Chapter 17

Food webs

Ross N. Cuthbert[1,3], Ryan J. Wasserman[2,3], Chad Keates[2,3] and Tatenda Dalu[3,4]

[1]*GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany,* [2]*Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa,* [3]*South African Institute for Aquatic Biodiversity, Makhanda, South Africa,* [4]*School of Biology and Environmental Sciences, University of Mpumalanga, Nelspruit, South Africa*

17.1 Introduction and overview

The trophic level concept organizes the biotic components of ecosystems into discrete compartments by trophic status (primary production, herbivory, predation). In tropical and subtropical systems (hereafter referred to as tropical), biodiversity within each trophic compartment is typically diverse (see Deemy et al., 2022a, Chapter 6; Piedade et al., 2022, Chapter 7; Dalu et al., 2022, Chapter 8; Brendonck et al., 2022a,b, Chapters 9 and 10; Dube et al., 2022, Chapter 11; Reichard, 2022, Chapter 12; Moraes et al., 2022, Chapter 13; Tarakini et al., 2022, Chapter 14), in turn facilitating food web complexity and cross-ecosystem fluxes or connections. For example, tropical wetland systems harbor high diversities of invertebrates, amphibians and fishes, which provide important foraging environments for birds (Heyer et al., 1975; Frederick et al., 2009; Polačik et al., 2014; Wasserman and Dalu, 2022, Chapter 1). However, in addition to diversity-driven complexity, food webs in tropical wetlands are further complicated by the fluctuating existence of various spatial compartments that can be connected directly via water, or are connected by mobile animals moving between aquatic environments (Winemiller, 2004; Vanschoenwinkel et al., 2011; Layman et al., 2012; Wasserman et al., 2018).

Water level fluctuations during the hydroperiod are a dominant force regulating community dynamics and ecological processes in many tropical freshwater wetlands, particularly in the subtropics (Nhiwatiwa and Dalu, 2017; Wasserman et al., 2018) (Fig. 17.1). The shallow nature of these systems, and their high surface area to volume ratios, make them sensitive to changes in water inputs (Mitsch and Gosselink, 1986; Talling, 2001; Nhiwatiwa and Dalu, 2017). While such changes in water inputs inevitably
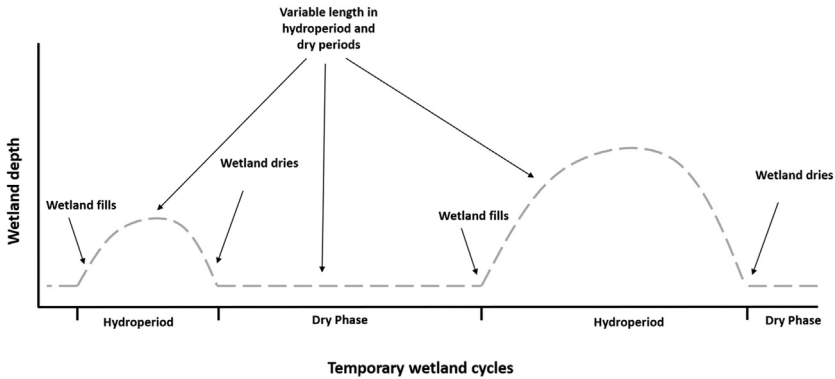
FIGURE 17.1 A hypothetical schematic diagram of temporary wetland cycles between dry phases and wet phases (hydroperiods), highlighting the variable nature of the ecosystems. Hydroperiods refer to periods of inundation when depressions/floodplains hold water. Dry phases represent those periods between the hydroperiods when the floodplains/depressions hold no water. *Modified from Tladi, M., 2021. Bioecology of Large Branchiopods in Central District, Botswana. MSc Thesis. Botswana International University of Science and Technology. 138 pp.*

have implications for physico-chemical water properties, the direct role of fluctuating water is the main driver of environmental heterogeneity, with implications for food web structure and trophic interactions in these environments. Indeed, tropical wetlands are frequently characterized by extremes—both wet and dry periods, driven by marked seasonal variations in temperature and precipitation patterns. Under these conditions, the necessity for rapid growth to facilitate reproduction during short hydroperiods can drive marked trophic interaction strengths among biota. Accordingly, the nature of trophic interactions in these wetlands frequently facilitate high rates of species turnover and potential "boom-bust" dynamics, making these systems important models for testing wider food web and community ecology theories (De Meester et al., 2005).

The wet-dry climate of tropical wetlands, in interaction with microtopography, drives seasonal patterns in food web dynamics. The characteristic hydrograph exhibited by temporary wetlands, isolated ponds, and bottomlands is a result of interactions between seasonal precipitation and fine-scale elevation differences, or microtopography. These elevation patterns can be the result of interactions and feedbacks among plants, sediment, water, and even animal activity (Nhiwatiwa and Dalu, 2017). Populations respond to changes in hydroperiod, water depth, and associated physico-chemical changes with corresponding changes in density, diet, and movement. As a result, food webs in tropical ecosystems are characterized by a high degree of plasticity, omnivory, and complexity. Wetting and drying cycles also impart important links between aquatic and terrestrial realms in wetlands, with consumers often supported by organic matter inputs from upland

catchments or adjacent areas (Carpenter et al., 2005). This high connectivity between terrestrial and aquatic environments necessitates quantitative understanding of how both allochthonous and autochthonous nutrient inputs alter food webs.

The primary objective in this chapter is to provide an overview of the structure, diversity, and intensity of trophic interactions in tropical wetland ecosystems. We begin by providing an appraisal of trophic groups and environmental factors which mediate food web dynamics in these systems. We then discuss trophic structure dynamics, distinguishing between endorheic wetlands and those temporarily connected to permanent waters, with emphasis on cross-ecosystem subsidies with permanent water bodies and adjacent terrestrial habitats. Then, a focus on predation is made in these systems. Further, approaches to quantify trophic dynamics are presented, which can be used to rapidly determine interaction strengths, food web structure and resource selectivities to inform wider food web models in wetlands.

17.2 Trophic groups

17.2.1 Aquatic primary production

Freshwater tropical wetlands tend to have high productivity, but are variable depending on factors such as plant types present, tidal energy, flooding, flow rates, soil nutrients, grazing, and toxins. There is a strong relationship between above ground biomass and summer temperatures, and therefore tropical wetlands are generally more productive than those in temperate systems. The flow of energy through any ecosystem starts with sunlight fixation by plants (i.e., phytoplankton, macrophytes) and other autotrophic organisms (i.e., certain bacteria). Thus, phytoplankton and macrophytes principally accumulate energy, forming an important component of aquatic food webs. The development of diverse plant communities within wetland systems often fuels complex food webs that not only sustain microbial communities through large detrital inputs to wetland soils, but also support diverse invertebrate and vertebrate animal communities that utilize these systems in part or for the entirety of their lives (Cherry, 2005).

Wetland productivity has been highlighted to be mostly affected by the flooding degree, duration and periodicity. Water movement in wetlands, through drainage and recharge processes, can promote enhanced productivity by increasing nutrient mineralization (Schlesinger and Bernhardt, 2020). For most freshwater wetlands, the inflow sources such as groundwater and precipitation, and outflows such as evapotranspiration, groundwater and surface flow, tend to change over time, making the hydrology unstable and causing fluctuations resulting in pulsing hydroperiods (Cherry, 2011). Thus, these hydrologic pulses have been shown to alter wetland productivity along a flooding gradient by altering the extent of wetland flood subsidies and

stresses (Odum et al., 1995). The flood pulses may also influence the function and structure of wetland ecosystems through their influence on species richness, organic matter accumulation, and nutrient cycling (Odum et al., 1995; Cherry, 2011).

