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Trends in research on shallow water food webs

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Abstract

Making sense of the spider–web networks of interactions between species in food webs has been a major pre-occupation of ecologists over the last 60 years. This review describes the early attempts to reduce this complexity through the grouping of individual taxa into functional categories (such as trophic levels), through adopting the energy flow or systems approach as epitomised by the International Biological Programme, and most recently by the derivation of web statistics by food web theorists. The strengths and weaknesses of these approaches are discussed in relation to empirical field experiments for unravelling the processes responsible for organising communities and an assessment made of the representation of these approaches in the marine biological literature. © 2000 Elsevier Science B.V. All rights reserved.

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1. Dealing with complexity

It has long been recognised in ecology that individual species are embedded in a network of interactions with other species, the food web. Perhaps nowhere is the complexity of these networks more clearly illustrated than in Hardy (1924) figure of the herring (*Clupea harengus*) in the open sea (Fig. 1). Hardy not only recognised that changes in other network elements were likely to influence the numbers of herring, but also that the configuration of the web was an instantaneous ‘snap-shot’ with respect to the connections (trophic links) between species: as herring developed from eggs to adult, their diet shifted and their trophic status (the level in the food chain at which they ate) increased. However, the complexity of spider–web diagrams like Hardy’s, conceal more than they reveal — interesting patterns may be obscured by the high level of detail.

The need to reduce this complexity so that general patterns can be appreciated has

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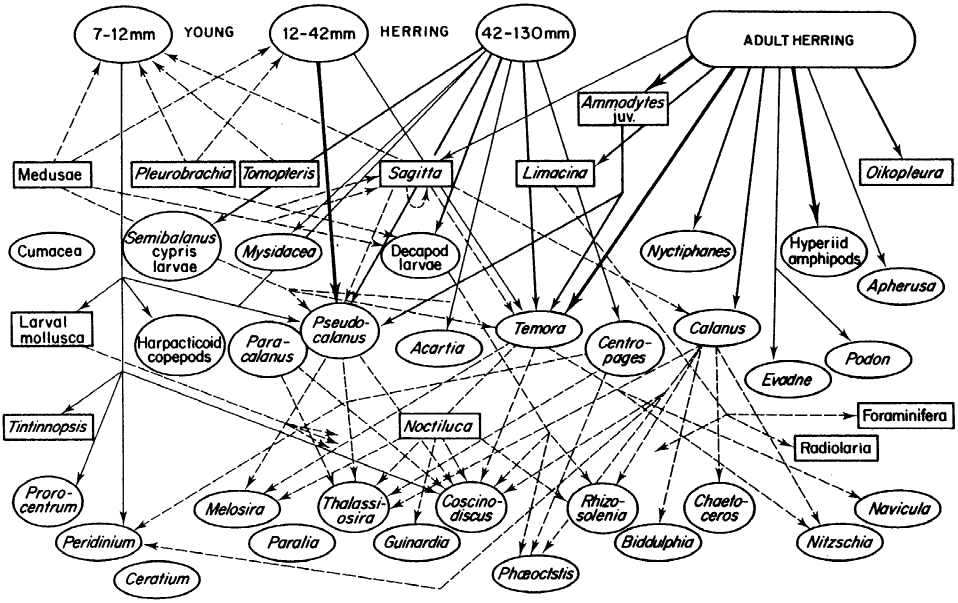

Fig. 1. The food web of the herring (*Clupea harengus*), as modified (broken lines added) by Graham (1987) from original by Hardy (1924). Note that the direction of arrows is the opposite of the normal convention.

been a major driving force in food web research over the last 50 years from the grouping of many species into fewer functional trophic types, such as producers and consumers at various trophic levels, to the more recent derivation of food web statistics (Cohen et al., 1990; Hall and Raffaelli, 1993, 1996). By providing summary statistics for individual webs, it becomes possible to start to make comparisons between different webs. If recurrent patterns emerge across different food webs, these patterns are likely to be important because they probably represent constraints on system architecture as well as important underlying processes. For example, the pyramids of biomass (a pattern) documented by earlier workers, such as Elton and Lindeman, revealed the low ecological efficiency of energy transfer (a process) between trophic levels. Such common patterns in real food webs may also be used to test predictions of conceptual and mathematical models (Pimm, 1982).

