *et al.* 2013). Comparing the roles of parasites in the networks at Palmyra and the estuaries provides insight into the role parasites play in food webs.
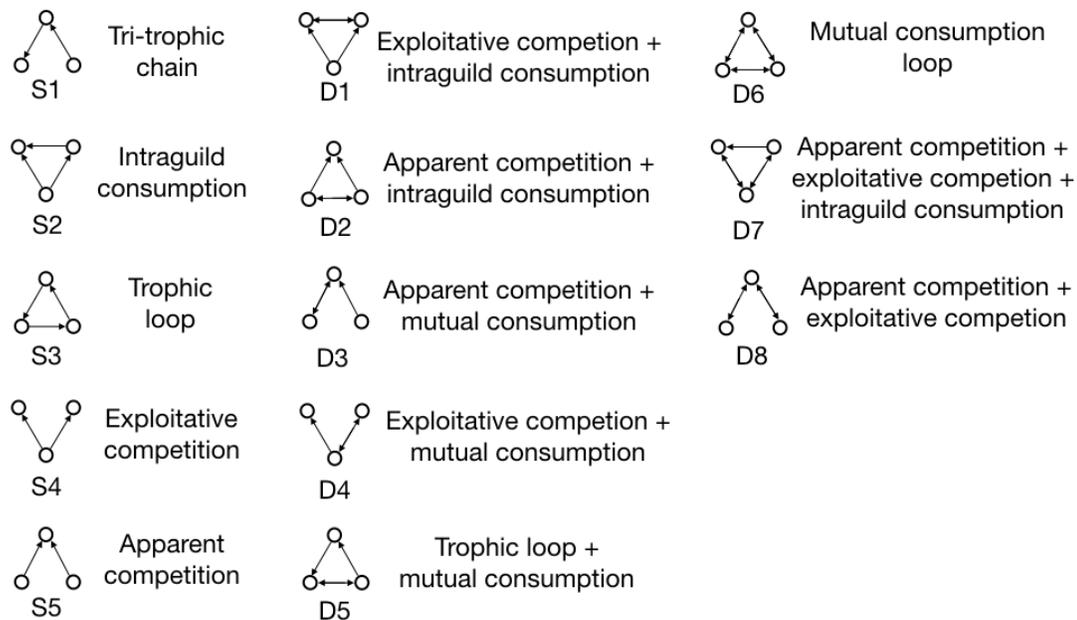
Figure 4. 1 Food web motifs. The 13 variations of three-node motifs possible in food webs. S1-S5 are single motifs. D1-D8 are double motifs.

4.2 Materials & methods

To compare parasite affects on community structure, we analyze two datasets describing the food webs for three Pacific estuaries and Palmyra (Hechinger, Ryan F. *et al.* 2011). Both datasets were assembled using similar quantitative, random sampling. Unlike most studies, that aggregated all life stages into a species node, the finest organismal units quantified in these datasets are species' individual life stages. We standardized the Palmyra data to match the less-finely resolved estuarine food web data by removing or aggregating nodes from Palmyra that were not adequately sampled in the estuaries. We removed from Palmyra, larval stages of free-living species (except gastropod trochophores and bivalve veligers), parasite

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eggs, oncomiracidia, miracidia, bacteria, heterotrophic flagellates, planktonic ciliates, tardigrades and free-living nematodes. When appropriate, we aggregated Palmyra nodes to make them comparable to aggregated estuarine nodes. We aggregated phytoplankton, benthic diatoms, benthic protists, calanoid copepods and harpacticoid copepods into their respective nodes and Palmyra detritus into five comparable nodes. Any links duplicated by node aggregation at Palmyra were removed. More detailed description of the sampling methods employed in both systems can be found in the original data sets described in chapters 1 and 2.

To compare parasite affects on community structure between Palmyra and the estuaries, we estimated free-living and parasite species diversity. Species richness was calculated from standardized surveys of free-living organisms in both systems. Sampling effort and method varied with the abundance and body size of target groups. For example, birds were counted in the field with binoculars, whereas polychaetes were collected with 10cm diameter cores, and then sorted and identified under microscope in the lab. Parasites were sampled in hosts collected by both random and targeted sampling. In both systems, most individual parasites were difficult to identify juvenile stages. To accurately estimate their diversity, expert taxonomists identified all parasites with morphological and molecular techniques (Hechinger and Miura 2014; Vidal-Martínez *et al.* 2012; Vidal-Martínez *et al.* 2017).

To compare how parasites affect abundance scaling relationships across systems, we plotted density versus body size after controlling for trophic level and temperature, as done for estuaries by Hechinger et al. 2013. We estimated short-weighted trophic level for Palmyra nodes in R (Team 2016) with the *cheddar* (Hudson *et al.* 2013) package. Ambient temperature corrections for abundance at Palmyra were based on the mean of 82,848

individual measurements taken over a month at 32 sites McLaughlin et al. (In review). We used general linear models to evaluate all abundance-body size scaling relationships. We used 95% quantile regressions to evaluate the under saturation of smaller species at Palmyra. Statistical controls were conducted for trophic level and body size in JMP 14 (Institute 2000) and general linear models evaluated in R. We conducted a one-way ANOVA to compare parasite trophic level across systems.

To compare parasite biomass in Palmyra with parasite biomass in estuaries, we estimated the biomass density for each node by multiplying the mean individual body size by density. For free-living organisms, body size is the mean body mass for individuals of each life-stage as they occurred in random sampling. For most birds in both systems, body size estimates are from the literature. Parasite body sizes are direct weights or were estimated by multiplying organismal volume by a tissue density of 1.1 g ml^{-1}. All biomass density comparisons were made with two-sample t-tests, with an FDR adjustment to control for multiple comparisons.

To compare parasite affects on trophic structure across systems, we first categorized links into four types: (1) free-living: links between free-living species, (2) predation on free-living infectious stages: free-living organisms consuming parasites in the environment, (3) concurrent predation: free-living organisms consuming parasites in hosts, (4) parasitism: parasites consuming hosts. We used two-sample t-tests (controlling for multiple comparisons with an FDR adjustment) to compare the fraction of total interactions that these link types comprise, and evaluate the contribution of parasites to trophic structure across systems. To determine if parasites extend the size range of consumer-resource interactions, we first compared the frequency distribution of parasite consumer body-size ratios to that of free-living species at Palmyra. To see if these effects are similar across systems we compare the

frequency distribution of parasite consumer body-size ratios at Palmyra to those of parasites in the estuaries. We used two-sample t-tests (adjusted with an FDR control) to compare the frequency distributions of the consumer body-size ratios within Palmyra and across systems.