17.2.2   Detritivory and consumers

In wetlands, most of the plant biomass dies and decays and is passed through the detrital food web where the major consumers are bacteria and fungi. This is one component that is the least studied within tropical wetland systems and more studies are needed to better understand detrital food web dynamics. These materials are then consumed by small invertebrate animals, such as worms, copepods, rotifers, and larval stages of benthic invertebrates. The larger benthic invertebrates are often either scavengers (e.g., crabs, snails) or filterers (e.g., mussels, fairy shrimp, and clam shrimp).

Most animal life in wetland systems consumes either phytoplankton directly, or smaller organisms that feed on phytoplankton. Others feed on detritus provided primarily by plant material. Consumers (heterotrophs) obtain their energy by consuming other organisms. Consumers can be plant eaters (herbivores), animal (invertebrate/vertebrate) eaters (predators), scavengers which eat dead animals or detritus (detritivores), or they can eat a variety of these sources (omnivores). Most of the energy within each trophic level is utilized for growth, respiration, reproduction and movement, but much energy is lost as heat.

Macroinvertebrates and zooplankton play important roles in wetland ecosystems as consumers at intermediate trophic levels. They have an important influence on nutrient cycling, material decomposition, translocation, and primary production (Merritt and Cummins, 1996). Detritivores, such as shredding insects and crayfish, can utilize dead plant material as their primary energy source, while others (e.g., snails, worms) help process organic matter for subsequent use by other organisms. Herbivory of phytoplankton by invertebrates and fish, and of plant biomass by some invertebrates, birds, and mammals, is a significant energy source for primary consumers in many wetlands. Secondary production by these primary consumers supports higher trophic levels, including predatory insects, fishes, reptiles, amphibians, birds, and mammals.

17.3   Trophic dynamics

17.3.1   Temporary endorheic wetlands

Temporary wetlands, among the most extreme of aquatic ecosystems, are ideal systems for the depiction of how complex and variable food web dynamics can be within tropical wetlands. These aquatic environments are

essentially temporarily available as a habitat for aquatic organisms, with water depth continuously shifting through precipitation and seeping dynamics. This makes for a temporally variable habitat, further complicated by spatial dynamics such as differing distances between isolated temporary wetlands of various shapes and sizes. In addition to complicated metacommunity dynamics between isolated temporary wetlands (see Gálvez et al., 2022, Chapter 18 on these processes), within-system complexities are considerable, driven by phenological processes associated with hydroperiod dynamics.

During dry (non-hydroperiod) phases, areas that get inundated are often overgrown with nonaquatic vegetation. In many instances, this vegetation community is dominated by pioneer species that are capable of survival in disturbed areas (Datry et al., 2018; Wasserman et al., 2022; Dalu et al., 2020). Following inundation as the hydroperiod commences, much of this vegetation dies off, providing detritus within the aquatic environment, which contributes to available nutrients within these systems. Phytoplankton, bacteria and fungi then arise from diapause states in the sediment during early hydroperiod stages, instigating primary productivity activities in these systems—driven primarily by depth dynamics and nutrient availability (see Job et al., 2022, Chapter 2; Deemy et al., 2022b,c, Chapters 3 and 4; Moyo, 2022, Chapter 5 for these processes). The consumer community in temporary wetlands is comprised of "internal" and "external" recruits, with their relative contributions to consumer community structure highly variable over the hydroperiod (Fig. 17.2).
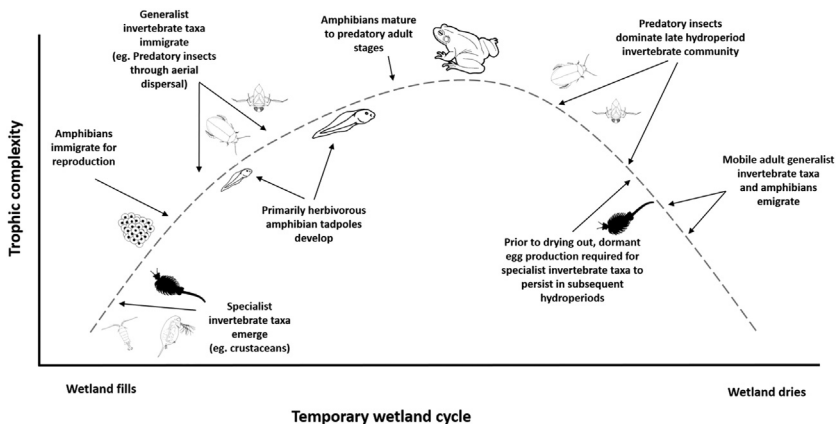

FIGURE 17.2 A hypothetical schematic diagram on temporary wetland consumer trophic complexity development over the course of a hydroperiod. Key consumer groups contributing to complexity dynamics are outlined. *Modified from Tladi, M., 2021. Bioecology of Large Branchiopods in Central District, Botswana. MSc Thesis. Botswana International University of Science and Technology. 138 pp.*

Upon inundation, populations of many specialist taxa are driven by hatching of dormant cysts that are present in the sediment. These "internal recruits" typically comprise the pioneer consumer community within temporary wetlands, most of which feed on primary producers (Dalu et al., 2016; Celewicz et al., 2018). Crustaceans (branchiopods, copepods and ostracods) feature in this community, along with planarians, annelids and molluscs (Bird et al., 2019). Given high levels of primary (phytoplankton) and secondary (specialist metazoans) productivity that rapidly develop in these systems, generalist aquatic invertebrate and vertebrate taxa start to invade these aquatic food patches (O'Neill and Thorp, 2014; Wasserman et al., 2016c; Dalu et al., 2017a). The invertebrate general fauna typically comprise numerous predatory insect species, many of which invade as semiaquatic adults (e.g., Notonectidae and Dyticidae), and some of which lay eggs that rapidly hatch to produce predatory early life stages (e.g., Odonata) (O'Neill and Thorp, 2014; Bird et al., 2019). Vertebrate generalist aquatic taxa that enter these environments are dominated by herpetofauna (amphibians and testudines) (Whiles et al., 2006; Channing and Rödel, 2019), which serve as apex predators in these systems. As the wetlands start to dry out near the end of their hydroperiods, the generalist taxa are typically required to emigrate to survive. Many taxa migrate to permanent water bodies during drier periods when temporary wetlands hold no water. Others, such as some frogs and testudines, may burrow in sediment in or near the wetland. The specialist "internal" recruiting taxa, however, persist locally through the production of cysts (dormant eggs). Viable cysts remain in the sediment over the dry period, ready to hatch in the following hydroperiods (Jocque et al., 2010).

