8.3 | CENTRAL ISSUES FOR AQUATIC FOOD WEBS: FROM CHEMICAL CUES TO WHOLE SYSTEM RESPONSES

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Aquatic ecosystems worldwide provide important resources for human populations. Estuarine and marine habitats provide many essential ecosystem services, including climate regulation, yet currently these systems are impacted over large areas through over-exploitation and degradation (Alongi, 2002; McClanahan, 2002; Verity et al., 2002). In many countries, freshwater is a scarce resource that requires sensitive political engagement to address the social, economic and environmental problems arising from reductions in freshwater availability. Moreover, aquatic ecosystems represent an integrative picture of environmental impacts and management practices operating in the terrestrial hinterland (Beeton, 2002; Hall, 2002; Malmqvist and Rundle, 2002; Kennish et al., 2005). As a consequence, an ecosystem approach to analyse food webs of these systems is increasingly valued by managers and research funding agencies alike, but major challenges lie ahead in the application of food web research to real-world issues of ecosystem management.

The understanding of food web structure, function, dynamics, and complexity is the central theme of food web research. Within this context, there is an array of approaches aimed at answering the ultimate question: "What drives food web dynamics?" A major goal is to be able to predict food web behavior under external (e.g., climate, human exploitation, extensive nutrient input) and internal influences (e.g., population dynamics, feedback, self-organization), in order to manage ecosystems sustainably. Scientists have as yet not been able to develop predictive whole ecosystem simulation models and, to our knowledge, no single method of food web analysis has been subjected to extensive validation of its predictive capabilities. Analytical methods targeting the smaller scale of populations or single species, on the other hand, have collected more credibility throughout their longer application history.

In the subsequent sections of this chapter, we discuss several areas, which, whilst they may not be peculiar to the aquatic environment, seem pivotal for future progress in understanding food webs. We deal first with factors that act at the level of individuals and populations (life history and storage effects, chemicals released by individuals and consumer-driven nutrient cycling) but whose influence on the food web dynamics and ecosystem functioning is as yet poorly understood. We suggest that the neglect of these factors, amongst others to be discovered and explored, contributes to the uncertainty of predictive ecosystem simulation models. We then emphasize the use of larger-scale network approaches and the need for quantitative descriptors of food webs, and conclude with challenges in application of food web theory to management issues in aquatic systems.

INDIVIDUAL AND POPULATION-BASED FACTORS THAT SHAPE FOOD WEB DYNAMICS

Influence of Life History on Aquatic Food Web Dynamics

Food webs are strongly influenced by life-history variation among populations (Polis et al., 1996b), and this is perhaps most apparent in aquatic systems. A fundamental aspect of life history is generation time and its influence on potential population growth rate and the storage effect (a sort of inertia in the biomass dynamics of the adult populations of long-lived organisms with relatively low vulnerability to mortality factors). Demographic and physiological tradeoffs that dictate limited suites of life-history attributes characterise three strategies, which represent endpoints in a triangular model of evolution of primary strategies (Winemiller and Rose, 1992). The *opportunistic strategy* characterizes populations with shorter generation times, which tend to have higher intrinsic rates of increase (r) and greater capacities to maintain positive population growth rates under density-independent environmental settings (e.g., following major disturbances). This strategy tends to be associated with small body size, early maturation, and continuous high reproductive effort, such as algae, decomposers, zooplankton, meiofauna, some aquatic macroinvertebrates (e.g., chironomids) and small planktivorous fishes. These organisms often occupy positions low within the trophic continuum of aquatic systems, but this is not always the case (e.g., parasites and small piscivores).

Species with longer generation times and life spans may be associated with either of two suites of life-history attributes. The *equilibrium endpoint,* associated with relatively low fecundity but high investment in individual offspring, presumably increases fitness (survival, growth, reproductive success, etc.) in environmental settings with frequent or chronic density-dependent population regulation via resource limitation, predation, or other biotic factors (Pianka, 1970), but the trade-off is a lower intrinsic rate of increase in density-independent settings (Lewontin, 1965). The equilibrium strategy, more common in tropical than temperate aquatic systems, is extremely rare among pelagic fishes, but predominant among marine birds and mammals. It is also observed among certain fishes and invertebrates inhabiting caves.

The second slow life-cycle strategy, associated with high fecundity but low investment per offspring, is the *periodic strategy* (Winemiller and Rose, 1992). This strategy is extremely common among aquatic macroinvertebrates and fishes and may promote fitness when environmental variation is predictable in space and/or time at relatively large scales (Winemiller and Rose, 1992, 1993). As a consequence, periodic strategists tend to have high inter-annual and regional variation in recruitment in which strong cohorts are produced in favorable locations or during favorable periods (Persson and Johansson, 1992; Scharf, 2000). In the absence of appropriate conditions for subsequent recruitment, strong cohorts of long-lived species may dominate the population for several years, yielding the phenomenon often referred to as the storage effect (Chesson and Huntley, 1989).

The periodic strategy tends to be associated with high dispersal in the egg and larval stages and can have major effects on the structure and dynamics of food webs. Seasonal mass movements of larval organisms into estuaries, that often are nurseries for marine crustaceans and fishes, provides pulses of food resources for predators (Deegan, 1993); the return of juvenile organisms to coastal marine waters results in a major reduction in consumers in the estuarine food web. Given the prevalence of the periodic strategy among aquatic/marine invertebrates and fishes, donor control, or supply-side, ecological dynamics should be common in aquatic ecosystems (Roughgarden et al., 1987; Menge, 2004). Thus, in addition to estimating effects of slow versus fast life cycles and concomitant intrinsic rates of increase and storage effects associated with life-history strategies, aquatic food web models will also have to include important migrations and subsidies (Polis et al., 1997) that connect local and regional food webs.