To compare how parasites affect network topology across systems we analyzed two different food-web assemblies for each system: (1) A version containing only stages of free-living species, and (2) a version containing stages of both free-living and parasitic species. To make our results comparable to previous analyses (Dunne, J. A. *et al.* 2013) we aggregated life stages at the species level. The food web version including parasitism also includes concurrent predation. We can evaluate network similarities by comparing descriptive topological metrics and motif representation. For both food-web versions we estimated nine metrics that describe network topology and trophic structure (Table 4.1). We also compared how parasites affect motifs that represent mutual consumption (also known as double motifs) across systems. We estimated parasite effects as the difference in double-motif proportions between free-living and parasite versions. However, because such versions differ in species richness (which can affect motif proportions), we used the niche model to simulate webs of equal richness but containing only free-living species. We used two-sample t-tests (adjusted with an FDR control) to compare parasite effects with richness effects. To evaluate the consistency of these contributions across systems, we plotted the parasites effects on double motifs in Palmyra vs estuaries. All network analyses were conducted in R (Team 2016) with the *cheddar* (Hudson *et al.* 2013) and *igraph* (Csardi and Nepusz 2006) packages which can accommodate large networks.

4.3 Results

4.3.1 Diversity

Parasites made similar contributions to community structure at Palmyra and in the estuaries (Fig. 4.2). The richness of both free-living and are parasitic consumers was consistent across systems, and we failed to reject the null assumption of no difference. Although there was no difference in total free-living richness (Palmyra = 119, Estuary mean = 107, SD ± 15), potential differences in sampling effort between the projects limit the determining which system has the most species. With respect to relative richness, birds were the richest vertebrates in estuaries ($p < 0.01$, Palmyra = 6, Estuary mean = 43, SD ± 2), whereas at Palmyra fishes were the richest vertebrate group ($p < 0.01$, (Palmyra = 41, Estuary mean = 41, SD = 0) (Fig. 4.3). It is remarkable that parasites comprised at least one-third (33-40%) of diversity in both systems (Fig. 4.2).
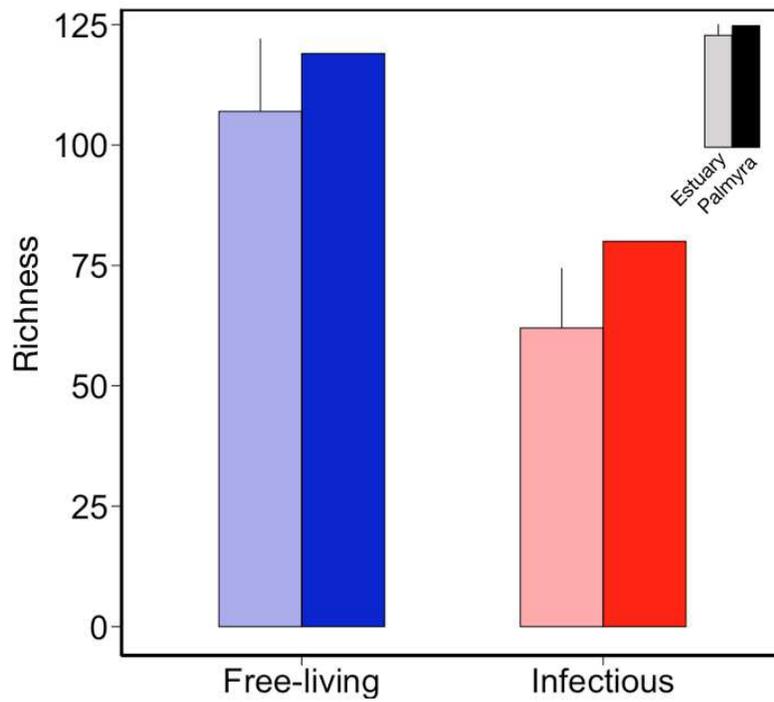
Figure 4. 2 Richness. Similar richness for free-living (blue) species in estuaries (light bars, mean +/- S.D.) and at Palmyra (dark bars), and similar richness for infectious (red) species in estuaries (light bars, mean +/- S.D.) and Palmyra (dark bars).
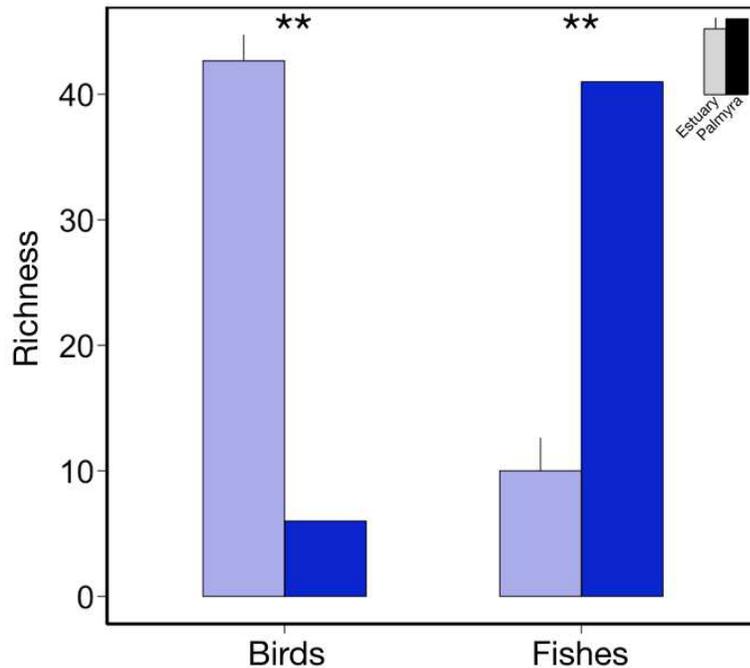
Figure 4. 3 Bird and fish richness. Bird diversity was higher in estuaries (light bars, mean +/- S.D.), whereas fish diversity was higher at Palmyra (dark bars). (** p < 0.01).