17.3.2 Temporary wetlands connected to permanent water bodies

Temporary wetlands, such as river floodplains and temporary lakes, that are connected to permanent water bodies function in similar ways to the endorheic systems mentioned above, in that fluctuating water levels facilitate environmental heterogeneity and phenological processes. Microtopographic patterns in temporarily inundated areas can facilitate very similar conditions to those of endorheic systems. However, their connection to permanent water usually means that fishes (often a diverse community in tropical regions, see Reichard, 2022, Chapter 12) are included in the food webs. Aquatic reptiles are also more of a major feature in wetlands associated with permanent waters, such as testudines, snakes, and crocodylians (Uzarski et al., 2009). The presence of larger-bodied vertebrate species has implications for "food chain length" in these wetlands, which can make overall food web structure more complex than the smaller endorheic systems. For example, large-bodied fish can assume the role of high trophic levels, while crocodylians feature at the highest levels in aquatic food webs (Bondavalli and Ulanowicz, 1999; Grigg and Kirshner, 2015; Villamarín et al., 2017, 2018).

Crocodylians play a particularly dynamic trophic role in tropical wetlands, given ontogenetic shifts in diet from aquatic and terrestrial invertebrates when young, to fish and even terrestrial vertebrates as they grow (Radloff et al., 2012). However, many taxa that inhabit tropical wetland environments exhibit high levels of trophic flexibility, facilitating their success in these dynamic systems.

A striking example of the complexity of floodplain systems is that of the floodplains on the Zambezi River system in Africa. Taylor et al. (2017) contrasted food web structure in the Upper Zambezi, Kavango and Kwando floodplains, all tributaries of the Zambezi River. While the majority of the fish species encountered in the study were ubiquitous between rivers, there was still evidence that food web structure differed among floodplains. They found that the Upper Zambezi and Kavango River food webs were likely supported by C4 riparian vegetation from the floodplain, whereas the Kwando River food web was likely driven by autochthonous filamentous algae and aquatic macrophytes. These differences were linked to floodplain pulses between the study areas. The Everglades provide another good example of aquatic food web complexity in flooded systems. In the Everglades, a regular microtopographic pattern of ridges (high, marsh dominated) and sloughs (low, inundated, periphyton dominated) occurs. Sloughs exhibit both long and short hydroperiods, and the density of large fish varies with hydroperiod (Chick et al., 2008). As a result, predation pressure on smaller omnivorous fish, and rates of herbivory on epiphytic algae, are also proportional to hydroperiod (Chick et al., 2008). Similarly, during the dry season when floodplain lagoons and waterholes become isolated, invertebrates and fish must shift their diets. Food webs in isolated waterholes are subsidized by allochthonous riverine resources in the wet season, but switch to become supported by autochthonous algal basal resources in the dry season (Pettit et al., 2016; Venarsky et al., 2020).

17.4   Wetlands as attractants and sources of predators

Tropical wetlands are productive environments, with high levels of secondary productivity. As such, these environments make for very good foraging patches for invertebrate and vertebrate predatory species. Many of the semiaquatic insects that make use of wetlands have complex life cycles, the adults of which are predatory. Through flight (e.g., odonates, notonectid hemipterans, dyticid coleopterans), these predators invade wetland environments for feeding and reproductive purposes. At times (e.g., in endorheic systems), invertebrate predator numbers can even reach levels where they dominate those of prey (O'Neill and Thorp, 2014; Wasserman et al., 2018). Other semiaquatic insects (e.g., dipterans) also reproduce in these environments (Bird et al., 2019), with the emerging adults serving as important food sources for terrestrial consumers such as spiders, herpetofauna, bats and birds

(Adler and Courtney, 2019). Given that nearly one-third (46,000 spp.) of all true flies (Diptera) have some affinity with the aquatic environment, the importance of dipterans in ecosystem functioning cannot be overstated (Adler and Courtney, 2019). In this way, aquatic habitats can be a major consumer attractant, even of terrestrial organisms, facilitating cross-ecosystem fluxes of energy.

Consumers with complex life cycles also disperse from aquatic habitats (Knight et al., 2005; McCoy et al., 2009; Semlitsch, 2008). Many insects reproduce in wetland habitats, the adults of which predate on terrestrial organisms (e.g., odonates). Similarly, amphibians participate in multiple levels of the food web, with larval stages feeding on algae and detritus (Whiles et al., 2006; Channing and Rödel, 2019), while the adult amphibians are exclusively predatory, with many taxa (e.g., anurans) feeding primarily in terrestrial habitats (Crump, 2009; Wells, 2010). Given that wetlands are typically embedded within a terrestrial matrix, fluxes of predators from aquatic habitats may have important impacts on the surrounding terrestrial environment, contributing to spatially-structured patterns of herbivore consumption and primary production in receiving environments (Knight et al., 2005; McCoy et al., 2009). As such, wetlands export substantial predation pressure from the aquatic habitat to the surrounding terrestrial landscape. For example, within some parts of the humid tropics, adult amphibians represent the most abundant land vertebrates (Pough, 1980), with many of these predators having originated from wetlands. The implications of adult amphibian export from wetlands to adjacent terrestrial environments, within the context of predation pressure, is, however, poorly reported in the literature. In temperate regions, the transfer of energy and predation pressure between wetlands and receiving terrestrial habitats would be highly seasonal (pulsed), whereas in the "true" tropics, the more consistent abiotic factors would result in a more consistent transfer, and in the subtropics, these processes would be driven primarily by rainfall dynamics.

17.5 How predator−prey interactions shape wetland communities

Predation is a fundamental biotic process that alters the structuring and functioning of ecological communities and is a key driver of evolutionary change (Dayton, 1971; Paine, 1980). Interactions between predators and their prey can result in both direct, lethal changes to prey abundance (i.e., density-mediated effects; Connell, 1972; Paine, 1980; Abrams, 1995), or can manifest in a plethora of indirect, nonlethal effects (i.e., trait-mediated effects; Abrams et al., 1996; Lima, 1998; Peacor and Werner, 2002). In the latter phenomena, predator presence alters key phenotypic traits in prey, including behavior, morphology, and physiology (Lima, 1998; Peacor and Werner, 2002). For example, predator presence can reduce activity rates in prey, in

turn negatively affecting foraging (Alexander et al., 2013), or can induce defensive structures that reduce predation rates (Tollrian, 1995).

In aquatic systems, the strength of trait-mediated effects is thought to be as strong as, or stronger, than density-mediated effects, owing to the immediacy and ubiquity of predator chemical cues in water bodies, which can influence entire populations across their life histories (Peacor and Werner, 2001; Trussell et al., 2002, 2004). In turn, the elicitation of such effects can be dependent on eco-evolutionary contexts between predator−prey participants (Barrios-O'Neill et al., 2014; Cuthbert et al., 2018b). Specifically, trait-mediated responses can be contingent on whether predator−prey pairings have shared evolutionary histories, and whether prey can recognize specific cues. The strengths of predatory interactions are also highly context-dependent, driven by a range of biotic and abiotic factors, such as temperature (Englund et al., 2011; Uiterwaal and Delong, 2018), habitat complexity (Barrios-O'Neill et al., 2015), salinity (Cuthbert et al., 2019a), predator−prey body size ratios (Rall et al., 2011; Barrios-O'Neill et al., 2016), predator density (Wasserman et al., 2016a; Sentis and Boukal, 2018), and prey supply (Alexander et al., 2012). These context-dependencies make derivations of empirical interaction strengths challenging to predict, with many effects often interacting to influence community dynamics and population outcomes.