2. The systems approach

The search for recurrent patterns and processes in ecological systems was given a major boost in the mid-1960s through the International Biological Programme (IBP). This initiative aimed to *"ensure a world-wide study of . . . .organic production on the land, in fresh waters and in the seas, and the potentialities and uses of new as well as of existing natural resources . . . .".* The vision of scientific endeavour and international co-operation presented in the reports, newsletters and briefings of the IBP seems staggering by today's standards. The role of the IBP faded in the mid-1970s, but not before the publication of a host of IBP manuals for the measurement and estimation of ecological processes and parameters relevant to the description of the flows of materials and energy between food web elements. These manuals permitted (and continue to do so) the development of an agreed, common approach to the interactions between species or their functional groupings, particularly the flows of material within an ecosystem and the construction of energy budgets. Many research programmes in shallow water marine environments were formally under the IBP banner (Table 1), but all subsequent food web programmes have benefited from the IBP springboard.

By constructing whole-system flow diagrams and energy budgets, ecologists were able to identify those processes most critical to the system and highlight parts of the system where more research was needed. For example, Steele's (1974) attempt to provide a budget for the North Sea ecosystem, revealed an urgent need to understand and unravel the processes taking place within the meiofaunal 'black-box' (Fig. 2). The early assumption that the main role of the meiofauna in marine benthic food webs was chiefly to remineralise or recycle nutrients (McIntyre, 1969) was overturned over the next two decades by detailed investigations of interactions between different meiofaunal species (Fig. 2), an appreciation of their importance for small epibenthic predators (Gee, 1989), and, more importantly, the significance of their small individual body size for production and energy flow (Vernberg and Coull, 1974; Gerlach et al., 1985). In this respect, developments in meiofaunal tropho-dynamics have great similarities with the appreciation of the importance of the equally neglected microbial assemblages in the marine plankton. The significance of these organisms for open water food webs, via the microbial loop, is also apparent in shallow water surf-zone food webs on sandy beaches (Brown and McLachlan, 1990). Of course, the systems approach continues to date, with a shift away from the making of empirical measurements, towards a suite of modelling approaches, such as Ecopath (Christensen and Pauly, 1992), network analysis (Ulanowicz, 1996), and exergy-orientated models (Jørgensen, 1998).

3. The experimental approach

Whilst the ecosystem approach provides quantitative estimates of the flow of material between system compartments or web elements, it is unlikely to identify those processes which are critical to sustaining a food web in its normal state. The point is well made by Paine's (1980) illustration of a simple rocky shore food web (Fig. 3). In the upper diagram the web is depicted in its binary form, a simple description of whom eats whom, which Paine termed the *connectedness* web. Such representations reveal little about which links are trivial and which are important dynamically. By quantifying the energy (or material) flowing from producer to consumer (the approach essentially adopted within the IBP), trophic links can be assigned different degrees of importance. In Paine's *energy flow web*, several links have much energy moving from producer to consumer, whilst other links have much less, and some links cannot even be depicted sensibly because the flows are trivial (Fig. 3b). One might expect the reduced subset of high-flow links in Fig. 3b to represent those links which are functionally important, but this is clearly not the case, as seen in Fig. 3c. This *functional web* shows those links

Table 1
Selected examples of national projects focusing on marine shallow-water systems under the International Biological Programme umbrella (data from IBP, 1969)