4.3.2 Abundance

After correcting for trophic level, a single linear model ($F_{2,203}$ = 91.06, p < 0.0001) described the abundance-body size scaling of parasites free-living and organisms at Palmyra ($\log_{10}$ abundance = 1.5 − 0.49 x $\log_{10}$ body size; r^2 = 0.47, slope 95% confidence limits ± 0.071) (Fig. 4.4), indicating that parasites at Palmyra have the same abundance-body size power law as comparable free-living species. Although, a shared power law for parasites and free-living species is consistent with past results for estuaries, the model parameters for free-living organisms and parasites were different at Palmyra than for the estuaries (p = 0.0001). Specifically, the model for all three estuaries ($F_{1,458}$ = 1387, p < 0.0001) had a steeper slope

and higher intercept ($\log_{10}$ abundance $= 2.1 - 0.72$ x $\log_{10}$ body size; $r^2 = 0.75$, slope 95%

confidence limits $\pm$ 0.039) (Fig. 4.4), indicating that abundance was lower at Palmyra, but

fell less sharply with body size than in estuaries, perhaps due to temperature, differences

between birds and fishes, differences in productivity, energetic subsidies from adjacent

habitats or tidal effects on transient species. 95% quantile regressions suggest that the

maximum slope at Palmyra (-0.70) may be closer to the mean estuary slopes (-0.74 - -0.77).

It may be a general finding that parasites are as abundant as similar free-living species (Fig.

4.4).
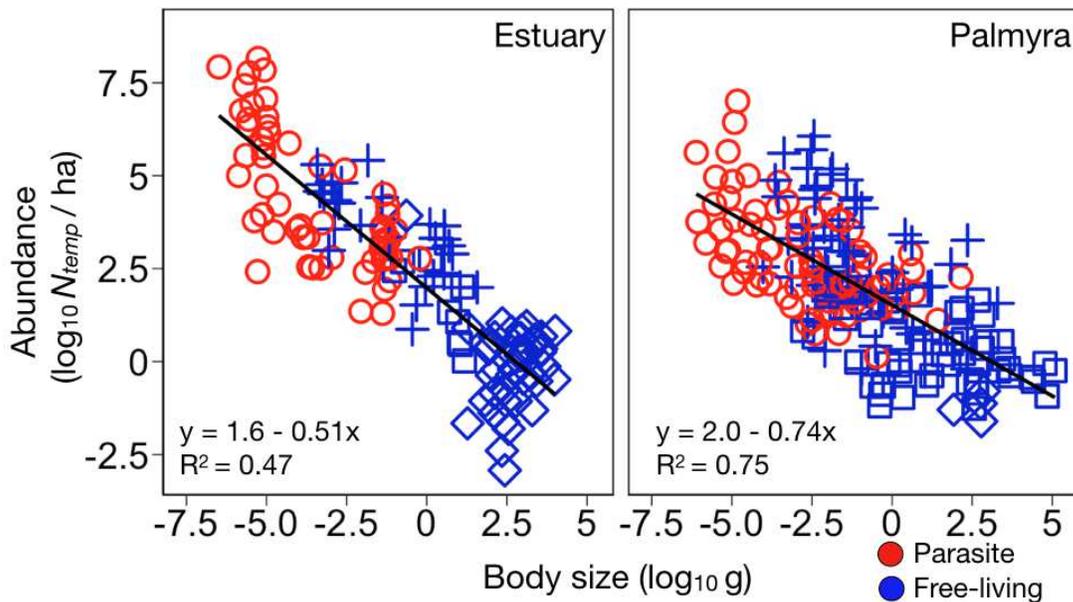
Figure 4. 4 Abundance. Parasites (red circles) are as abundant as similar-sized free-living species (blue) in estuaries and at Palmyra. Crosses are invertebrates; squares are fishes; diamonds are birds. Abundances are temperature corrected and statistically control for trophic level.