Life-history responses to variable environmental factors (e.g., productivity) have profound influence on food web dynamics. For example, phytoplankton in pelagic systems are opportunistic populations with fast life cycles. These populations respond relatively fast to changes in resources and sources of mortality. Moving up pelagic food chains, life cycles tend to become progressively slower but with a greater storage effect. As a consequence, species high in the food web tend to be relatively less responsive to short-term variation in food resources, however time lags in the responses of physiological, behavioral, and demographic parameters could yield complex population dynamics. Whereas opportunistic species should be more variable and responsive to short-term changes in resources, the storage effect should allow equilibrium and periodic strategists to remain more stable through periods of resource fluctuation. Because of the strong tendency for life cycles to become slower in successively higher levels of aquatic and marine food webs, models that employ simple linear Lotka-Volterra consumer-resource dynamics probably will be poor predictors of dynamics in these systems. To some degree, food web models must capture the essential ecological features that yield time lags and non-linear responses among populations with different life history strategies. For instance, Persson et al. (2003) analyzed shifts in trophic cascades caused by intrinsically driven population dynamics. Trophic cascades were explored experimentally in aquatic systems at the ecosystem level (Polis, 1999) and have been a central paradigm in explaining the structure of ecological communities. Yet, trophic cascades may alternate over time between two different configurations. By using empirical data and a size-structured population model, Persson et al. (2003) showed how according to the energy extracted from their prey, which constrains the reproduction, the size structure of a fish population may shift from a dominance of dwarfs to a dominance of giants. This intrinsically driven population dynamics limits the whole community and is the driving force behind distinct abundance switches observed in zooplankton and phytoplankton (see also De Roos and Persson, Chapter 3.2; Koen-Alonso and Yodzis, Chapter 7.3; Persson and De Roos, Chapter 4.2).

The Chemical Matrix and Food Web Dynamics

Whilst life history shapes food web dynamics on a population level, chemicals released by plants and animals modulate both trophic and competitive interactions with consequences to the entire natural food web. Dicke and Vet (1999) coined the term information web, or information network, for the combined effects of infochemicals on interactions in multitrophic communities (also see Vet, 1999; Vos et al., 2001). Here we extend this perspective and propose that food webs are embedded within a chemical matrix that includes both infochemicals and allelopathic substances. The effects of this matrix manifest themselves at the individual level in modified behaviors or rates of feeding, growth, and mortality, inducible defenses or shifts in competitive interactions. At the community level, plant- and animal-released chemicals affect both direct and indirect interactions in food webs, often through trait-mediated effects (Werner and Peacor, 2003). The study of these processes in aquatic systems requires specific approaches because the physical aspects of the medium are different from terrestrial ecosystems. For instance, the diffusion of chemicals in the medium depends on their solubility but also on the viscosity of the medium. Here we choose to focus on infochemical effects on trophic interactions and allelopathic effects on competitive and trophic interactions.

Infochemical Signals and Trophic Interactions

Infochemical signals affect trophic interactions in a variety of ways. Prey use predator-released chemicals as cues to tune refuge use and other induced defenses to actual predation risk. Such defenses affect functional responses and, as a consequence, interaction strengths (Jeschke and Tollrian, 2000; Vos et al., 2001; Vos et al., 2004a; Vos et al., 2004b). Predators, on the other hand, may use prey-released waste products and pheromones to locate resource species. This implies that trophic interactions may have an information aspect. Empirical ecologists have accumulated an impressive body of knowledge on the ecology and evolution of such interactions (Kats and Dill, 1998; Tollrian and Harvell, 1999). Kats and Dill (1998) reviewed prey responses to predator-released chemical cues and described changes in prey behavior, life history, and morphology in more than 200 species. Despite this wealth of information at the level of individuals, much less light has been shed on the implications for food web dynamics. Theoretical work predicts that infochemical use as manifested in induced defenses affects community persistence (Vos et al., 2001; Vos et al., 2002), stability (Edelstein-Keshet and Rausher, 1989; Abrams and Walters, 1996; Underwood, 1999; Vos et al., 2004a), resilience (see Vos et al., Chapter 3.4) and trophic structure (Abrams and Vos, 2003; Vos et al., 2004b). This suggests that infochemical-mediated effects may play an important role in the functioning of food webs in nature (also see Bolker et al., 2003; Werner and Peacor, 2003). In terrestrial plant-insect systems, extensive experimental work has focused on infochemical-mediated mutualisms between plants and the predators that attack their herbivores. Such research on the scope for infochemical-mediated multitrophic interactions is relatively underdeveloped in aquatic systems and deserves more attention (also see Vos et al., Chapter 3.4).

Allelopathic Interactions

We define allelopathy here as the inhibitory effects of chemicals released by one species on a sensitive species. For instance, chemicals of some cyanobacteria species have a targeted toxic effect by inhibiting the photosystem II of other primary producers (Mason et al., 1982; Gleason and Paulson, 1984; Gross et al., 1991). Allelopathy has also been reported in zooplankton species, with effects including reduced feeding and growth and increased mortality (Halbach, 1969; Folt and Goldman, 1981; Matveev, 1993; Lürling et al., 2003). As a consequence, allelopathy can modulate competitive interactions. Allelochemicals produced by macrophytes affect the composition of algal communities, both in marine and freshwater systems (Gross, 2003; Mulderij et al., 2003), whilst inhibitory effects reported between zooplankton species suggest a regulatory role for allelopathy in zooplankton communities.

