6.01 Introduction to Food Webs in Coastal and Estuarine Ecosystems

JG Wilson, Trinity College Dublin, Dublin, Republic of Ireland
JJ Luczkovich, East Carolina University, Greenville, NC, USA

Abstract

This introduction covers the main components of coastal and estuarine food webs along with the selected examples of such systems. The food web is instrumental in the structuring of the system and the pathways for the transfer of energy provide the routes along which other substances, including contaminants, are passed. The contributions emphasise not just the functional roles in the system and their importance, but also the problems faced, particularly in terms of anthropogenic pressures. An understanding of how these systems work is vital for sustainable development.

6.01.1 Introduction

Food has been one of the major drivers of human interaction with coastal and estuarine ecosystems, and this has impelled much of the study of these systems. In its initial phase, greater understanding would have brought direct payoffs in the form of greater catches and, now, greater understanding is necessary to not just to counter past mistakes (such as overexploitation, habitat loss, and pollution) but also future pressures (such as climate change). The key change has been in the recognition that the oceans were not an infinite resource, and that sustainability of the resources was the key not only regarding commercial returns, but also in terms of socioeconomic stability of the human populations. As a result, scientific investigations in the cause of exploitation of the fisheries' resources, for example, has progressed from a simple goal of maximizing the catches through one where long-term yields (e.g., MSY or maximum sustainable yield) of single species were the required model outputs to the present situation in which the sustainability of the ecosystem itself is the overriding goal.

Along with this has come the realization that such exploitation may cause a number of unintended changes in the ecosystem, including the removal of nontarget species ('by-catch'), physical disturbance of the sea bottom (dredges and trawling) and other anthropogenic impacts, such as the introduction of contaminants and physical modification of the system through port facilities and land reclamation. The recent rise in aquaculture has lessened some of the impacts (by, e.g., substituting farmed catch for wild) but also introduced others, most notably through the introduction of invasive species (including parasites and diseases) and through the taking of 'waste' fish from coastal systems as food for the farmed finfish and has also changed the ecological and genetic balance of species (most notably, salmon) by the sheer volume produced in the farms. These topics are explored at more length in Volume 8 of this treatise.

This widening of appreciation of the impacts of the harvesting of food resources has coincided with a greater appreciation of the value of the 'natural goods and services' of the system. In this regard, the seminal work of Costanza et al. (see Volume 12) not only drew attention to the global contribution (and economic value) of these services, but also highlighted the value of coastal and estuarine ecosystems and wetlands which, per unit area, were the most valuable of the global systems with coral reefs not far behind, and both higher than, for example, tropical rainforest.

As a result of these recent advances in understanding, we know now that no single component can be considered or treated in isolation, and that changes in one part of the system may have unintended, and indeed unexpected, consequences in another. Clearly, the better we understand the system, and especially the nature of the connections between components, the better the chance we have of rational and sustainable management.

In this volume, what we have tried to do is to set out the major compartments in coastal and estuarine systems, to describe their functioning and to show both their drivers and their limiting factors. We have done this by considering the structuring of coastal and estuarine food webs: what sustains the productivity of the system as energy inputs, and how (and whence) the energy is transformed and passed to higher trophic levels.

This structuring serves a number of functions. First, it is a familiar image of a system, one which is process-based and one for which considerable information, albeit perhaps still rather scattered and patchy in distribution, is available. Second, trophic structuring reflects not just the transfer of energy through the system, and of course is directly relevant to food resources, but also provides pathways through which other materials, such as nutrients and contaminants, can be transferred, accumulated (sinks), or released (sources) throughout the system. Finally, the trophic structuring approach highlights the important role of top consumers in the system, in which they may play the role of 'key' or 'keystone' species, such that although relatively few in number, their presence (or absence!) determines the balance and functioning of the system as a whole. In addition, many of the top consumers in the system have, from a management perspective, considerable public visibility and sentiment, not to mention commercial implications – think of the numbers of bird watchers, for example, or the money spent annually by sports anglers in the pursuit of fish, such as large-mouth bass.