4.3.3 Biomass

Parasite biomass density was lower at Palmyra than in the estuaries ($p < 0.001$; Palmyra = 1.8 kg ha^{-1}, Estuary mean = 21.8 kg ha^{-1}, SD ± 13.2 kg ha^{-1}) (Fig. 4.5). Monogenes ($p < 0.001$, Palmyra = 0.0005 kg ha^{-1}, Estuary mean = 0 kg ha^{-1}) and nematodes ($p < 0.001$, Palmyra = 0.97 kg ha^{-1}, Estuary mean = 0.07 kg ha^{-1}, SD ± 0.01 kg ha^{-1}) had more biomass at Palmyra, but other groups did not differ in their biomass density (Fig. 4.6). This lower parasite biomass occurred even though Palmyra had more free-living biomass ($p < 0.05$; Palmyra = 2960 kg ha^{-1}, Estuary mean = 1856 kg ha^{-1}, SD ± 905 kg ha^{-1}), resulting in a lower parasite:free-living biomass ratio for several host groups at Palmyra (Fig. 4.7). The lower parasite biomass ratio was due, in part, to several lightly parasitized invertebrate groups (especially hemichordates, holothuroideans and polychaetes) that are less abundant or not present in estuaries, but contributed substantial biomass at Palmyra ($p < 0.001$, Palmyra = 29.8 kg ha^{-1}, Estuary mean = 3 kg ha^{-1}, SD ± 3.5 kg ha^{-1}) (Fig. 5). Fish ($p < 0.01$, Palmyra = 176.4 kg ha^{-1}, Estuary mean = 22.1 kg ha^{-1}, SD ± 10.9 kg ha^{-1}) and polychaetes ($p < 0.01$, Palmyra = 480 kg ha^{-1}, Estuary mean = 19.5 kg ha^{-1}, SD ± 13.4 kg ha^{-1}) also had more biomass at Palmyra than the estuaries (Fig. 4.8). There were no significant differences in the biomass of small arthropods, bivalves, snails, crabs, burrowing shrimp or birds. Bivalves and snails drove the