When released by a prey (see examples in Landsberg, 2002), extracellular compounds that are toxic for a predator act as a defense. Such inhibitory effects on higher trophic levels are very similar to allelopathic effects on competitors. The production of compounds that are toxic against competitors and predators alleviates the producer from controls, which implies a potential for strong impacts on community dynamics (Hulot and Huisman, 2004). For instance, a variety of factors may explain shifts between turbid and clear water states in shallow lakes or be involved in the maintenance of such alternative states (Scheffer, 1998). Toxic compounds released by macrophytes may be among these factors, although their importance relative to other factors is poorly understood. Similarly, whether allelopathy against predators or competitors plays an important role in the development of toxic phytoplankton blooms is an open question (Hulot and Huisman, 2004).

There is great potential for the chemical matrix to affect both trophic and competitive interactions in food webs. We expect that incorporation of the chemical matrix in food web theory will result in a more complete understanding of how food webs function. One particular challenge is to explore to which extent infochemicals and allelopathic substances, which manifest themselves at the individual level, may affect the ecosystem dynamics.

Consumer-Driven Nutrient Recycling (CNR)

Consumer-driven nutrient recycling (CNR) is an important component of aquatic ecosystem dynamics that has recently gained considerable attention among food web ecologists (DeAngelis, 1992a; Vanni, 1996; Sterner, 1997; Elser and Urabe, 1999; Vanni, 2002). Consumptive interactions within food webs are inextricably linked to the excretion or egestion of nutrients that exceed an organism's metabolic or reproductive requirements (Elser and Urabe, 1999). These recycled dissolved or particulate nutrients are released into the aquatic environment and may be reincorporated into the food web at all levels from basal species to top predators. Such dynamic recycling of essential elements may have strong implications for the structure, productivity, and stability of aquatic food webs (Kitchell et al., 1979).

Recent studies of consumers in lakes and streams (Elser and Urabe, 1999; Vanni, 2002) reveal a large degree of interspecific variation in dissolved nutrient recycling which is often correlated with the nutrient content of consumers. For example, Vanni et al. (2002) demonstrated that the N:P ratio of excreted nutrients by stream fish and amphibians was negatively related to organism body N:P ratios. Similar variation in nutrient recycling ratios has been discovered among species of zooplankton (Sterner et al., 1992; Elser et al., 1998) that differ largely in their body nutrient content. Such relationships between species identity and nutrient cycling imply that community composition, or even the presence of one dominant species, can determine the availability of essential nutrients and productivity of the system. Understanding the importance of CNR to whole-system nutrient dynamics will likely require a combination of detailed empirical studies of individual interactions in addition to analysing the system as a whole. Ulanowicz and Baird (1999) describe a promising whole-ecosystem approach which uses information on nutrient content, metabolic and recycling rates for all species or trophospecies in the system for various nutrients simultaneously (e.g., C, N, P etc.) to identify the limiting nutrient and the limiting source for that nutrient for each species in the food web. Network analysis techniques underscore and incorporate the importance of species connectedness via nutrient recycling, in addition to the more commonly recognized connectedness via direct consumption.

Although most empirical and theoretical studies of CNR focus on dissolved nutrients (i.e., excretion), consumers can potentially have large effects on nutrient availability through recycling of particulate nutrients (i.e., egestion). If large elemental imbalances exist between consumers and resources, the nutrient content of egested material will be lower than that of ingested food items because of nutrient sequestration by consumers. Alternatively, consumers may increase the nutrient content of egested material by altering its size-structure (i.e., surface:volume ratio) and susceptibility to nutrient-rich microbial colonization (Turner and Ferrante, 1979; see Cross et al., Chapter 5.4). In aquatic systems, coprophagy is relatively common (Wotton and Malmqvist, 2001; Pilati et al., 2004), and particulate nutrient recycling may have important ramifications for the dynamics of these food webs. Although food web linkages via egestion are well recognized in the analysis of trophic flow networks, empirical studies of this process are few (Short and Maslin, 1977) and considerable research is needed to identify when and where food web flows are dependent upon nutrient cycling through egestion.

Understanding the importance of CNR in aquatic food webs will require a great deal of empirical research in a wide variety of systems. Investigation of CNR in non-pelagic communities (e.g., benthic lake, stream, or marine communities; Frost et al., 2002; Sterner and Elser, 2002) will undoubtedly provide valuable insight into the generality of current theory.

A MACROSCOPIC APPROACH TO ECOSYSTEM STUDIES

The factors influencing the structure and dynamics of food webs often differ in scale in both signal and response. We previously considered selected issues such as life-history strategies, chemical interactions, behavioral responses, and nutrient stoichiometry. They all describe interactions on the relatively small scale of species and populations. Frequently a broader scale to view the ecosystem is required to understand interactions between species within an ecosystem context, as well as ecosystem level descriptors, which result from such direct and indirect species interactions.

Such a macroscopic or holistic approach, which can reveal descriptors of food web structure and processes, can be applied to quantified trophic flow networks. In these networks, the biomass of each node and the trophic exchanges between species and the surrounding environment are quantified using currencies of energy or material (e.g., C, N, P, S;

Wulff et al., 1989). The magnitude of material transfer between species is a result of a multitude of factors such as new nutrient availability and nutrient recycling, detritus production, interaction patterns between species (e.g., predator–prey interactions), recruitment patterns, habitat availability and exchanges with the environment (detritus and migration). They constitute as such an integration of environmental and biotic factors. Stable isotope ratios, which are now routinely employed for tracing trophic connections (see Layman et al., Chapter 7.4), also provide valuable information to build such quantified flow networks. They are used to estimate basal energy sources and overall patterns of flow of material through webs as a time-integrated measure of feeding relationships, reflecting all pathways of material flow from the base of the food web to an organism of interest. Especially where stomach content analyses prove futile (e.g., nutrients, primary producers, small organisms, etc.), stable isotopes provide valuable information of feeding interactions.