Programme	Location	Scientist responsible
Biology of the interstitial sand bottom fauna of the German North Sea Shore.	Sylt, Heligoland, Germany	P. Ax
Metabolism of the benthic fauna investigated by tracer methods (by radioactive substances).	North Sea, Germany	W. Ernst
Investigations on metabolism at the sea bottom of the German Bight.	North Sea, Germany	S. Gerlach
The relevance of *Corophium* to the return of nutrients from the sediment into the water.	North Sea, Germany	K. Lillelund
Mytilus growth rates, dry matter production, variation in production of different races, transplantation experiments.	Danish fjords, Denmark	B. Muus
Biology and productivity of the brackish water in the Baltic along the coast of Finland.	Baltic coast, Finland	H. Luther
Dynamics of primary and secondary production of plankton and benthos.	Mediterranean, France	
Food-chain, quantitative studies, biomass, and losses of food at different trophic levels.	Dutch Wadden Sea, Netherlands	J.J. Beukema
Benthic algae on intertidal flats.	Dutch Wadden Sea, Netherlands	G.C. Cadee
Food chains from benthic algae to young fish.	Loch Ewe, Scotland, UK	J. H. Steele
Quantitative study of the food relations in an estuarine community.	Ythan estuary, Scotland, UK	G.M. Dunnet
Primary productivity of mangrove swamps and lagoons.	Canaeia, Sao Paulo, Brazil	C. Teixeira
Biological associations.	Mundau lagoon, Brazil	L. Cavalcanti
Productivity in a small marine bay.	St Margarets Bay, Nova Scotia, Canada	L.M. Dickie
Organic production and the marine food chain.	Cochin estuary, India	N.K. Panikkar and S.K. Qasim
Productivity of estuarine, inshore and offshore marine environments.	Panjai, Goa, India	N.K. Panikkar
Comparative ecology of estuaries, lagoons and mangrove swamps.	India	R.V. Seshaiya
Comparative studies on the productivity of fresh water, brackish water and marine lagoon communities.	South India	S. Krishnaswarni
Climate and hydrography of intertidal and shallow-water areas.	Leigh, New Zealand	W.J. Ballantine
Productivity of *Spartina*.	Auckland, New Zealand	V.J. Chapman
Estuarine research, production in tidal pools.	Aransas Refuge, USA	B.J. Van Tries
Surf clam ecology.	USA	R.M. Yancey
Biological reworking of marine sediments.	USA	D.C. Rhoads
Ecology of eelgrass communities.	Aleution Islands, Alaskan Peninsula, USA	C.P. McRoy
Ecological investigations of the flora and fauna of the littoral.	White Sea, USSR	L.A. Zenkerich
Productivity of the high boreal littoral.	Behring and Okhotsk Sea, USSR	O.G. Kusakin