parasite-biomass : host-biomass relationship in estuaries (Fig. 4.8). While these hosts were not less abundant at Palmyra they supported less parasite biomass (Fig. 4.8). The lower parasite biomass at Palmyra is a result of few parasites in the most abundant hosts. This shows how a few key hosts can affect parasite biomass at the ecosystem level.
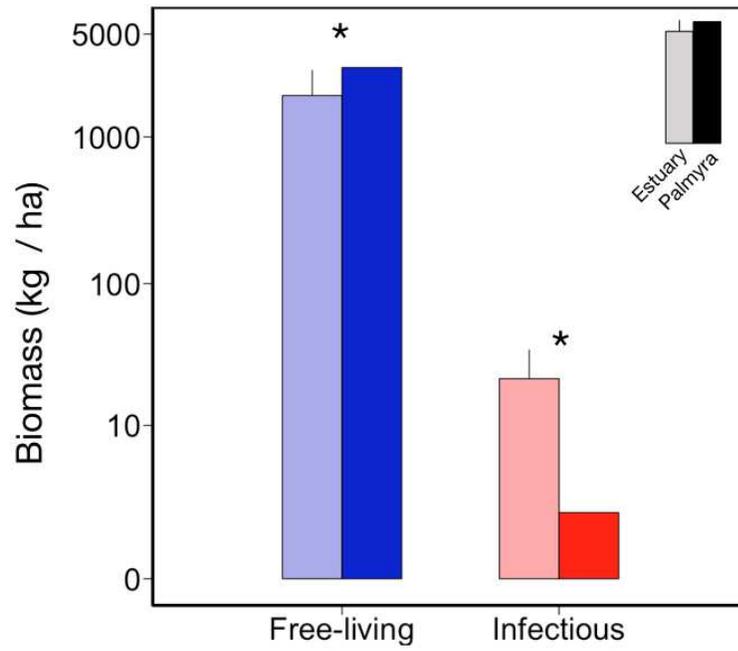
Figure 4. 5 Total biomass. Estuaries (light bars, mean +/- S.D.) had less free-living biomass (blue) but more parasite biomass (red) than Palmyra (dark bars). (* $p < 0.05$).
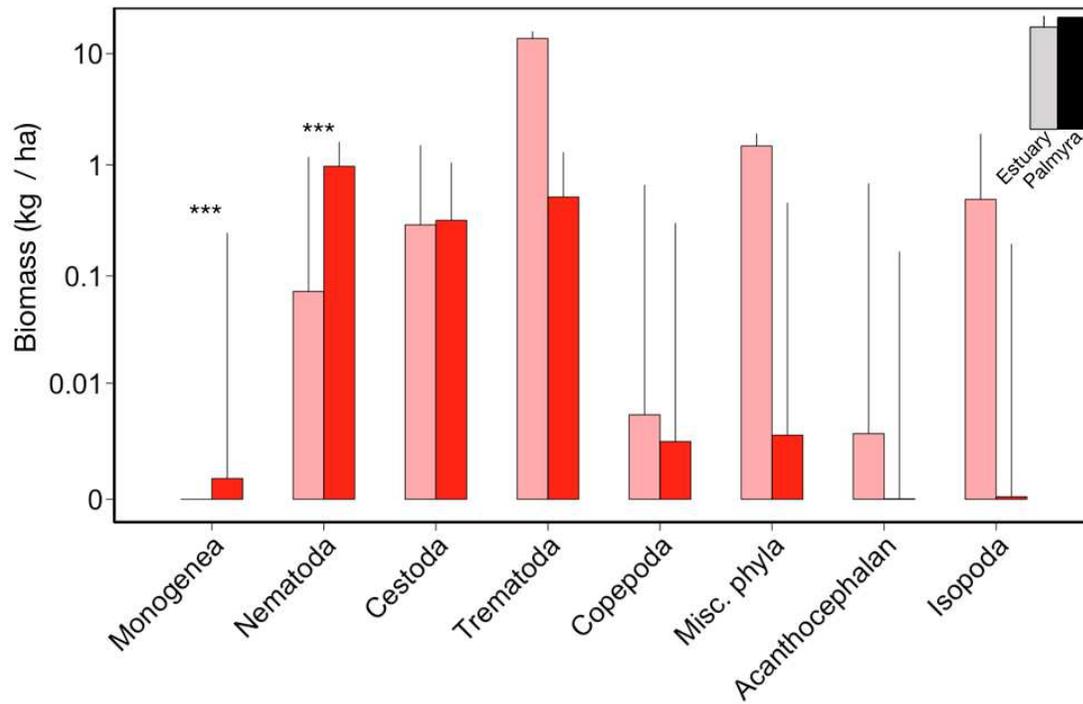
Figure 4. 6 Parasite biomass. Mongeneans and nematodes had lower biomass density in estuaries (light bars, mean +/- 95% C.I.) than at Palmyra (dark bars). (*** p < 0.001). Taxa ordered from relatively lower in estuaries than at Palmyra to relatively higher in estuaries than at Palmyra.
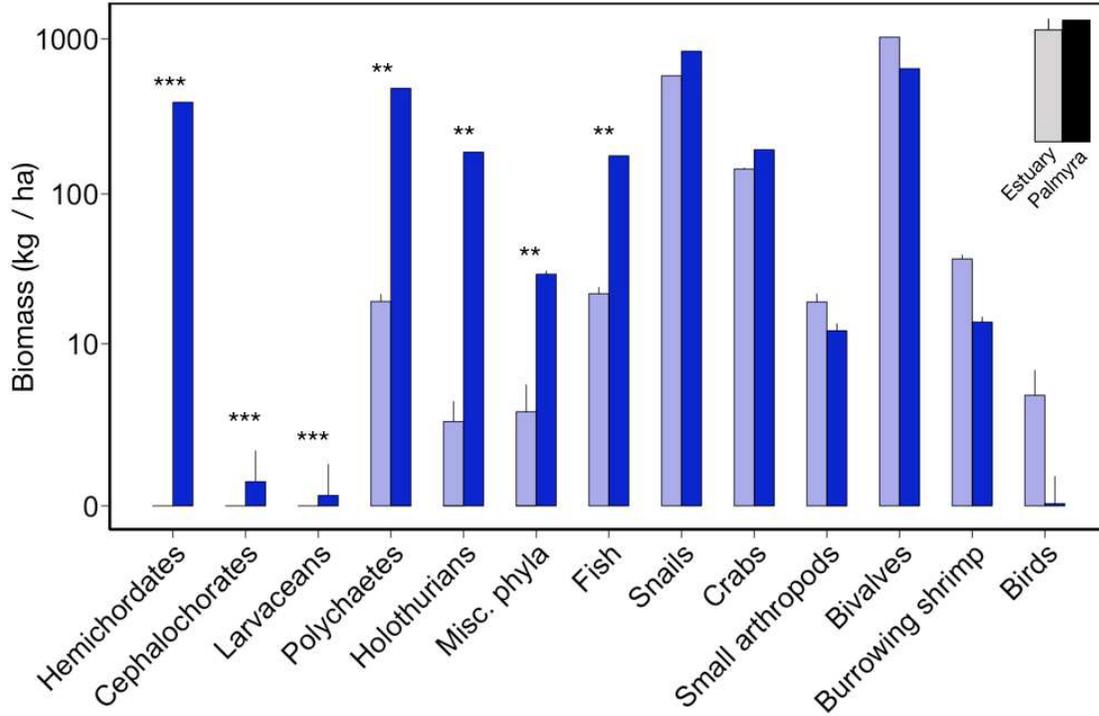
Figure 4. 7 Free-living biomass. Fishes and several invertebrate groups had lower biomass densities in estuaries (light bars, mean +/- 95% C.I.) than at Palmyra (dark bars). (** p < 0.01; *** p < 0.001). Taxa ordered from relatively lower in estuaries than at Palmyra to relatively higher in estuaries than at Palmyra.
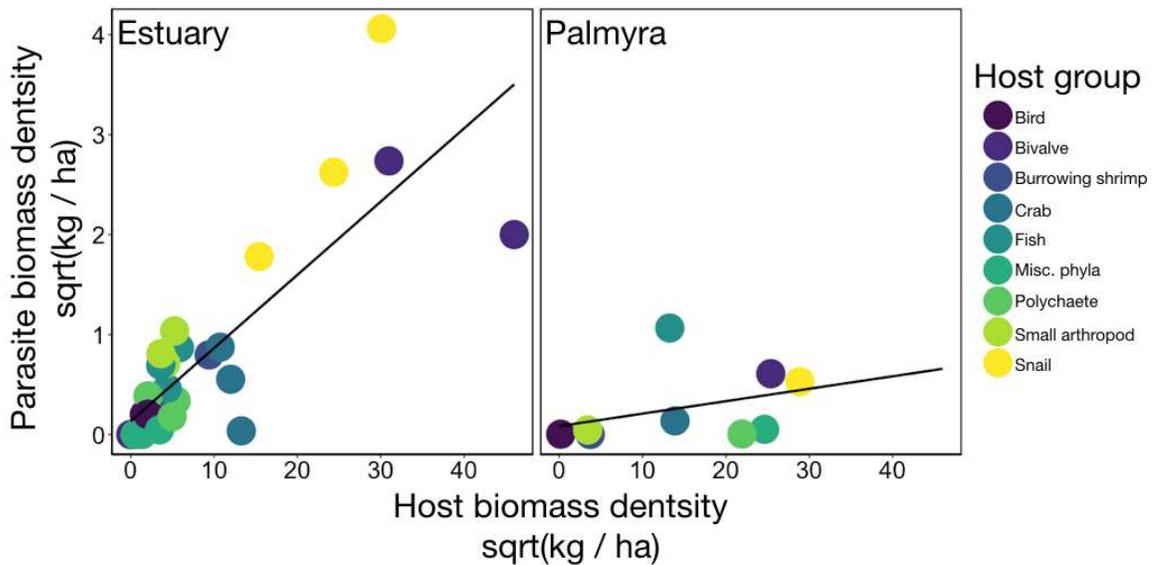
Figure 4. 8 Host biomass versus parasite biomass. The association between host biomass and parasite biomass is much stronger in estuaries, because the most abundant estuarine hosts had the most parasite biomass, whereas this relationship was less strong at Palmyra.