The magnitudes of transfers between species so measured by and calculated from, amongst others, above observations shape a number of species-, community-, and ecosystem-level properties, which can be calculated from a transfer matrix of material (i.e., species j (column) consuming species i (row)). Ecological Network analysis (ENA) is a tool used to analyze such quantified flow networks and comprises several types of analyses that are briefly mentioned here. The quantitative data describe direct and indirect effects between species. By applying Input-Output Analysis to weighted networks (Szyrmer and Ulanowicz, 1987), the combined direct and indirect effects reveal dependencies of any one species on any other species in the network, which can be quantified in terms of material transfer. It is thus possible to track the dependencies (also called 'extended diets') of, for example, a commercially exploited species, or a 'keystone' species. The dependencies are expressed as the fraction of the total ingestion by j which has passed through compartment i on its way to j, over all direct and indirect pathways (Szyrmer and Ulanowicz, 1987). In addition to transfers between any two species, cycles can be enumerated and the amount of material flowing through cycles of various lengths computed with ENA. The amount of material flowing through cycles (or recycling) can be quantified as opposed to straight through flows (material entering the system and leaving it without being cycled once), and gives, together with the cycle structure, a clue about the developmental state of the system. In the light of human exploitation and the urgent question of ecosystem resilience, information inherent in the flow structure (including the magnitudes of flows) can been calculated to express the development capacity, organization, and resilience of ecosystems as information theoretical indices (Ulanowicz, 2004).

The importance of quantitative data in food web studies has more recently been highlighted by, for example, Bersier et al. (2002) who compared several qualitative and quantitative food web descriptors to show that there is more information inherent in quantitative data than in a qualitative approach. Another recent example for a quantitative descriptor of food webs includes the assignment of a 'loop weight' to cycles (Neutel et al., 2002), which has allowed interaction strength and cycle length to be related to the stability of ecosystems.

The analysis of quantified networks is used to compare ecosystem attributes on local and global scales (Baird et al., 1991; Monaco and Ulanowicz, 1997) and to illustrate changes in system behavior over time (Baird and Ulanowicz, 1989; Baird et al., 1998). Other studies highlight the effects of environmental impacts such as the construction of a dam (Baird and Heymans, 1996), nitrogen overloading in an estuary (Christian and Thomas, 2003), or a change in freshwater inflow into estuaries (Scharler and Baird, 2005). In such circumstances, the network approach gives valuable insight into food web attributes through (1) changes in the topology of the food web and (2) changes in the magnitude of energy or material transfers. The latter constitutes a more subtle response of ecosystems to perturbations compared to changes in food web topology (i.e., a loss of links).

ENA as a whole ecosystem approach describes effects of abiotic and biotic interrelationships through numerous parameters. The advantage of such an approach lies in the inclusion of several species interactions, including feedback mechanisms, in an ecosystem context as opposed to single species interactions and dynamics. As such it describes patterns arising from the structure and magnitudes of flows, which is valuable information required for the management of ecosystems. Such an analysis can be complementary to dynamic ecosystem simulation models.

THE APPLICATION OF FOOD WEB THEORY IN MANAGEMENT

Food web theory has broad application in relation to management issues, yet there is often reluctance on the part of modellers and theoreticians to put their models to the test by addressing the concerns of regulators and the public. Of course, the contrary argument can be made that managers themselves can often be suspicious of models and distrustful of their predictions, and models are seen as either too complex to convey meaning to the end-user or too simplistic to apply in situations which are economically or politically sensitive (in the sense that they might not stand up to close public scrutiny). To date, the use of food web models in environmental management has largely been restricted to two areas: the trophic transfer of contaminants (Camphens and Mackay, 1997) and the management of marine fisheries (see Koen-Alonso and Yodzis, Chapter 7.3).

Trophic transfer models have generally been applied in the study of persistent organic pollutants (e.g., PCBs), where it is possible to predict the movement of substances through food webs by a combined knowledge of their chemical properties, and the structure and functioning of the food web itself. Such models remain highly simplistic, however, and it is perhaps surprising that little progress has been made in refining these models beyond the pioneering work of the Canadian Environmental Modelling Centre (http://www.trentu.ca/cemc/). There is a need here to introduce more ecological thinking into the fugacity approach (Camphens and Mackay, 1997), and this should be a fruitful area for future collaborations between ecologists and environmental chemists.

The use of food web models in fisheries management should constitute the greatest success story for the use of such models in environmental management. However this is not the case: there has been some reluctance on the part of regulators and operators to fully engage in the application of these models in regulation of fishing activity. This is further exacerbated by the unwillingness on the part of the fishing industry to accept the social and economic consequences of the management actions suggested by the model predictions. Even in marine fisheries management, decisions continue to be taken on a species by species basis, even though this is clearly failing to address the consequences of fishing, which inevitably involves exploitation of food webs rather than individual species (Pauly et al., 2003).