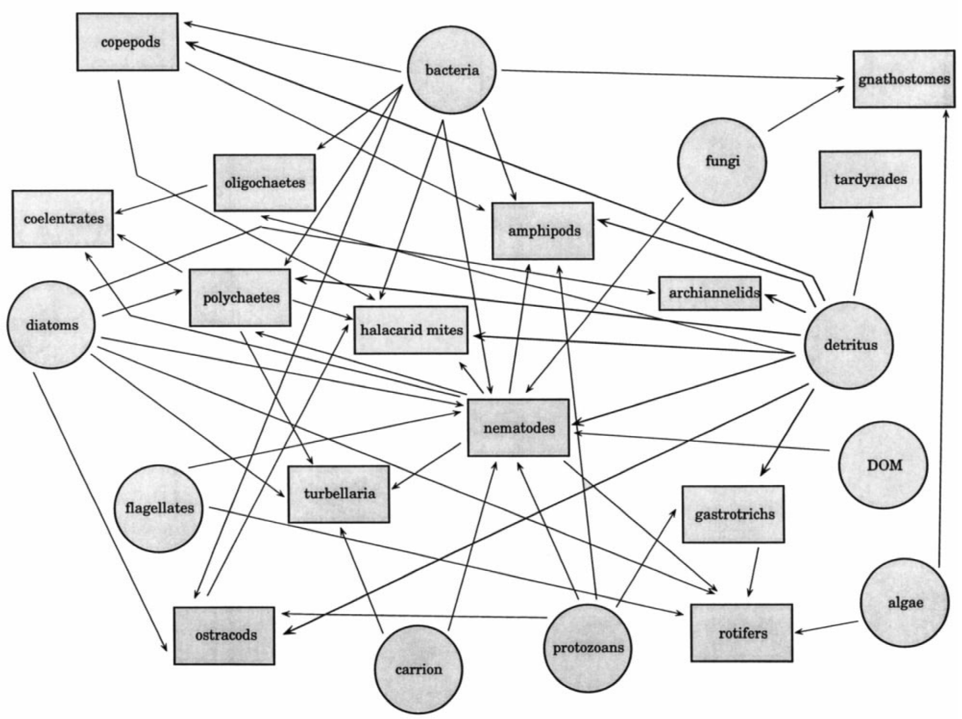

Fig. 2. Trophic interactions within the meiofauna, based on Coull and Bell (1979).

which maintain the web in its normal state. It is in effect an experimental test of the hypothesised important links in Fig. 3b. If these links are disrupted (for example, by excluding or removing the consumer), then the system changes dramatically. Thus removal of the limpet *Acmaea* does not result in any detectable change to this food web, but removal of the urchin *Strongylocentrotus* has a huge impact. In this respect, the most interesting functional link is that between the urchin and the large kelp *Hedophyllum*. Removal of the urchin releases *Hedophyllum* which quickly becomes the dominant seaweed. Yet, a glance at Fig. 3b shows that this link is energetically insignificant, a paradox explained by the inclusion of energetically insignificant sporeling stages of the kelp in the urchin’s diet. Clearly, there is a mismatch between those links considered important in terms of energy flow, and those which are functionally significant. Nowhere is this more evident than in the interactions between pathogens and parasites and their host species. These interactions are often functionally much more significant than traditional predator–prey interactions, yet energy flows are usually trivial (Huxham et al., 1995).

If we are to understand the dynamics of food webs then construction of connectedness webs (*sensu* Paine, 1980), or pursuance of the energy flow approach alone, are unlikely to deliver answers; these approaches are essentially hypothesis-generating tools. There is