4.3.4 Trophic structure

Parasites made consistent contributions to the fraction of link types across systems (Fig. 4.9). As a proportion of total links, free-living links (Palmyra = 0.36, Estuary mean = 0.33, SD ± 0.02), concurrent predation links (Palmyra = 0.33, Estuary mean = 0.37, SD ± 0.02), predation on infectious stages (Palmyra = 0.19, Estuary mean = 0.09, SD ± 0.04) and parasitism links (Palmyra = 0.11, Estuary mean = 0.21, SD ± 0.05) were not significantly different from estuaries (all p > 0.08). Parasites had the same affects on the range of consumer-resource body size ratios in both systems (Fig. 4.10). Notably, parasites extended

the range of consumer-resource body size ratios at Palmyra across nine orders of magnitude (min = 1: $8.3e^{-14}$), whereas in the estuaries parasites extended the range over two orders of magnitude (min = 1: $1.0e^{-9}$). Micropredators (i.e. mosquitoes) with small consumer-resource body size ratios, which are present in the estuaries but not Palmyra are the primary reason for the estuaries already having a wide range in body size ratios without parasites. The mean parasite-host body size ratio (1:$5.1e^{-3}$ g) was 10 orders of magnitude lower than the mean predator-prey body size ratio (1:$9.6e^{7}$ g) at Palmyra (p < 0.0001), in the estuaries the difference in means was between nine and ten orders of magnitude (CSM p < 0.0001, parasite mean = 1:$2.6e^{-3}$, predator mean 1: $2.3e^{7}$; BSQ p < 0.0001, parasite mean = 1:$4.3e^{-3}$, predator mean = 1:$4.6e^{5}$ EPB p < 0.0001, parasite mean = 1:$3.9e^{-3}$, predator mean = 1:$2.0e^{6}$). The mean parasite-host body size ratio at Palmyra was not significantly different from the estuaries (CSM p = 0.3; BSQ p = 0.8; EPB p = 0.7). The extent that parasites dominate food web links in estuaries and Palmyra greatly extends consumer-resource body-size ratios.
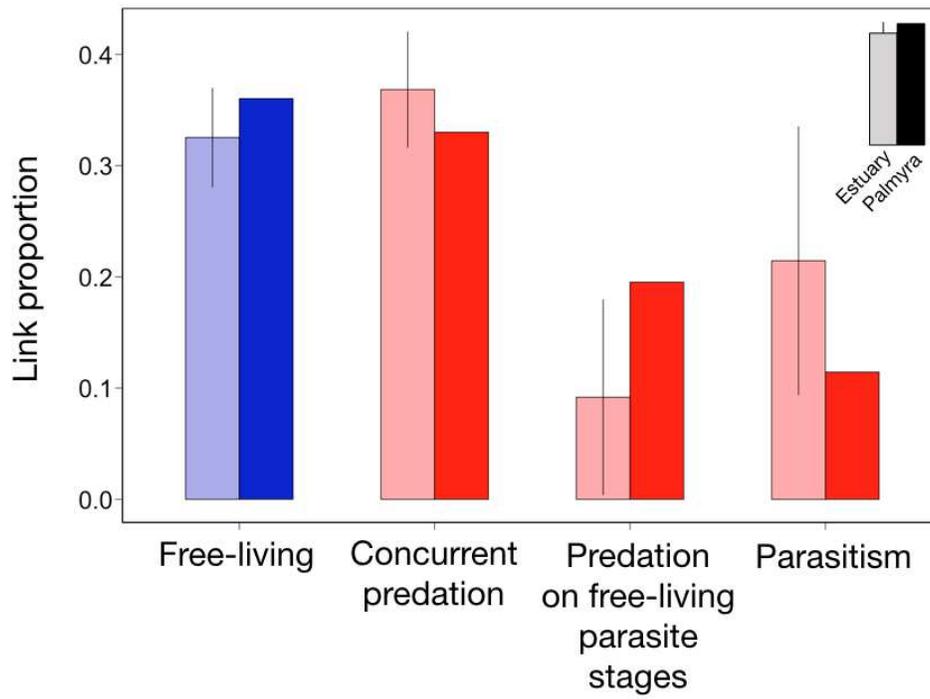
Figure 4. 9 Link proportions. Similar link proportions in estuaries (light bars, mean +/-95% C.I.) and at Palmyra (dark bars) for links that don't include parasites (blue bars) and links that do include parasites (red bars).
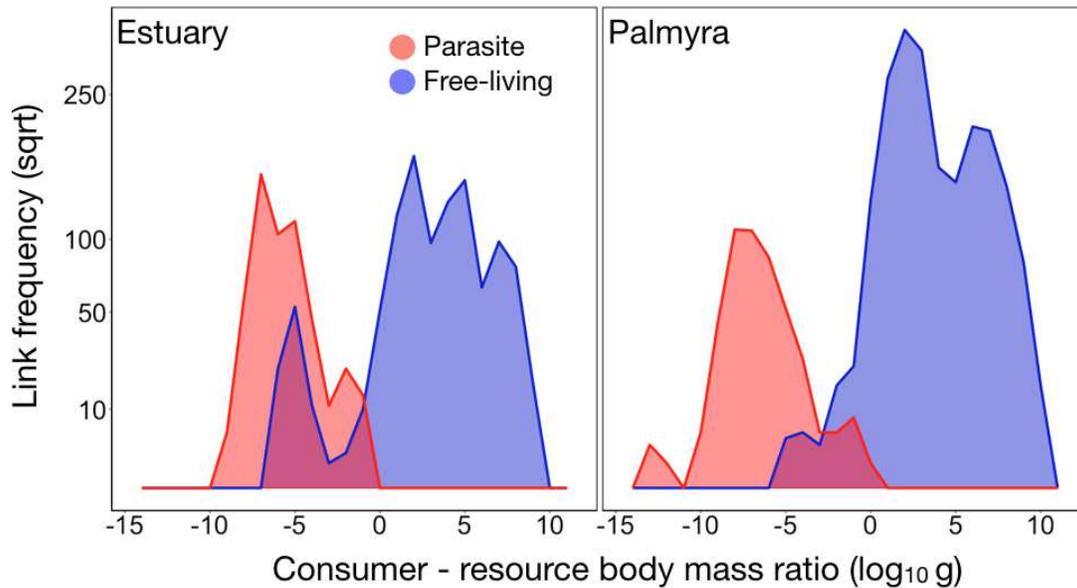
Figure 4. 10 Consumer-resource body size ratios. Parasites (red curve) extended the range of consumer-resource body size ratios in estuaries less than they do at Palmyra. The blue curve represents free-living links. The left mode in free-living links in estuaries (which is lacking at Palmyra) represents mosquitoes feeding on birds.

4.3.5 Network topology

Parasites had similar affects on network topology at Palmyra and in the estuaries (Table 4.1). In particular, including parasites increased directed connectance and degree distribution, but had little effect on mean distance and maximum chain length. Parasites increased the double motifs by between 0.1 - 12% relative to generic increases in free-living diversity (all p < 0.05), with slightly larger effect in estuaries (Fig 4.11). The biggest increases associated with adding parasites were for motifs that combine mutual consumption with either apparent

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competition (D3) or exploitative competition (D4). The mutual consumption in these double

motifs results from concurrent predation on parasites.

System	Pal	Pal	CSM	CSM	BSQ	BSQ	EPB	EPB
Assembly	FL + P	FL	FL + P	FL	FL + P	FL	FL + P	FL
Nodes	209	129	166	109	172	120	215	140
Links	3689	1303	3709	1008	3721	1087	5654	1703
Connectance	0.08	0.08	0.13	0.08	0.13	0.08	0.12	0.09
Degree distribution	17.65	10.10	22.34	9.25	21.63	9.06	26.30	12.16
Clustering coefficient	0.30	0.23	0.37	0.27	0.28	0.21	0.32	0.31
Generality	1.28	1.06	0.93	1.01	1.05	1.29	1.08	1.05
Vulnerability	0.91	0.92	0.72	1.01	0.69	0.99	0.70	0.98
Max chain length	7	6	6	5	5	5	6	6
Intervality	4264	1343	3798	858	3133	621	6277	1152
Mean distance	2.55	1.90	2.20	2.29	2.13	2.25	2.25	2.22

Table 4.1 Network topology metrics. System indicates networks from Palmyra (Pal) and
the estuaries (Carpinteria salt marsh, CSM; Bahia San Quintin, BSQ; Estero de Punta
Banda, EPB). Assembly indicates networks that include parasites (FL + P) and those that
only include free-living species (FL).
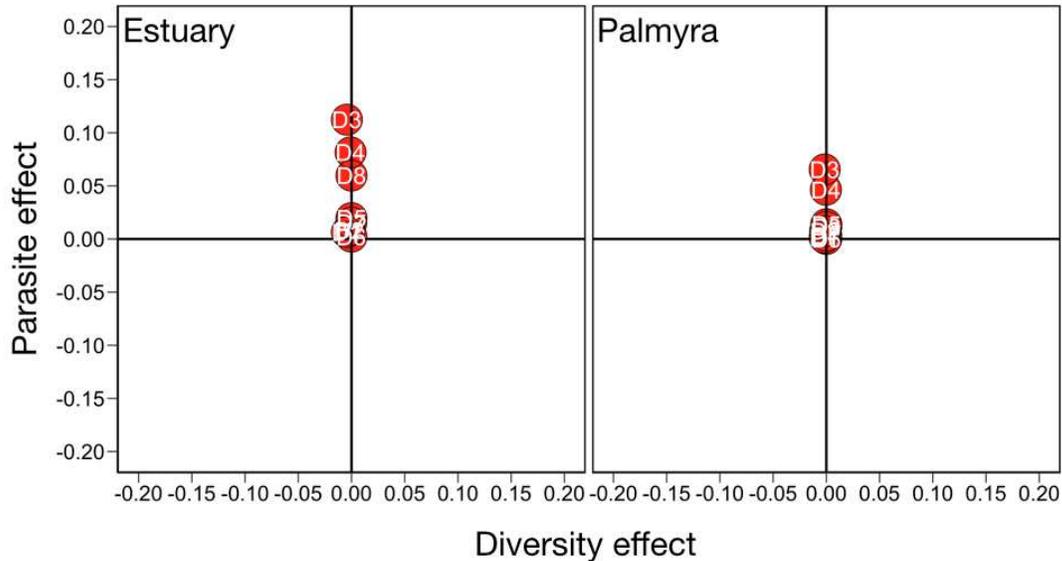
Figure 4. 11 Parasite affects on double motifs. Parasites increased double motifs in ways that free-living species did not in estuaries and at Palmyra. Axes indicate the difference in motif proportions between free-living webs and those containing increases in diversity. The y-axis indicates the effect of increasing parasite diversity on motif proportions, whereas the x-axis indicates the effect of increases in generic free-living diversity