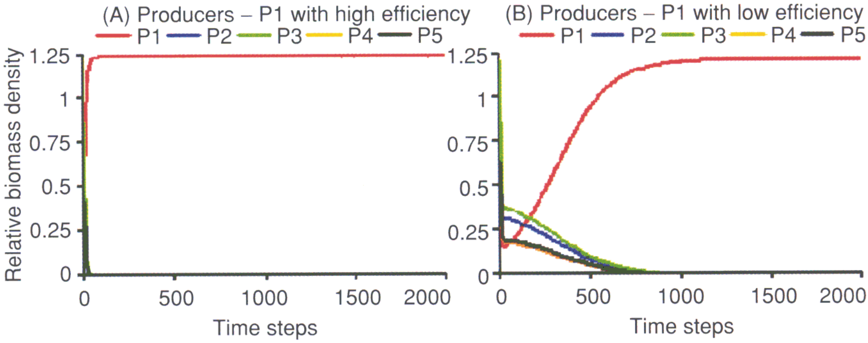
Food web models clearly have much to offer the field of environmental management: they can be used for forecasting the consequences of management actions, or the impacts of environmental pressures. Alternatively, they can be employed to hindcast the historical state of existing, degraded systems and to provide target images for ecological restoration schemes. They have particular value in the field of environmental risk assessment, where they can form the basis of a diagnostic methodology to tease apart the effects of multiple stressors (Baird et al., 2001; see Culp et al., Chapter 7.1), and it is in this complex area where adoption of a food web approach can perhaps offer the greatest immediate advantages to the environmental manager.

DISCUSSION AND CONCLUSIONS

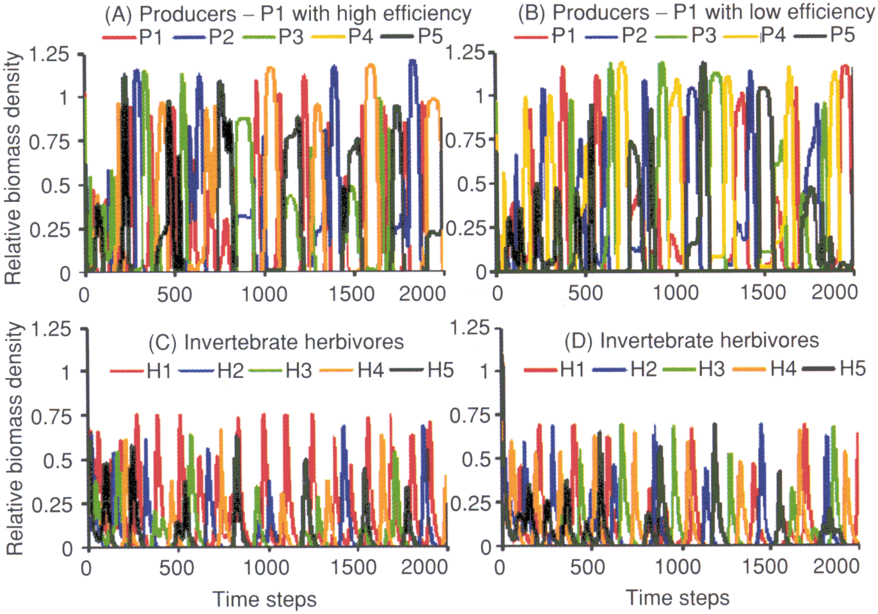
The issues previously discussed are examples of study areas that provide insights into the structure, function, and dynamics of aquatic food webs, and which the authors feel deserve increased attention. They also illustrate how new perspectives may emerge from their combination. Importantly, these study areas range in scale from the population and species level (e.g., life history strategies, chemical cues and defenses, nutrient consumption and sequestration), to the community and ecosystem level (e.g., nutrient cycling, nutrient transfers, indirect effects, organization, development and resilience, management). However, the degree of influence on food web dynamics and ecosystem functioning of the processes described at these different scales are still poorly assessed. For instance, processes linked to specific organisms such as long-lived species with a great storage effect or seasonal mass dispersal of egg and larval stages may drive, at different time and spatial scales, the dynamics of food webs. However, the extent of their effects is poorly known and opens questions as to which temporal and spatial scales to consider in such studies. The issues described at the population and species level are also examples of processes, which may contribute to the uncertainty of food web model predictions. One important challenge is therefore to reduce this uncertainty by identifying the non-trophic processes influencing food web dynamics, and including them in models of predictive capability.

Despite the increasing number of food webs documented in the literature and on the World Wide Web, there is a need for the identification of pathways and the quantification of matter transfer in ecosystems to facilitate analyses of entire ecosystems and not only parts thereof. This is even more relevant if we aim to extend the analysis to interaction networks by including information transfer and allelopathy, or the size-structure of populations as a driving factor of aquatic communities.

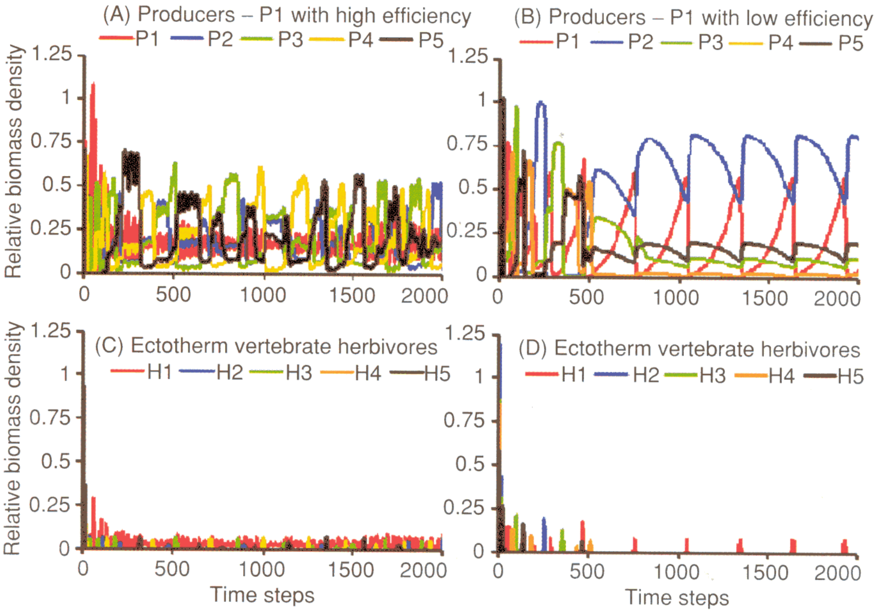
The area of food web research has great importance for the management of ecosystems to ensure performance under circumstances of continuous exploitation by humans. Ecosystem approaches facilitate taking a step towards 'whole ecosystem management' and away from reductionist approaches such as single species management. Although the predictive capability of ecosystem models has a poor record of validation, the analysis of a given structure of ecosystems can already provide valuable information on several issues important to their management. A major challenge of food web research is to reduce modellers' and managers' reluctance to respectively test and apply food web theory.