17.6   Predation in temporary wetlands

Temporary wetlands represent excellent model systems to test ecological theory, owing to their relatively small size, rapid succession, accessibility, abundance, high heterogeneity and structural simplicity (De Meester et al., 2005). They also host a diverse array of predators that mediate population structure (Brendonck et al., 2002). Trophic dynamics and community composition in these systems are atypical, differing substantially from permanent freshwaters, such as lakes and reservoirs. That is, because temporary wetlands are internally drained and dry out completely for extended periods of time, community composition spatiotemporally is contingent on dynamics of internal and external recruitment (Brendonck and De Meester, 2003; O'Neill and Thorp, 2014). Wind is a key dispersal mechanism in temporary wetlands during dry periods (Brendonck and Riddoch, 1999; Vanschoenwinkel et al., 2009), as well as ingestion and transportation of eggs by predators (Rogers, 2014, 2015) and adherence to mobile organisms (Vanschoenwinkel et al., 2011). Both predation and demographical constraints associated with pond drying are key structuring processes in these systems.

17.6.1   Temporary wetlands in southern Africa

Austral temporary wetlands are particularly understudied and are at high risk of degradation due to land-use changes, invasive species and pollution (Dalu

et al., 2017a; Mabidi et al., 2018). Many temporary wetlands are dredged and deepened to facilitate fish stocking or for water storage purposes in drought-risk areas, in turn, risking the high and often endemic biodiversity of these systems (Bird et al., 2019). Indeed, environmentally protected areas have been shown to foster higher pond biodiversity than those that are degraded anthropogenically (Dube et al., 2020). The trophic structure of temporary wetlands in southern Africa has been recently delineated using stable isotope analyses (Dalu et al., 2016, 2017b, 2017c; de Necker et al., 2020; Box 17.1). These food webs have been found to comprise of three-to-four distinct trophic levels, whereby top predators are notonectids and diving beetles and intermediate trophic groups include zooplankton, tadpoles, macroinvertebrates and mollusks (Dalu et al., 2016). Other studies have also found frogs and killifish to occupy the top trophic level (de Necker et al., 2020). Furthermore, generalist species have been found to typically dominate higher trophic levels, while lower trophic groups are more specialist (Dalu et al., 2016). However, owing to the transient nature of these systems and the aforementioned recruitment dynamics, the length and shape of temporary wetland food webs changes markedly over time (Dalu et al., 2017b; de Necker et al., 2020). Specifically, food webs in the early hydroperiod are highly simplified, with trophic chains lengthening depending on the timing of external predator "invasion." In turn, basal food resources become more heterogeneous during the hydroperiod initially, before then again decreasing in later stages. Moreover, resource partitioning and specialization can differ both within and between species in temporary wetlands (Dalu et al., 2017c).

Predatory copepods can dominate the upper trophic levels in the early to middle stages of hydroperiod, depending on the phenology of dormant egg hatching events and other colonization dynamics (Wasserman et al., 2016b, 2018). Such predators can also act as regulatory species for abundant crustacean and dipteran groups such as daphnids (Wasserman et al., 2016b) and larval mosquitoes (Cuthbert et al., 2018a), and can show strong prey selectivities (Cuthbert et al., 2020a). Moreover, sex-skewed ratios have been shown to develop empirically in southern African temporary wetlands over time (Wasserman et al., 2018), caused principally by selective predation processes. Furthermore, predation can cause trophic cascades through the elimination of consumer types that impact other organisms in ponds. For example, the high voracity of notonectids has caused periphyton increases through extirpation of grazing taxa (Blaustein, 1998), with "boom-bust" dynamics thus common in temporary wetlands (Wasserman et al., 2018) (e.g., Cladocera, Fig. 17.3).

In the Eastern Cape province of South Africa, Wasserman et al. (2018) found female-biased copepod sex ratios to develop temporally over the hydroperiod, which coincided with notonectid (i.e., higher predator) colonization dynamics. Notonectid colonization can also correspond tightly with intermediate copepod predator declines (Fig. 17.3). Results from that

BOX 17.1 Copepod trophic niche specialization in response to shifts in resource diversity over a temporary wetland hydroperiod (Dalu et al., 2017c).

In Dalu et al. (2017c), a small temporary wetland was sampled over a hydroperiod to test for trophic niche specialization in response to shifting basal resource diversity. Differences in isotopic $\delta^{13}C$ and $\delta^{15}N$ signatures between two closely related copepod species (*Lovenula raynerae* and *Paradiaptomus lamellatus*) and between sexes within these species, in relation to heterogeneity of basal food resources over the course of the pond's hydroperiod, were assessed. The study showed that basal food resource heterogeneity increased over time initially, before decreasing toward the end of the hydroperiod (Image 1), reflective of the expected evolution of trophic complexity for these systems (as in Fig. 17.2). Resource partitioning also varied over the hydroperiod with evidence of intra- and inter-specific specialization in relation to resource availability, whereby increased resource availability facilitated increased trophic specialization (Image 2). This study is one of the few to show that trophic specialization at both the intra- and inter-specific level is likely, as least partly, driven by food resource availability.
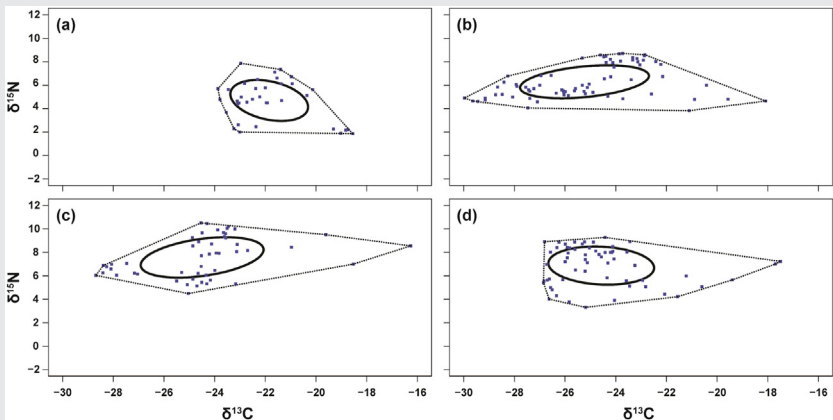

IMAGE 1   Overall trophic diversity ($\delta^{13}C$ and $\delta^{15}N$) of the entire food web over a hydroperiod. The temporary wetland food web was characterized on four consecutive sampling occasions (a = 2 weeks, b = 7 weeks, c = 12 weeks, and d = 16 weeks after inundation). *Adapted from Dalu, T., Wasserman, R.J., Vink, T.J.F., Weyl, O.L.F., 2017c. Sex and species specific isotopic niche specialisation increases with trophic complexity: evidence from an ephemeral pond ecosystem. Scientific Reports 7, 43229.4*

