The ubiquity of omnivory

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Introduction

The textbook view of ecology is of communities assembled from linear food chains, where predators feed on grazers, which feed on plants. Species can then readily be placed into trophic levels. This view of communities has been perpetuated by studies that have illustrated trophic cascades (Paine 1980), where perturbations at one trophic level have effects that are transmitted along food chains in an alternating pattern of positive and negative effects. However, this traditional view has been challenged by authors who have suggested that in real food webs, species can not tidily be attributed to a particular trophic level. This view is supported by detailed descriptions of real food webs (Hall & Raffaelli 1991, Polis 1991, Woodward & Hildrew 2001) and recent meta-analyses (Arim & Marquet 2004, Williams & Martinez 2004, Thompson et al. 2007).

A weakness of the studies to date is that they have relied on food webs that are binary matrices of trophic interactions, meaning that infrequent or incidental ingestion of material is given equal weight to frequent and deliberate feeding events. While omnivorous feeding has now been shown to occur frequently, we have no clear assessment of the dynamic importance of omnivorous trophic links. If omnivorous links are generally weak, then trophic dynamics may still closely approximate a linear food chain. Using highly detailed food webs collected from ponds, we assessed the prevalence of omnivory in terms of both the frequency and intensity of the trophic links involved. Specifically, we sought to ascertain the dynamic importance of omnivory, based on the strength of energy flows through omnivorous food chains.

Key words: food web, pond, trophic level, trophic structure

Methods

Food webs were described from two 100 m^2, 3-m deep artificial ponds on the University of British Columbia campus (see Bell et al. 2003 for details) in August 2004. The ponds are surrounded by deciduous trees (predominantly alder, *Alnus rubra* Bong.), the leaves of which dominated the substrate. The benthic and limnetic components of the food webs were sampled at 3 discrete locations in each pond. A 20-cm diameter, 100-cm long plastic pipe was inserted into substrate at a location where the water depth was 80 cm. All water and biological material to a depth of 10 cm of substrate were sampled using a suction pump and stored in 1 % formaldehyde for later processing.

Samples were sorted at 40× magnification, and all individuals identified to at least genus using Pennak (1989), Thorp & Covich (1991) and Merritt & Cummins (1996) and keys listed therein. A subsample of leaves (10 cm^2) was scrubbed with distilled water to sample benthic algae. Limnetic algae were sampled by placing the water sampled in a settling chamber overnight. Three 20-ml subsamples were taken from the bottom of the chamber and inspected using an inverted microscope. Algae were identified with reference to Wehr & Sheath (2002).

All invertebrates in a sample were used for gut analysis, unless more than 100 individuals were present, in which case a random sample of 100 individuals was used. Invertebrates were processed for gut analysis as described elsewhere (Townsend et al. 1998). Algae, unidentified detritus, algal remains, and macrophytes were given a Trophic Position = 0. Unidentified invertebrates were given a Trophic Position of 1. Each dietary item was given a Trophic Interaction Score (TIS) from 1 to 5 based on its occurrence across all individuals inspected; 1 indicated a single fragment (invertebrate) or cell (algae) observed; 5 indicated material comprising >25 % of the gut volume.

Trophic positions were calculated for every taxon using the 'prey-averaged technique' (Williams & Martinez 2004). Taxa with non-integer Trophic Position scores are considered to be omnivores (Thompson et al. 2007). For the individual sample food webs from each pond we calculated number of species in each trophic level (TL) and number of omnivores. For each web overall, and for the food chains containing omnivores only, we calculated total number of trophic links, summed TIS, and average TIS.

Results

The food webs were diverse, with the majority of taxa either algae or detritivorous invertebrates (Fig. 1). There were a relatively small number of omnivores in these
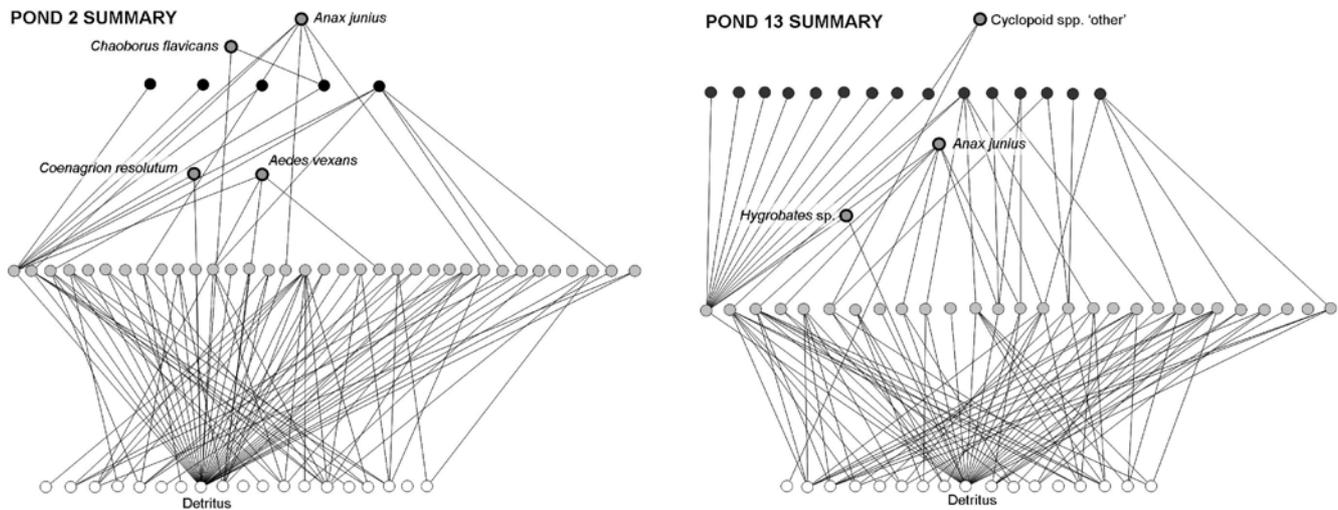
Fig. 1. Food webs summarized from the 3 webs from each pond. Circles indicate taxa arranged in trophic levels, with omnivores labeled by species.