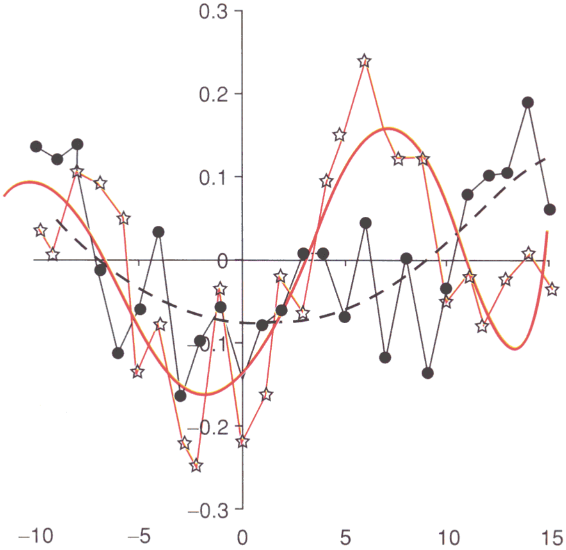
CHAPTER 2.1 FIGURE 1 | Biomass evolution in producer communities. The guzzler (P1) is strong **(A)** or weak **(B)**.



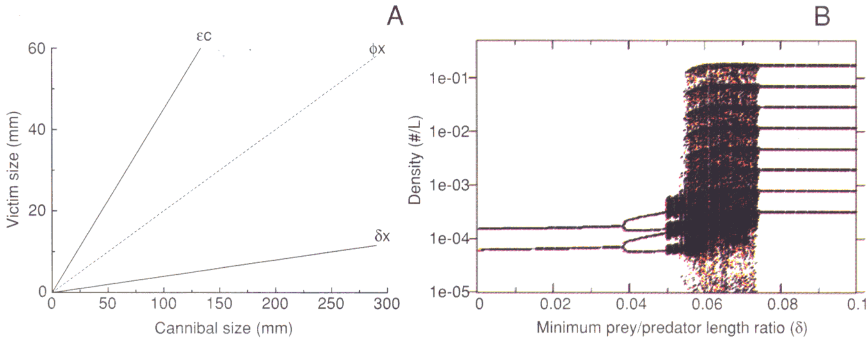
CHAPTER 2.1 FIGURE 2 | Biomass evolution in producer-invertebrate herbivore communities. The guzzler (P1) is strong **(A, C)** or weak **(B, D)**.



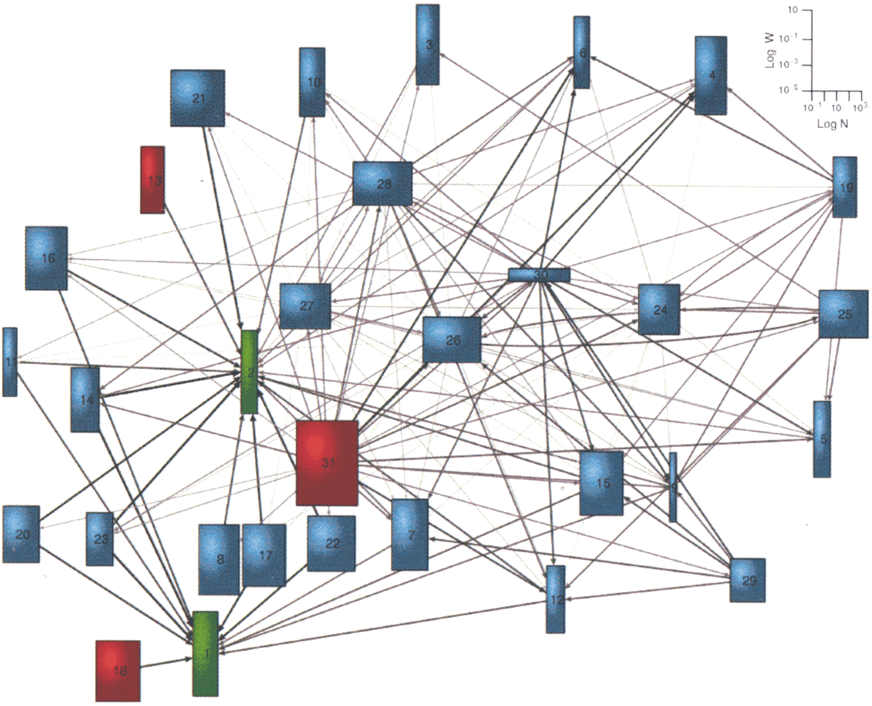
CHAPTER 2.1 FIGURE 3 | Biomass evolution in producer-ectotherm vertebrate herbivore communities. The guzzler (P1) is strong **(A, C)** or weak **(B, D)**.



CHAPTER 2.2 FIGURE 3 | Time series cross-correlation analysis of log-biomass of edible algae against zooplankton. Black dots show data (averaged across 4 replicates of each treatment each with 20 data points) for the cross correlation function for cases where *Daphnia* are the only grazers present, red stars indicates cases where there are three species (*Daphnia*, *Ceriodaphnia* and *Chydorus*). The X-axis is time lag (days), the Y-axis is the correlation coefficient. The graph shows lines that connect the data and smoothed estimators for each function (dashed black line for *Daphnia* only, solid red for three species together).