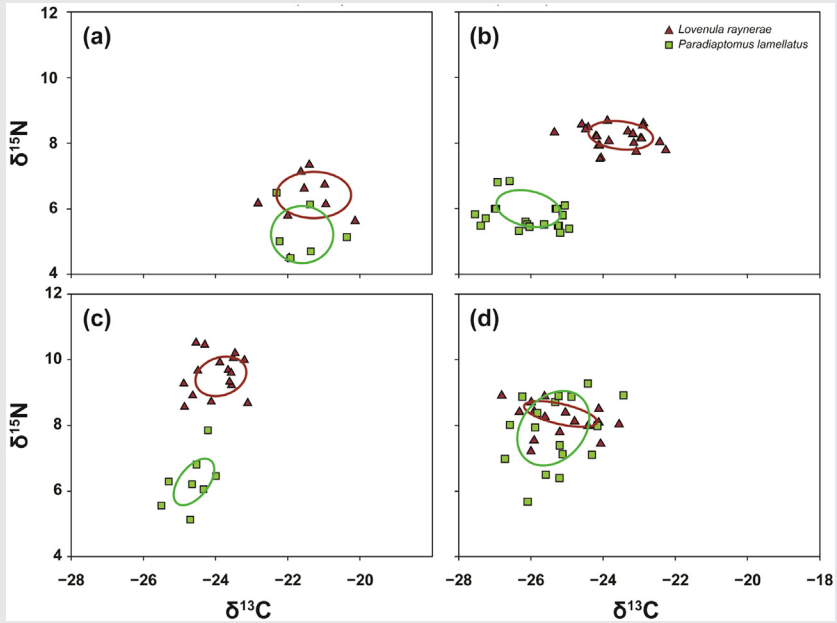*(Continued)*

BOX 17.1 (Continued)

IMAGE 2 Stable Isotope Bayesian Ellipses for male and female *Lovenula raynerae* and *Paradiaptomus lamellatus*, showing increased levels of interspecific and intraspecific (between sexes) specialization in response to increased basal resource heterogeneity (a = 2 weeks, b = 7 weeks, c = 12 weeks, and d = 16 weeks after inundation). *Adapted from Dalu, T., Wasserman, R.J., Vink, T.J.F., Weyl, O.L.F., 2017c. Sex and species specific isotopic niche specialisation increases with trophic complexity: evidence from an ephemeral pond ecosystem. Scientific Reports 7, 43229.*

laboratory study suggested that these patterns were due to selective predation during copepod copulations. Specifically, while female and male copepods were consumed similarly as individuals, as copulating pairs, males were significantly more vulnerable as females orientated males toward predators when at risk, releasing males following their capture. This study concerned predatory *L. raynerae*, the largest species of freshwater copepod in Africa, and possibly globally (Suárez-Morales et al., 2015). Other experimental predation studies have shown gravid females of this species to be significantly more voracious than males, and to be more affected by the presence of habitat structure (Cuthbert et al., 2020b). In other systems, such as temporary rock pools in Botswana, flatworms (turbellarians) and dragonfly juveniles (odonates) have been identified as key predators which influence the
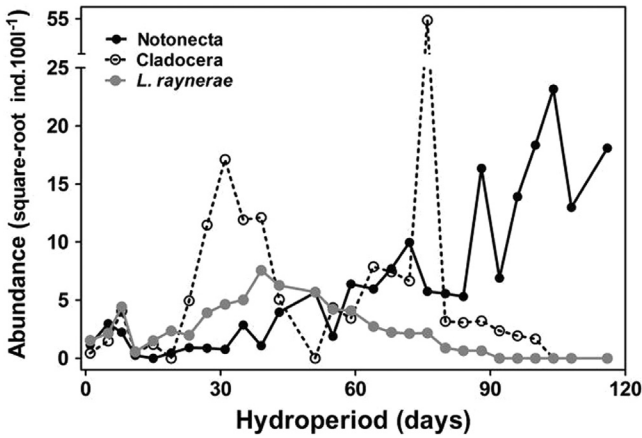
FIGURE 17.3 Abundances of notonectids, cladocerans, and copepods (*Lovenula raynerae*) through a hydroperiod, illustrating boom-bust dynamics among taxa through time. *Adapted from Wasserman, R.J., Weston, M., Weyl, O.L.F., Froneman, P.W., Welch, R.J., Vink, T.J.F., et al., 2018. Sacrificial males: the potential role of copulation and predation in contributing to copepod sex-skewed ratios. Oikos 127, 970–980.*

population dynamics of internally recruited prey groups (e.g., fairy shrimp: anostracans) (De Roeck et al., 2005).

17.6.2 Context-dependencies and trait-mediated effects

The small size and simple structuring of temporary wetlands communities lend these systems to empirical mesocosm experiments. Experimental research has also demonstrated emergent effects of temperature and habitat structure in temporary wetlands ecosystems, whereby the effects of habitat structure on predation by top predators are contingent on levels of warming (Wasserman et al., 2016c). As well as trophic structure, vegetation colonization dynamics are highly variable over the course of the hydroperiods in temporary wetlands, and such habitat structure is known to have a marked effect on trophic interactions in food webs more generally (Barrios-O'Neill et al., 2015). Aquatic plants (i.e., submerged macrophytes) generally colonize later in the hydroperiod and could provide physical refuge for prey. Furthermore, given their shallowness, temperature is known to undulate considerably in these ecosystems (Wasserman et al., 2018). Therefore a suite of abiotic characteristics is known to modulate predation rates in these systems, challenging predictions of trophic dynamics therein. From an applied perspective, recent works in temporary wetlands have highlighted a novel ecosystem service, whereby internally -recruited species are able to contribute to mosquito regulation via predation (Cuthbert et al., 2018a). The primacy of context-dependencies as a mediator of predator effects is thus of great relevance in a

public health context. This is especially pertinent in southern Africa, where there are high incidences of several mosquito-borne diseases.

Trait-mediated effects of predators can also be pertinent in temporary aquatic ecosystems. Time stresses associated with temporary wetlands necessitate rapid development—species must reach maturity before the pond dries. As such, morphological phenotypic traits are thought to be more pronounced than behavioral in this respect, so that species can retain foraging intensities even when faced with predation risk (Richter-Boix et al., 2007; but see Schalk, 2016). One key example concerns species' egg banks in substrate, which are reported to employ "bet-hedging" strategies to reduce total recruitment into conditions that are potentially unsuitable. That is, not all eggs hatch during one wet phase, with some remaining dormant to reduce the risk of the pond drying before the population reaches maturity, and to alleviate intraspecific competition (Simovich and Hathaway, 1997; Brendonck et al., 1998). Importantly, these strategies can also be mediated by the presence of predators, with hatching success reduced under predation risk (e.g., De Roeck et al., 2005; Pinceel et al., 2015). In tropical regions of Africa, killifish can additionally be important predators in temporary wetlands, and can bridge hydroperiods through the production of dormant eggs (Watters, 2009). Trait-mediated effects have been demonstrated in annual killifish, whereby higher predators that invade following flood events heighten peak and total fecundity levels, potentially allowing for killifish life stages that can persist until the predation risk has been removed (Grégoir et al., 2017). Conversely, intermediate copepod predation has been shown to be unaffected by invasive fish predatory cues (Cuthbert et al., 2018b), indicating naiveté that could heighten the impacts of higher predators; trait-mediated effects can thus be congruent on shared eco-evolutionary histories (but see Cuthbert et al., 2019b). Overall, the profound presence of both density- and trait-mediated effects in ephemeral wetland ecosystems makes these systems highly dynamic, and exceptional platforms for studying trophic interactions.