4.4 Discussion

Parasites had similar effects on two food webs with different physical and biological features. Parasite diversity was comparable between Palmyra and estuaries and parasites in both systems were as abundant as were similar free-living species. Parasite biomass in both systems exceeded that of bird biomass. At Palmyra and the estuaries, parasites made similar contributions to trophic structure and increase double motif frequencies. This suggests that the remarkable roles that parasites play in estuaries are not an anomaly.

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The host community drove parasite richness and parasite community composition at Palmyra and in the estuaries. Thus, differences in free-living communities led to differences in their parasite communities. It might be surprising that host diversity was comparable between a tropical and temperate system, but because it is small and remote, Palmyra is difficult to reach for free-living species (MacArthur and Wilson 2001). Hosts often leave their parasites behind when colonizing new places (Lafferty *et al.* 2010; Torchin *et al.* 2003; Torchin *et al.* 2001), but parasites able to reach Palmyra are likely to thrive in the relatively pristine and trophically intact system (Lafferty, K. *et al.* 2008; Sandin *et al.* 2008; Vidal-Martínez *et al.* 2012; Vidal-Martínez *et al.* 2017). Parasite diversity in the estuaries is dominated by parasites that mature in birds, which dominate upper trophic levels in estuaries. Whereas, fish were the most diverse definitive hosts at Palmyra and the parasite community was dominated by parasites that mature in fish, including bucephalid trematodes, tetraphyllid cestodes and *Pulchrascaris* nematodes. Thus, parasites at Palmyra add a new dimension to the theory, first proposed for estuaries that host diversity begets parasite diversity (Hechinger and Lafferty 2005), namely that host composition begets parasite composition. For this reason, parasite composition in estuaries can indicate ecosystem integrity (Hechinger *et al.* 2007) and parasite composition in the fore reefs adjacent to intertidal sand flats indicates fishing pressure across the Northern Line Islands(Lafferty, K. *et al.* 2008; Wood *et al.* 2014). Thus, parasites are likely to make similar significant contributions to richness in other systems with intact host communities regardless of composition, but parasite composition should follow from host composition, which varies considerably from system to system.

Although parasites were as abundant as similar free-living species in both systems, the relationship between abundance and body size differed between systems. Specifically,

small organisms (i.e. parasites and invertebrates) were less abundant and large organisms were more abundant at Palmyra relative to estuaries. One possible explanation is that at Palmyra, large fish like jacks, sharks and rays are more abundant than expected because they augment their diets with resources from adjacent habitats (e.g. deep-water lagoon, fore reef), which they move to at low tides (McCauley *et al.* 2012). At Palmyra, these mobile species tend to be large, whereas smaller species may be under saturated relative to their maximum abundances, as suggested by quantile regressions. Accounting for subsidies to large mobile organisms would steepen the abundance-body size scaling relationship at Palmyra, making it more similar to the estuaries, with parasites and free-living organisms exhibiting similar abundance-body size scaling across systems.

Differences in host identity led to higher parasite biomass densities in estuaries than at Palmyra. A few taxa explained the higher free-living biomass at Palmyra. The significantly higher polychaete biomass at Palmyra was driven by a single spionid species (*Malacoceros* sp.) that was abundant in low-flow habitats where few other infauna can survive. Furthermore, bioturbators like hemichordates (acorn worms) and small infaunal sea cucumbers made important contributions to free-living biomass at Palmyra but do not have ecological analogs in the estuaries. For example, hemichordate biomass was greater than shark biomass. Despite their disproportionate contributions to free-living biomass at Palmyra, these groups hosted few parasites. Because parasite biomass is a simple product of host abundance and parasite biomass per host, most of the variation in parasite biomass (and its taxonomic compostion) is determined by parasites in the most abundant host species. For instance, *Conomurex luhuanus* had the highest biomass density of any species at Palmyra and hosts two parasite species (both cestodes), which therefore comprise substantial parasite

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biomass at Palmyra. Likewise, in the estuaries, the abundant snail, *Cerithideopsis*

(Cerithidia) californica is host to 23 parasite species, which, together, dominate parasite

biomass in estuaries. One key measure for parasite biomass was the same for both systems;

parasite biomass exceeded bird biomass. Thus, although parasite biomass varied across

systems, parasite biomass in both systems compares with the biomass of free-living taxa that

most ecologists consider to be important in food webs.

Being smaller than their resources, parasites extend the range of consumer-resource body

size ratios in a new direction (Lafferty and Kuris 2002). This contrasts with current

assumptions for how body size ratios constrain food-web structure and dynamics (Cohen,

Pimm*, et al.* 1993; Yodzis and Innes 1992). In particular, when parasites invert consumer-

resource body size ratios these ratios, it challenges both the niche model that underlies food

web structure (Warren *et al.* 2010; Williams and Martinez 2000) and predictions for how

size-ratio distributions facilitate stability (Emmerson and Raffaelli 2004; Loeuille and Loreau

2005). New theory is needed to consider how parasite-host body size ratios affect network

dynamics.