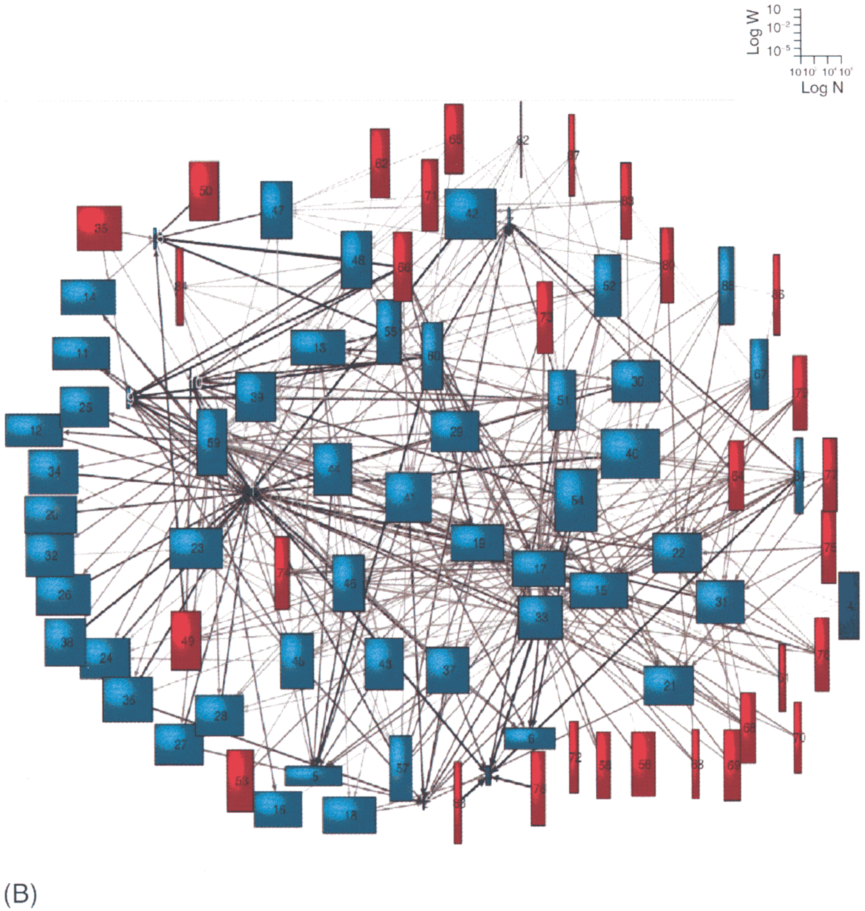


CHAPTER 4.2 FIGURE 3 | **A,** Two-dimensional plot of the cannibalistic window showing the minimum size ratio (δ), the optimum size ratio (φ) and the maximum size ratio (ε) of victims to cannibals for which cannibalistic interactions take place. **B,** Bifurcation plot showing the effects of the lower size limit (δ) on cannibalistic population dynamics for β = 200 and ε = 0.45. Densities reflect all cannibals excluding young-of-the-year individuals.

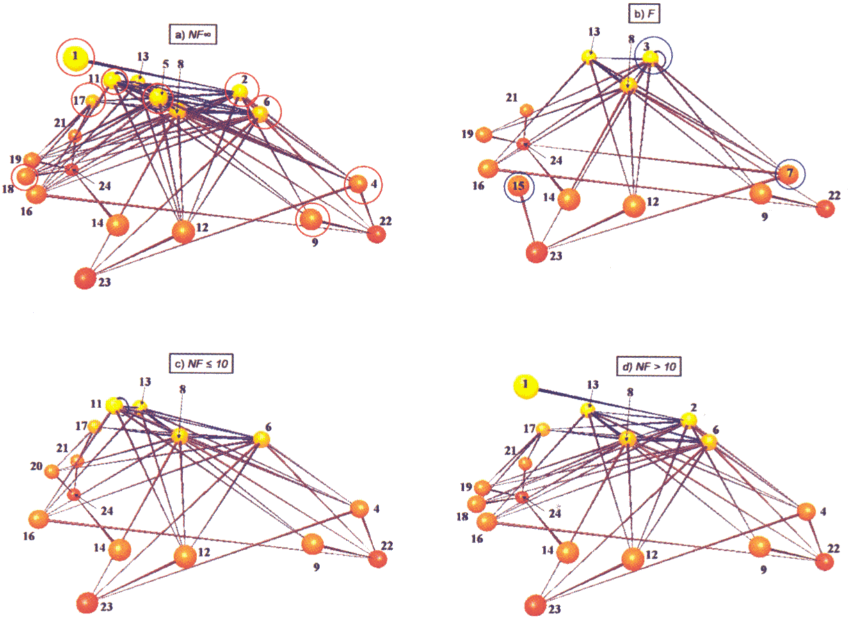


(A)