17.7 Models and experimental approaches to quantify trophic interactions

17.7.1 Functional responses

A combined use of experimental and statistical modeling approaches is frequently used to quantify the strength of trophic interactions between consumers and resources. From an overall perspective, food webs comprise a network of interacting "nodes," with the strength of these pairwise interactions differing largely. Functional responses are fundamental to the quantification of *per capita* (i.e., individual-level) consumer-resource interaction strengths (Holling, 1959). Definitively, functional responses quantify resource use as a function of resource density and can be applied to any

consumer-resource system. That is, all organisms require resources, and thus all organisms exhibit a functional response, from plants, to detritivores, to herbivores, to predators.

Functional responses have been readily applied to quantify interaction strengths in aquatic ecosystems, and especially freshwaters. Both the functional response type and magnitude provide information pertaining to the interaction strength of a consumer. Three types of functional response are typically thought to ensue from consumer-resource interactions (Hassell, 1978) (Fig. 17.4). The type I functional response is linear, whereby resource use increases with resource availability until an immediate plateau:

$$N_e = aN_0T \tag{17.1}$$

where N_e is the initial resource density, α is the attack rate, N_0 is the initial density of prey and T is the time available. This type of functional response is mechanistically restricted to organisms which do not need to "handle" their resources, such as filter feeders (Jeschke et al., 2004). The type II functional response is hyperbolic, characterized by high rates of resource acquisition at low resource densities, which declines until a plateau is reached. Most commonly, Holling's disk equation is classically used for type II functional responses where resources are replaced as they are consumed (Juliano, 2001):

$$N_e = (aN_0T)/(1 + aN_0h) \tag{17.2}$$
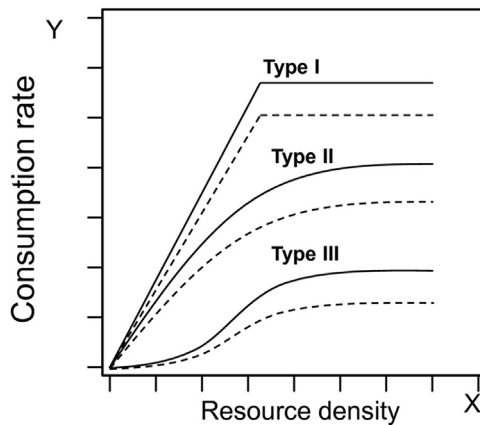
FIGURE 17.4 Three common functional response types, considering resource use as a function of resource density. Within each type, the dashed line illustrates lesser consumer impacts than the solid line. *Adapted from Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, J.R., et al., 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54, 1259−1267.*

where h is the handling time. For situations where resources are not replaced, Rogers' random predator equation is commonly fit instead for type II functional responses (Rogers, 1972):

$$N_e = N_0(1 - exp(a(N_e h - T))) \tag{17.3}$$

Studies have found that use of the random predator equation is suitable even when resources are totally depleted at certain densities (Cuthbert et al., 2020c). In contrast, the type III functional response is sigmoidal, whereby consumption rates are reduced at low resource densities, increase initially as densities grow, before again falling and plateauing as in the type II functional response. Where this functional response is exhibited, Hassel's Type III functional response model can be fit for experimental designs that replace resources following consumption:

$$N_e = (dN + bN^2)/(1 + cN + dNT_h + bN^2 T_h) \tag{17.4}$$

where b, c, and d are constants, which can be optimized or removed to aid model fitting. For situations where resources are not replaced, Hassel's Type III functional response model can be modified as follows:

$$N_e = N_0(1 - \exp((d + bN_0)(T_h N_e - T)/(1 + cN_0))) \tag{17.5}$$

Importantly, these functional response types and their parameters can allow for quantification of the strength of feeding interactions, whereby type II functional responses have been typically associated with destabilizing effects for resource populations, and type III functional responses deemed to be more stabilizing (Dick et al., 2014). This is because low-density prey populations are more likely to be extirpated in the case of the type II functional response.

Depending on the functional response model, there are several key parameters that can be used to quantify the strength of feeding interactions. The attack rate (or search coefficient) can be used to deduce the strength of feeding interactions at low resource densities, and thus high attack rates are more likely to destabilize resource populations. Further, the handling time (time taken to capture, subdue and digest) of resources can be used inversely to infer maximum feeding rates, that is, the functional response curve asymptote. Both the attack rates and handling times can be used to infer the potential of consumers to impact upon resources (Cuthbert et al., 2019c) (Fig. 17.5). Furthermore, classically, the consumer functional response has been combined with the consumer numerical response to quantify population-level effects (Solomon, 1949; Holling, 1959). While the functional response quantifies individual effects, the numerical response accounts for population-level changes of a consumer resulting from differences in resource densities, including both predator aggregation and reproduction. The functional response and numerical response product, deemed the total
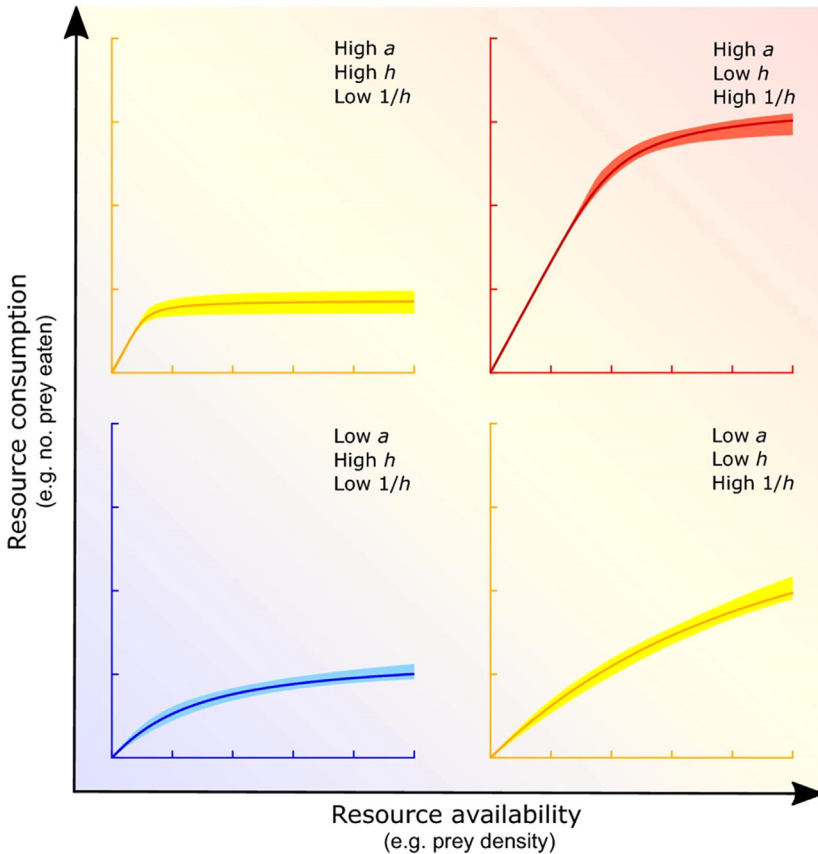
FIGURE 17.5 Functional response "heat map" demonstrating differences in consumer impact based on attack rates (a; initial slope of curve) and handling times (h; which inversely gives maximum feeding rates, i.e., $1/h$, curve asymptote). Increasing *per capita* impact is illustrated from bottom-left to top-right. *Adapted from Cuthbert, R.N., Dickey, J.W.E., Coughlan, N.E., Joyce, P.J., Dick, J.T.A. 2019c. The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. Biological Invasions 21, 2543−2547.*

response, allows for insights of population-level interaction strengths based on the assimilation of individual and population effects. While the numerical response is more difficult to quantify in a laboratory setting, recent advances have sought to use proxies such as consumer abundance or fecundity as a supplement (Dick et al., 2017). Therefore the combination of functional response and numerical response can be used to quantify the offtake rates by consumers in wetlands.