Parasite impacts on network metrics are similar to previous analyses, with one

important exception. Unlike previous analyses, we found parasites increased connectance, a

fundamental measure of network structure (Dunne, J. A. *et al.* 2013). This also runs counter

to the negative interaction between connectance and species richness that is generally

reported (Dunne, J. A. *et al.* 2002). Robustness indices increase with connectance because

consumers have broader diets in well-connected networks (Dunne, Jennifer A. *et al.* 2002).

Therefore it seems important to understand why our results differ. One possibility is that

Dunne et al. (2013) compared webs that varied in resolution and assembly method, whereas

here, we standardized network assembly methods across the systems, because without standardization it is difficult to tell if differences in topology derive from parasite effects or assembly differences. This calls into question previous studies that compared structure between networks whose assembly methods generate different resolutions.

Parasite affects on motif distribution were primarily due to concurrent predation (Cirtwill and Stouffer 2015), which describes how parasites are eaten along with their hosts. Double motifs featuring mutual consumption (Fig. 1) become common when parasites are included in food webs (Dunne, J. A. *et al.* 2013), but are otherwise rare (Stouffer *et al.* 2007). In particular, parasites increased D3, the double motif that illustrates apparent competition and mutual consumption. Although double motifs are little studied, apparent competition (without mutual consumption) is thought to be a transient phenomenon, persisting only in stable systems (Holt and Bonsall 2017). Those effects are not likely to apply to D3 motifs involving parasites, as parasites are not usually important resources for consumers. Furthermore, although an increase in double motifs suggests that parasites should increase system robustness to secondary extinction, concurrently predated parasites do not expand predator diets and therefore do not increase robustness (Rudolf and Lafferty 2011). Although predators don't gain additional energy from digesting parasites, infected prey might be easier to catch, or have reduced energy content.

Not only do parasites compete with their host's predators they are killed by them. Therefore, the importance of the D4 motif that depicts exploitative competition with mutual predation depends on the extent that parasites compete with predators. If this occurs concurrent predation might amplify perturbations, such as predator loss, if following a reduction in predation, parasite densities increase faster than competing predator densities.

For instance, removing predatory spiny lobsters increases the abundance of their urchin prey, which both destabilizes kelp forest dynamics and increases bacterial epidemics in sea urchin populations (Lafferty 2004). Furthermore, classic models show that parasite-induced host mortality can regulate parasite population dynamics (Anderson and May 1978). Therefore, if heavily infected hosts are selectively predated, concurrent predation could regulate parasitism by the same mechanism. How parasite affect network stability through double motifs is still uncertain, but a better understanding could improve our ability to control parasites and predict indirect effects when parasites are removed (Johnson *et al.* 2010).

In showing that metazoan parasites have important effects on food webs across systems, we give an example for how to add more detail to food webs. Many other taxa deserve better inclusion in food webs. Notably, fungal, protist, bacterial and viral pathogens have yet to be systematically incorporated in any food web. As microparasites, these groups are likely to be important in habitats with high host densities (e.g. plankton, temperate rocky intertidal) or clonal host populations (e.g. coral reefs). On land, different host compositions and transmission strategies will favor parasite taxa different from those seen in Palmyra and estuaries. For example, many terrestrial insects will function as parasites or pathogens on plant hosts (and such insects will have their own parasitoids), whereas parasites with aquatic larval stages like trematodes seem likely to be less successful in purely terrestrial food webs. Finally, future efforts could consider how network resolution and assembly rules, such as disaggregating species into ontogenetic life stages, can affect the role parasites play in food webs (Rudolf and Lafferty 2011)

Our results suggest that parasite contributions to ecosystem structure are both important and general. Their intimate life style makes parasites more susceptible to secondary

extinctions (Lafferty and Kuris 2009), and they are easily lost when food webs simplify. If an ecosystem were to lose its parasites, the change in richness, abundance and energetics would be equivalent to that incurred by losing other consumer groups, such as birds. Perhaps most importantly, losing parasites is not just about reducing species richness. Parasites make contributions to network structure that are distinct from those made by free-living consumers. For all these reasons, we have an incomplete understanding of food-web structure without parasites (Fig. 4.12).
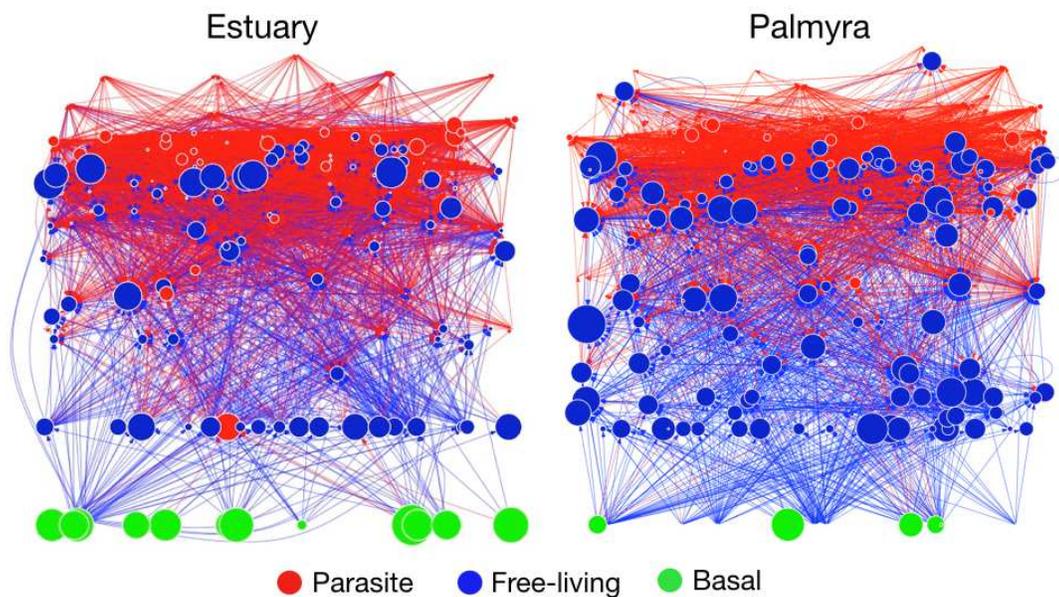
Figure 4. 12 Parasites dominate food web links in estuaries and at Palmyra. Blue lines indicate free-living consumer feeding interactions, red indicates parasitism. Node size indicates species biomass. Green nodes indicate basal species, blue nodes indicate free-living species, red nodes indicate parasites. Vertical height indicates node trophic level.

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