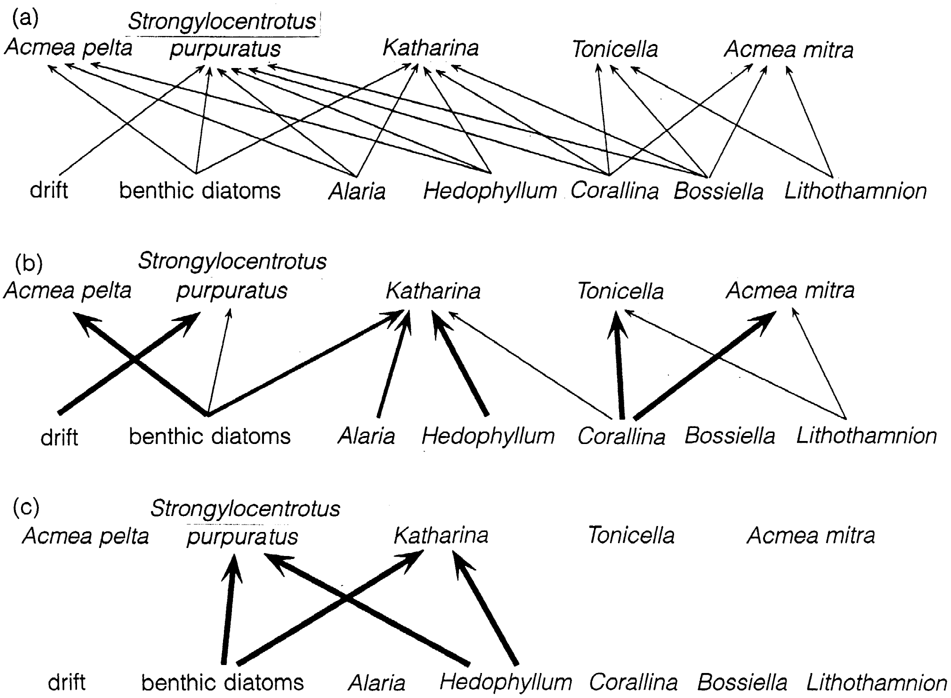

Fig. 3. Three perspectives on a simple rocky shore food web comprising interactions between marine algae and their invertebrate consumers. (a) Connectedness web, showing binary links; (b) energy flow web, where thickness of lines reflects amount of energy channelled; (c) functional web, based on consequences of species removals (after Paine, 1980).

a clear need for experimental testing of hypotheses about which links or pathways are likely to be important.

Experimental approaches to food web dynamics have been spectacularly successful in revealing much about the way marine systems function, and they have formed the basis of paradigms in mainstream community ecology concerning trophic cascades and keystone or critical species. Surprisingly, the experimental approach has not been a conspicuous feature of recent terrestrial food web research, despite its early application to community ecology in the UK and North America (Paine, 1994). The early manipulation experiments by Lodge (1948) on intertidal rocky shores in the Isle of Man illustrated most vividly the power of the experimental approach for clarifying the important role of limpet (*Patella vulgata*) grazers, but it was not until the publication of the dramatic results of manipulations obtained by Connell (1961–3) and Paine (1966) that ecologists began to use the experimental approach in earnest. This was probably because both Paine (1966) and Connell (1961) were able to place their results within mainstream conceptual ecology, (unlike Lodge (1948) — see citation in reference list). From the 1970s onwards, experimental manipulative approaches have become commonplace in marine food web research, but not to the same extent in terrestrial systems. The reasons for this are largely practical, but may also involve cultural differences between terrestrial and aquatic ecologists (Moller and Raffaelli, 1996; Raffaelli and Moller, 2000). Carrying out terrestrial manipulative experiments at the correct spatial and temporal scales with adequate replication is extremely difficult, the organisms of interest often being long-lived, large and, (in the case of predators) with home range sizes of many thousands of square metres. Large-plot, long-term experiments on food webs have been attempted in terrestrial systems but often at the expense of replication. In contrast, marine shallow water benthic systems (including rocky shores) offer tremendous potential for highly replicated, small-scale, short-term manipulative experiments, well within the capabilities and funding cycles within which researchers have to operate (Raffaelli and Moller, 2000).

4. Food web statistics

Over the last 10–15 years, the main thrust of food web research has moved back towards documenting recurrent patterns in the hope that such regularities may infer something about important underlying mechanisms or enable parameterisation or testing of food web models (Cohen et al., 1990). Unlike Elton and Lindeman’s functional grouping approach, the new generation of pattern-seekers — the food web theorists — have generally derived species-based statistics from pictures of webs which have appeared in the published literature. A list of such statistics is shown in Table 2. Most of these statistics can be readily extracted from a food web diagram and over 100 such diagrams can be found in the literature. Analysis of these properties revealed a number of recurrent patterns (Table 3). For example, food chain lengths are typically short (3–4 links), and the frequency of omnivorous species (species which feed at more that one trophic level) is typically small. Whilst many of these patterns are consistent with the assumptions and predictions of conceptual and mathematical models, their significance has been called into question by a number of authors (e.g. Hall and Raffaelli, 1991, 1993, 1996). This is mainly because many of the food web diagrams used are hopelessly inadequate for this kind of analysis (indeed, they were never intended for such analysis

Table 2
Examples of statistics which can be calculated from food web diagrams

Statistic	Definition
Web size	Number of species in web
Linkage density	Number of links divided by number of species
Connectance	Proportion of potential links between species which are realised
Proportions of top intermediate and basal species	Top species have no predators, basal species have no prey, and intermediate species have both predators and prey
Food chain length	Chain length is the number of links along a path running from a basal to a top species
Proportion of omnivores	Species which feed at more than one trophic level