17.7.2 Resource preferences and switching

One further important component of consumer-resource interactions concerns resource preferences. Many consumers are generalists and are thus simultaneously exposed to a range of resource types at varying relative proportions in their environment. Preferences among resource types at different proportions can mediate stability within communities, and data on the diets of consumers can inform understandings of resource partitioning (Shoener, 1971). In particular, consumers may avoid prey which are relatively rare in their environment, and instead preferentially select abundant prey (i.e., "switching"; Murdoch, 1969). This patterning can thus allow rare resources to persist in the environment, allowing for species coexistence, while regulating relatively abundant resources. Such processes can be driven by phenomena such as "predator learning," whereby a "search image" for abundant prey is developed and targeted (Tinbergen, 1960).

As with functional responses, numerous models have been developed to quantify and compare consumer-resource preferences (Manly, 1974; Chesson, 1978, 1983). Model selection can, again, depend on whether resources are replaced as they are consumed during a given experiment. Where replacement occurs, Chesson's index can be used to derive preferences:

$$a = \frac{r_i/n_i}{\sum_{j=1}^{m}(r_j/n_j)} \tag{17.6}$$

where α is the selectivity index for resource type i, n_i is the amount of resource type i available at the start of the experiment, r_i is the amount of resource type i consumed, m the number of resource types, r_j is the amount of resource type j consumed and n_j the amount of resource type j available at the start of the experiment. Conversely, where a given resource is not replaced (i.e., it depletes), the following equation can be applied:

$$a = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^{m} \ln((n_{j0} - r_j)/n_{j0})} \tag{17.7}$$

For both of these selectivity metrics, output values are between 0 and 1, with values closer to 1 indicating increased preference for the focal resource, and $1/n$ indicating null preference. The converse is true for prey avoided (i.e., values closer to 0 are disproportionately avoided).

Experimentally, controlled feeding trials can be used to quantify functional response and prey preferences in aquatic systems, and typically in a laboratory environment. The often simplified structure of ecosystems such as temporary wetlands makes representing natural communities relatively straightforward (De Meester et al., 2005). Broadly, these experiments typically expose consumers, standardized according to body size or another

measure, to different densities (for functional responses) or proportions (for resource preferences) of singular or multiple resource types. For aquatic study systems, mesocosms can be used to examine feeding rates toward resources over fixed experimental durations; modeling is typically based on quantifications of resources consumed as a function of initial levels supplied over that time interval (see above equations). This approach additionally allows for comparative examination of other environmental contexts (e.g., temperature, habitat complexity) while controlling for other factors, depending on the specific hypotheses of a study. However, feeding experiments could also be conducted in field-based conditions (Novak, 2010), and this may be particularly practical in small-sized tropical wetlands.

17.7.3 Stable isotopes use in aquatic food webs

Stable isotope analysis provides a powerful and important tool for identifying energy sources which fuel consumers, and enables us to better understand trophic interactions and infer consumer trophic positions (Quezada-Romegialli et al., 2018). The assessment of food web structure cannot be discerned using only short-term, traditional methods (e.g., stomach contents, regurgitates and fecal matter), but can be advanced by employing stable isotope analysis which provides understandings of diet over a longer period of time (Post, 2002). Stable isotopes provide time-integrated information on the material assimilated by organisms, with carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope composition being most commonly used in ecological studies (Cornwell et al., 2006). The δ^{13}C isotopes change little from primary producer to consumer, hence it reflects consumer diet closely. Whereas, the d^{15}N isotope values are generally high and are mostly used as a trophic position indicator (Post, 2002; Layman et al., 2007). Thus, the use of δ^{13}C and δ^{15}N isotope analysis can provide substantial information about different food sources, trophic relationships and energy pathways utilized by aquatic organisms (Jones et al., 1998; Dalu et al., 2017a,b; Jackson et al., 2020). Other elements such as hydrogen (H) and sulfur (S) show little change between trophic levels, and oxygen (O) is mostly used to investigate changes in water temperature. A limited number of studies have been conducted using stable isotopes within tropical wetland systems (e.g., Wantzen et al., 2002; Frings et al., 2014; Dalu et al., 2016; 2017b,c; De Necker et al., 2020).

17.7.3.1 Hypervolumes

Consumer trophic niches are difficult to characterize. However, new tools, such as hypervolume analysis, allow for more definitive quantification (see Newsome et al., 2007; Blonder et al., 2014, 2018; Shipley and Matich, 2020). These can be of great use, particularly within wetland environments, although were initially developed for the marine environment. This new tool has already been applied in assessing the degree of recovery of ecosystem

energy flow and success of habitat restoration (see James et al., 2020) and to test for trophic niche partitioning in an adaptive radiation of Hawaiian *Tetragnatha* spiders (see Kennedy et al., 2019) with great success. Therefore, hypervolumes offer useful insights that enable us to understand interactions at many ecological resolutions (i.e., individual, population, community, and ecosystem levels). This approach is based on the conceptual framework of Hutchinson's *n*-dimensional niche, where *n*-variables represent multiple axes which define a hypervolume that quantify the role of a species in its environment (Blonder et al., 2014). Depending on the variables included (e.g., abiotic factors, basal resources), hypervolume geometries and locations in *n*-dimensional space are particularly useful to gain insight into complex ecological processes that depend on multiple drivers, such as energy flow in a food web (Blonder et al., 2014, 2018). However, a variety of intrinsic and extrinsic factors may drive isotopic variability and influence the ultimate geometry of observed hypervolume niche dimensions within the natural environment (see Shipley and Matich, 2020). The hypervolume size varies with the values of the input data (i.e., larger hypervolume = more variation) and can be used to characterize resource use variation in food webs. The overlap between two hypervolumes (i.e., food webs from two different habitats) can be used to determine the similarity between two food webs, because overlap increases as two hypervolumes occupy more of the same *n*-dimensional space. This approach presents an opportunity for quantification of resource use within tropical wetland ecosystems through the use of stable isotope analysis. These metrics have the potential to be used at the system scale by combining resource use data from multiple species to quantify and compare food web-level resource use among habitats.

17.7.3.2 Best practices for use of stable isotope mixing models

The best practices for using stable isotope mixing models are presented in detail in Philips et al. (2014). For proper implementation of stable isotope mixing models, it is important to note that models can only be as good as the study design and/or data collected (Philips et al., 2014). Clear questions for studies are therefore important and these should be informed by study system knowledge, with strong sampling designs needed to characterize resource and consumer isotope variability at spatiotemporal scales. One of the implicit assumptions of any mixing model is that all the food sources are included, and researchers should thus strive to ensure that this is the case to get the most reliable results. It is also imperative to note that decisions on source grouping or incorporation of concentration-dependence can influence results, and studies should be careful about model output interpretation. Combining some sources to reduce the total number may sometimes lead to more constrained, less diffuse solutions, and should be considered to be an option if the sources examined have isotopically distinct signatures (Gannes et al., 1998; Phillips et al., 2005).