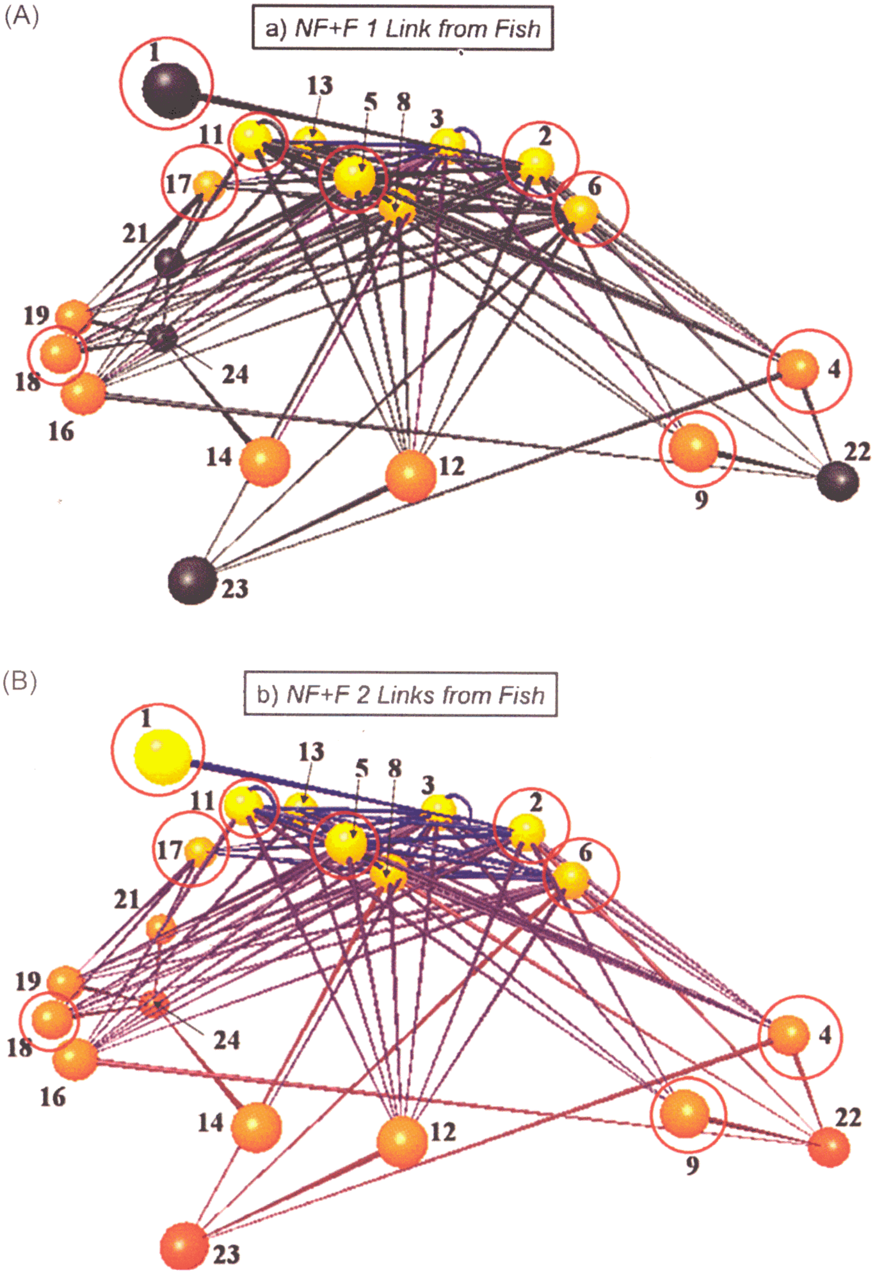
CHAPTER 7.2 FIGURE 1 | Representation of Broadstone **(A)** and Ythan **(B)** food webs. Arrows point from predators to prey, and line thickness and darkness correspond to predator per capita interaction strengths (a_{ij}) in the community matrix. Rectangles correspond to species (most of them taxonomic species), and green, blue and red correspond to basal, intermediate and top species respectively. The base of the rectangle corresponds to species' numerical abundance (number/m^2), and its height to body size (mg of mean individual or mean adult, for the Broadstone and Ythan respectively).



CHAPTER 7.2 FIGURE 1 | *Cont'd* All data are log-transformed, and the scales for abundance and body size are indicated. For the Ythan web, we do not have direct measurements of some species abundances, so we have estimated them from their body size using observed allometric relationship between abundance (X) and body size (W) for the species whose abundance was already known: $X = 177.51^{*}W^{-1.185}$ (r^2=0,84; p<0.0001) (after Leaper and Raffaelli, 1999; Emmerson and Raffaelli, 2004b). This type of representation might be very helpful for visualizing the temporal variability in food webs (e.g., exploring how abundances, body sizes, or interaction strengths change through time), or the effects of the introduction and extinctions of species in complex food webs. Figures have been generated using the program Pajek.



CHAPTER 7.5 FIGURE 1 | Food webs for the four lake categories: (a) "*NF∞*" = Never any Fish, (b) "*F*" = Fish present, (c) "*NF ≤ 10*" = No Fish ≤ 10 years, (d) "*NF > 10*" = No Fish > 10 years. Each node is a separate trophic species which may consist of one or more taxa that share all the same predators and prey. Webs are oriented so that the basal species are at the bottom in dark orange and the top predators are at the top in yellow. Link shape indicates the direction of the feeding relation, with the wider end being the predator and the narrow end the prey. If two species eat each other, the link is narrowest in the middle. Cannibalistic links are indicated by a loop returning to the same node. In the *NF∞* web, red circles highlight the trophic species that are lost in the *F* web. In the *F* web, blue circles indicate new trophic species relative to the 'Never Stocked' web. For a list of taxa and trophic species, see Table 2.



CHAPTER 7.5 FIGURE 2 | A hypothetical *NF+F* web showing the *NF*∞ condition with fish added. **A,** All direct feeding links from trout are highlighted in color, with all other links and nodes blackened. **B,** All nodes and links two feeding links away from trout are shown in color, which includes the entire web. Red circles indicate trophic species that are lost in lakes where fish are present. For a list of taxa and trophic species, see Table 2.