Table 1. Summary attributes of the 3 food webs from each pond.

	2a	2b	2c	13a	13b	13c
# taxa in trophic level 1	17	18	19	19	19	19
# taxa in trophic level 2	22	25	26	17	17	20
# taxa in trophic level 3	4	2	1	8	8	6
# omnivorous taxa	3	1	1	2	2	2
Total no. of trophic links	76	77	73	73	92	83
Proportion trophic links via omnivorous food chains	0.07	0.04	0.05	0.11	0.10	0.10
Total trophic interaction score (TIS)	159	163	155	134	161	150
Proportion TIS via omnivorous food chains	0.09	0.02	0.03	0.10	0.09	0.09
Average TIS	2.09	2.12	2.12	1.84	1.75	1.81
Average omnivore TIS	1.56	1.00	1.25	1.75	1.67	1.75
Average TIS from omnivores to least connected trophic level	1	1	1	1	1	1

food webs, with 94 % (Pond 2) and 93 % (Pond 13) of taxa attributable to an integer trophic position (Table 1). Considering only animal taxa, this represents 12 % and 14 % of animal taxa being considered omnivorous (Table 1). Between 4 and 11 % of the total trophic links and between 2 and 10 % of the total TIS occurred in food chains with omnivores. Average link strengths to omnivores were lower than the average for the whole food web, and the link score from omnivores to the least frequently occurring trophic level in their guts were weak (an average score of 1).

The majority of omnivory was due to small amounts of organic matter being ingested by predators (e.g., the dragonfly *Anax junius*), or by small amounts of unidentified invertebrate remains appearing in taxa that fed predominantly on plant detritus (e.g., the mite *Hygrobates*

spp. and the mosquito *Aedes vexans*). Only a cyclopoid morpho-species and the damselfly *Coenagrion resolutum* had an equal representation of food items from 2 trophic levels in their gut. The phantom midge *Chaoborus flavicans* was the only taxa found to feed on TL 1 (herbivores and detritivores) and TL 2 (intermediate predators). Interestingly, the damselfly *Coenagrion resolutum*, which is considered a predator (MERRITT & CUMMINS 1996), frequently contained plant material, and must be considered an omnivore in this system.

Spatial variability in omnivory was higher in Pond 2 than in Pond 13, where food webs were extremely consistent from location to location (Table 1). Omnivory was overall less important in Pond 2, with stronger trophic links overall contrasting with weaker links to omnivores (Table 1).

Discussion

The food webs described here had low rates of omnivory compared to those found in our review of aquatic food webs (Thompson et al. 2007). Consistent with that review, however, we found that trophic levels became less defined as food chains increase in length. One of the reasons that so few species were found to be omnivores in this system may be that food chains were relatively short. Omnivory showed some evidence of being spatially variable both within ponds (Pond 2) and between ponds. Factors that determine the local importance of omnivory in real systems have been little explored, although there is a rich vein of theory suggesting that relationships should exist with productivity (Hairston & Hairston 1997, Hillebrand & Shurin 2005, Thompson et al. 2007).

The food webs described here were strongly based on detritivory, and instances of omnivory may have resulted from animals incidentally consuming animal material from the detrital compartment. Gut contents analysis can not distinguish these events from active predation. Sections of exoskeleton consumed by detritivores might seem to indicate a predation event but might actually be detritivory on dead remains, and thus may provide extremely limited energy inputs to the consumer. The evidence here suggests that while these events do occur, the strength of the trophic link is weak, and may be dynamically unimportant. This observation may explain why dynamics consistent with linear food chains, such as trophic cascades, are observed even in food webs where omnivores are common. To obtain an actual understanding of the energetic role of omnivory we need to combine stable isotope approaches with traditional gut content analysis and analysis of food web topology. Such an approach is likely to be highly informative in understanding the real prevalence and importance of omnivory.

The frequency of omnivory in food webs is likely to reflect an interaction between factors that act to linearise food chains and factors that favour omnivory. There is some evidence that competition may favour specialists through evolutionary time (Le Vay et al. 2001, Diehl 2003). Size hierarchies may also tend to favour trophic levels by constraining species to a particular size range of prey (Cohen et al. 1993, Loeuille & Loreau 2005). Omnivory may be expected to be favoured where species feed relatively indiscriminately (e.g., drift feeding in salmonids), change size, and therefore diet ontogenetically (e.g., crayfish), or there is high temporal or spatial variability in availability of some food species. Understanding the role of omnivory in food web dynamics presents itself as a challenge to combine evolutionary and ecosystem ecology in a way that may ultimately inform ecosystem management.

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