Table 3
Patterns claimed in food web statistics (but see Hall and Raffaelli, 1993, 1996)

The proportions of top, intermediate and basal species are scale-invariant, or constant with web size.
The ratio of predators to prey is constant across food webs.
Linkage density initially thought to be constant but now known to increase with web size.
Connectance declines with web size.
Food chains are typically short (3–4 links).
Omnivory is less common than expected in real webs.

by their authors), but also because of the lack of scientific rigour employed in performing and interpreting the analyses (Hall and Raffaelli, 1993). Nevertheless, some intriguing patterns may remain once (if?) the food web data sets and their analyses can be suitably sanitised.

A particularly intriguing approach in this respect is the emerging use of network analysis to derive functional statistics or properties of food webs, such as ascendancy, system throughput and recycling (Baird and Ulanowicz, 1989, 1993; Ulanowicz, 1996). Unlike the binary (connectedness) webs analysed by food web theorists, network analysis demands relatively high quality, quantitative webs, such that many of the criticisms levelled at food web theory may not apply. However, some of the web properties derived are not easily related to more traditional web metrics and this may slow the recognition and incorporation of this approach into mainstream food web ecology.

5. Food web research in the marine literature

Experimental tests of the putative relationships between these patterns and their underlying dynamic processes is an area where shallow-water marine ecologists have clear and obvious advantages: the systems are easily documented because they contain relatively few species and these species are readily identified, they occur in a structurally simple environment and statistically powerful experiments can be conducted with relative ease (Raffaelli and Hawkins, 1996; Raffaelli and Moller, 2000). Yet with a few exceptions, such as the relationship between food web infrastructure (compartments) and strong predator–prey links (Paine, 1980; Raffaelli and Hall, 1992), this potential has not been realised. I find this surprising, but it may simply reflect the dominance of food web research by terrestrial ecologists, for whom the experimental approach is less tractable (Raffaelli and Moller, 2000). In fact, many of those who do work on the dynamics of marine shallow-water food webs have a terrestrial ecology background or approach their science from a conceptual ecology rather than marine biological perspective. This is reflected by the occurrence of food web papers in learned journals. Using the keyword ‘food web’, I searched the BIDS database from 1981 to 1999 and recorded 1397 hits (at time of writing). Adding the keyword ‘marine’ reduced the tally to only 39 hits, split between 16 journals, the largest proportion (9) coming from *Marine Ecology-Progress Series*. In contrast, the journal *Ecology* alone provided 59 hits for ‘food webs’. It is clear that most researchers on food webs do not publish in marine biology journals. Those few groups working on shallow-water food webs tend to publish in more general ecological journals, such as *Ecology*, *Ecological Monographs*, *Oecologia*, *Oikos*, *Journal of Animal Ecology*, *Nature* and *Science*, rather than marine biology journals. Not surprisingly, inspection of the contents indices of JEMBE from Volume 1 to 210 (1997) revealed only a handful of papers dealing with food webs.

The reason for the apparent under-representation of food web papers in marine journals is probably due to a combination of factors. There are relatively few marine ecologists whose research is driven by mainstream ecological theory and those researchers probably see their work as having applications for ecology in general, rather than the marine environment. Related to this is the desired target audience, which may be other ecologists rather than marine biologists. In addition, the impact factor of most marine journals is relatively low. At the time of writing the impact factor for *Journal of Experimental Marine Biology and Ecology* was 1.35 and the marine journal with the highest impact factor, *Marine Ecology-Progress Series,* was 2.04. Regardless of the problems of interpreting and using impact factors, the pressures from funding agencies and peer assessment tend to promote targeting of journals with a high impact factor (i.e. non-marine). Given all of these factors, it seems likely that ecologists working on shallow water food webs will continue to publish in ecological journals and that food web research will remain under represented in the marine literature. [RW]

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