6.01.2 Food Webs in Coastal and Estuarine Ecosystems

At the foot of the food chain (*see* Chapter 6.02) is the detritus, which Wikipedia defines as "non-living particulate organic material (as opposed to dissolved organic material (DOM)). It typically includes the bodies or fragments of dead organisms as well as fecal material." As thus defined, it is particulate in form, that is as particulate organic matter (POM), but a considerable portion of the OM in the system may also be present in dissolved form (DOM). Although also the definition specifically excludes living matter, detritus does of course also include the microorganisms that decompose it, during which nutrients such as N and P are remineralized and other elements and components made available again. Wood's (1965) classic text indeed questioned whether there were enough bacteria in the sea to carry out all the transformations attributed to them! Contrast this with the reports from Ventner et al. (2004) which, in what was little more than an exploratory study in the Sargasso Sea, described 1.2 million new genetic sequences, and suggested that there is a much greater microbial diversity and that the microorganisms play a greater role than previously suspected. DOM can be allochthonous in origin (brought down in rivers, e.g., or released from waste-treatment plants), but of course includes exudates and mucus from both plants and animals in the system. DOM is a major substrate for microbial degradation, but many studies have shown that invertebrates also have the ability to take up DOM, often against the concentration gradient. However, both the uptake and the release of DOM is ignored or treated cursorily in many trophic studies, but the same cannot be said of POM, whose consumption from the water column by suspensivores or from the sediment by deposivores underpins many coastal systems.

Mixed in with the POM thus consumed are not only the decomposer organisms, such as bacteria and fungi, but also the unicellular primary producers, the phytoplankton and microphytobenthos in the water column and in the sediments, respectively (*see* Chapter 6.03). This compartment constitutes one of the primary differences with terrestrial systems, in that the bulk of primary production in some systems may be contributed by the smallest (individual) size fractions, which because of their small size, may have been ignored, or more properly underestimated, until relatively recently. Perhaps the most telling difference with terrestrial systems is that these primary producers do not physically structure the system. Nevertheless, they have influence beyond that of simply fixing C and providing the basis, through direct consumption, for much of the higher-level productivity. An excess, as with any other compartment, can unbalance and disrupt the ecosystem, and those phytoplankton that produce toxins (commonly referred to as harmful algal blooms or HABs) can induce a variety of impacts, up to and including death, in higher consumers (including humans). On the positive side, the extracelluar polymeric substances (EPSs) produced by microphytobenthos stabilize sediments against erosion and provide a valuable defense against the loss of valuable mudflat and wetlands.

The fringing vegetation, salt marshes (Chapter 6.11), and mangroves (Chapters 6.04 and 6.12) are major contributors of production into coastal and estuarine systems, and in addition play an important role as buffer zones between the land and the sea. In the former role, their position on the fringes means that relatively little of the production is consumed directly, but their input through detritus and decomposition (*see* Chapter 6.02) dominates many systems. As the latter, not only do they buffer the land from the effects of the ocean, but they also buffer oceanic systems from land influence, in particular the outflow of freshwater and the transport of river-borne sediments, both of which can be extremely harmful to corals. They also impart physical structuring to the systems, with the mangroves in particular offering a complexity of habitat through their root systems, not to mention the aerial component of trunks and branches. Salt-marsh plants are smaller, and in the case of European salt marshes, are composed of smaller species (than in the USA) restricted to much higher on the shore, so there is a lesser degree of modification. Nevertheless, both salt marsh and mangrove are amongst the most valuable of systems in terms of ecological goods and service (Volume 12), which range far beyond their value as primary producers.

The copepods (*see* Chapter 6.05) are the main grazers in the water column in coastal and estuarine systems, and in turn provide food items for those further up the food chain, particularly the gelatinous zooplankton (*see* Chapter 6.06) and the fish. It is through the latter link that the copepods have served as models for the primary consumers linkage in coastal ecosystems, going back to the preacoustic days when an experienced fishing skipper could tell from the color of the water (color due to the density of copepods) was worth shooting the nets in that location. They have also taken on another importance as signals of climate change, in that the various (often closely related) species serve as sensitive indicators of different water masses. Other primary consumers in the planktonic system can be equally as important as the copepods, but they do not exert such a universal influence throughout the system. In terms of system function, the major difference between this group and the copepods has less to do with their feeding, as they too consume phytoplankton (and suspended particulate matter (SPM)), but they can be selectively taken by the higher consumers, with some fish showing strong preferences for larger (and more energy-rewarding) forms.

The gelatinous zooplankton (*see* Chapter 6.06) has sprung to prominence in the past few decades, not least because of their invasion of complete systems such as the Black Sea. In particular, there have been strong suggestions that their prominence, indeed dominance in some systems, indicates a phase shift in the ecosystem, in which the ecological control has shifted into a new, and different, pattern. In turn, this shift has been linked to pressures on the system, pressures linked to human activity either directly in the case of fishing, where the removal of other predators has left vacant niches for the gelatinous zooplankton to exploit, or indirectly through eutrophication or climate change altering the bottom-up control.