17.7.3.3 Tissue sample collection choices

Bone collagen and fish otoliths provide dietary information that spans an organism's entire life history, while metabolically active tissues have a turnover of days (e.g., liver) or months (e.g., muscle) (Philips et al., 2014). However, sampling of tissues such as bone collagen and otoliths requires the scarification of consumers. When such destructive sampling is not possible or ethical, there are nondestructive options available, such as blood which can be separated into two components: (1) plasma, which rapidly turns over and reflects diet from previous days, depending on the metabolic rate of the study species and (2) red blood cells, which represent diet from the previous few weeks and have a slow turnover. Tissues (i.e., claw, hair, feather) that are metabolically inert after formation offer scope for constructing time series (Philips et al., 2014).

17.7.3.4 Layman community metrics for food web structure analysis

Six community-wide Layman metrics that reflect important aspects of trophic structure are described below. The first four metrics are measures of the total extent of spacing (i.e., community-wide trophic diversity measure) within $\delta^{13}C-\delta^{15}N$ biplot space, and the last two metrics reflect relative species position within a trophic niche space and are also used for estimating the extent of trophic redundancy (see Findley, 1973; Winemiller, 1991; Cornwell et al., 2006; Layman et al., 2007 for details on the underlying theory, mathematics, and methodological considerations). In summary, the following community metrics are described:

1. The $\delta^{15}N$ Range (NR) is the distance between two species with the most enriched (maximum $\delta^{15}N$) and most depleted (minimum $\delta^{15}N$) values, and represents the vertical structure (i.e., trophic levels) within a food web. The organism's trophic position must be calculated in relation to the $\delta^{15}N$ values of a standardized baseline (i.e., normally a primary consumer) and, a larger $\delta^{15}N$ range among consumers suggests more trophic levels and high trophic diversity (Post, 2002; Layman et al., 2007).
2. $\delta^{13}C$ range (CR) is the distance between two species with the most enriched (maximum $\delta^{13}C$) and depleted (minimum $\delta^{13}C$) values. High CR is common in food webs with multiple basal food sources with varying $\delta^{13}C$ values, providing food web base niche diversification.
3. Total area (TA) is the convex hull area of all species in a $\delta^{13}C-\delta^{15}N$ biplot space. Thus, TA is a measure of the total amount of niche space occupied by all organisms, and is a proxy for the total food web trophic diversity. The TA value is influenced by species with extreme positions on either the $\delta^{13}C$ axis, $\delta^{15}N$ axis or both.
4. Mean distance to centroid (CD) is the mean Euclid-distance of each species to the $\delta^{13}C-\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and

δ^{15}N value for all food web species. The CD value is important as it provides a measure of the mean degree of food web trophic diversity and also as a function of species spacing degree.

5. Mean nearest neighbor distance (MNND) is the average of the Euclidean distances to each species' nearest neighbor in the δ^{13}C−δ^{15}N biplot space, and thus MNND is a measure of the overall species packing density. For example, food webs with a large species proportion with similar trophic ecologies will exhibit a smaller MNND (i.e., increased trophic redundancy) than a food web in which species are, on average, more divergent in terms of their trophic niche (Layman et al., 2007).

6. Standard deviation of nearest neighbor distance (SDNND) is a measure of the species packing evenness in a δ^{13}C−δ^{15}N biplot space that is less influenced than MNND by sample size. Generally, low SDNND values indicate trophic niches which are evenly distributed.

17.7.3.5 Calculating trophic position using stable isotopes

The calculation of trophic position for one baseline follows standard equations linking ^{15}N enrichment per trophic level and the trophic position of the baseline (e.g., a primary producer or primary consumer). In the case of two baselines, a simple mixing model incorporating $\delta^{13}C$ allows for the differentiation between two distinct nitrogen sources, thus including heterogeneity derived from alternative $\delta^{15}N$ sources (Quezada-Romegialli et al., 2018). Statistical analysis packages integrate three Bayesian models, depending on the baseline number and carbon (C) trophic discrimination factor inclusion. The simplest model is:

$$\delta^{15}N_c = \delta^{15}N_b + \Delta N(TP - \lambda) \tag{17.8}$$

where $\delta^{15}N_c$ and $\delta^{15}N_b$ refer to the consumer and single baseline $\delta^{15}N$ values, respectively, ΔN is the nitrogen (N) trophic discrimination factor, TP is the consumer trophic position, and λ is the baseline trophic position (Vander Zanden et al., 1997).

The dual baseline Bayesian approach includes a mixing model to discriminate among two distinct C and N sources, for example, pelagic versus benthic, and extends the single baseline approach using two equations:

$$\delta^{15}N_c = \Delta N(TP - \lambda) + \alpha\left(\delta^{15}N_{b1} + \delta^{15}N_{b2}\right) - \delta^{15}N_{b2} \tag{17.9}$$

and

$$\delta^{13}C_c = \delta^{13}C_{b1}\alpha + \delta^{13}C_{b2}(1 - \alpha) \tag{17.10}$$

where $\delta^{15}N_{b1}$, $\delta^{13}C_{b1}$, $\delta^{15}N_{b2}$, and $\delta^{13}C_{b2}$ refer to the $\delta^{15}N$ and $\delta^{13}C$ values of baselines 1 and 2, respectively, and α is the N proportion derived from baseline 1 (Post, 2002; Vander Zanden and Rasmussen, 2001). The full

model is based on the former, but α includes the carbon trophic discrimination factor:

$$\alpha = \frac{\left[\delta^{13}C_{b2} - \left(\delta^{13}C_c + \Delta C\right)\right]/(TP - \lambda)}{\delta^{13}C_{b2} + \delta^{13}C_{b1}} \tag{17.11}$$

where $\delta^{13}C_c$ is the consumer $\delta^{13}C$ value, and ΔC is the C trophic discrimination factor (see Quezada-Romegialli et al., 2018 for further details).

17.8 Conclusions

Wetland habitats, particularly floodplain areas, represent buffer zones between rivers and adjacent terrestrial systems, and these habitats often support high densities of organic matter and consumers. They provide ideal growth conditions to biota as a result of the resource exchange between aquatic and terrestrial habitats. Further, the wetting and drying phases that often characterize tropical wetlands drive highly dynamic trophic interactions that provide excellent model systems for testing food web and community theory (De Meester et al., 2005). Nevertheless, there remain pervasive knowledge gaps regarding trophic interactions in many types of tropical wetlands, regions and taxonomic groups. In particular, there is a general need for ecologists to transcend from a single-population (i.e., autecological) to a multicommunity perspective of feeding connections (i.e., multitrophic), especially when developing strategies for resource management or conservation. Thus, further research that encapsulates this need is required, such as by approaching the question of connectivity through trophic linkages and subsidies via aquatic organisms at the holistic level of a catchment within tropical wetland systems. For example, freshwater wetland systems are linked to land through a variety of passive and active transfers of plant, animal and human matter. Acknowledging the movement of nutrients and consumers within and among adjacent habitats is critical to our general understanding of trophic dynamics, as the health and sustainability of wetland aquatic food webs can be strongly influenced by these factors. Further studies in wetland ecosystems are also required to unravel how contributions of terrestrial versus aquatic resources, in sustaining secondary production, drive community structuring. Emergent effects associated with ongoing climate change and habitat degradations should additionally be examined in the tropical wetland context.

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