The meiofauna (*see* Chapter 6.07) represent a compartment traditionally regarded as somewhat specialized, and one which, until relatively recently had been studied rather in isolation than as integral components in full ecosystem studies. There has been less emphasis on internal structuring, partly due to a difficult taxonomy, although the latter is also rapidly changing with the advent of molecular and genetic probes. Despite this, the meiofauna have had a long history of taxonomic studies – not least because of the size- and taxonomic overlap with macrobenthos – which, based on morphological characteristics, facilitated trophic conclusions founded on the structure of the mouthparts. Their roles in the system and particularly their trophic contribution through high productivity and turnover have long been set out in a number, admittedly somewhat limited, of studies. However, their actual prey items had been largely a matter of conjecture, save for those species which had, for example, diatom frustules in the gut, and it is only recently that the advent of stable isotope analysis (SIA) has allowed a much clearer picture of their food sources and their position in the trophic chain.

The fish (*see* Chapter 6.08) are, in the public mind at least, at the focus (if not the apex) of the coastal food web. This preoccupation has had two, rather contradictory, consequences. The first is that, compared to some of the other compartments, there is a plentiful amount of information about fish, from their feeding habits, their environmental tolerances and preferences, their biomass, production, reproduction, and survival to detailed process models for food consumption and assimilation efficiency. This enables their role in the coastal ecosystem to be set out with rather less uncertainty than for most other groups. The second consequence has been that commercial fishing especially has been treated almost in isolation from the system that supports it, with, for example, the seas being regarded as an inexhaustible resource for which the only control necessary was one relating solely (pun intended) to the species in question. Fortunately, this view is changing, and not only are we seeing ecosystem sustainability being brought to the forefront for consideration in fisheries policy, but we have also become very aware of the other changes (e.g., bycatch and physical disturbance) that the pursuit of fish has brought in its wake. Fish feed at many levels in the trophic system, providing food in their turn for higher consumers (including humans) and effect on coastal ecosystems of the removal of its top predators is starting now to be investigated.

By contrast, there has been comparatively little in the way of the role of some of the other vertebrates in the system, such as the amphibians or marine reptiles (*see* Chapter 6.09). There is no doubt that in previous times they were even larger and more formidable carnivores than the present day, and their impact or degree of control of the system can only be guessed at. Today, however, many species are threatened: the International Union for Conservation of Nature (IUCN) Red Data Book lists seven coastal/estuarine turtle species as ranging from critically endangered to vulnerable as are some crocodile species such as the American crocodile (*Crocodylus acutus*), which only in the past 20 years or so has progressed from endangered to vulnerable. Marine amphibians are rare because of the osmotic gradient, but the reptiles feed at the bottom and at the top of the trophic chain. The marine iguana (*Amblyrhynchus cristatus*), which feeds on seaweeds, is listed as vulnerable, not only because of its restricted distribution (Galapagos islands only) but also because the population has been shown to be significantly affected by El Nino episodes, and future climate change may exert greater pressures. The great majority are predators, such as the loggerhead (*Careta careta*), which has powerful jaws, and feeds on a variety of benthic prey, whereas the leatherback (*Dermochelys coriacea*) appears to subsist largely on jellyfish, and the latter species' decline has been suggested to be a contributing cause to the increase in some forms of gelatinous macroplankton (*see* Chapter 6.06). The crocodiles are active predators of fish, and also of terrestrial prey, which strictly speaking is outside the remit of this chapter, but increases their importance in public perception, as does the venom of the sea snakes.

The remaining chapters (Chapters 6.10, 6.11, 6.12, and 6.13) in this volume cover the entire food-web studies in selected habitats. These are intended as examples or case studies, to show how the various compartments, considered in more detail in the preceding chapters, are interlinked and to put their individual contributions into the context of the system as a whole. It has been structured by habitat, as this is often the primary discriminant: see, for example, the European University Information system (EUNIS) classification of biotopes and to try to draw out some general characteristics and principles for shallow coastal ecosystems.

Four habitats are considered. The first, sandy coastal ecosystems (*see* Chapter 6.10) is structured by the grain size of the sediment, while both salt-marsh systems (*see* Chapter 6.11) and mangroves systems (*see* Chapter 6.12) are not only physically structured by the respective primary producers, as are oyster reef and mussel bed systems (*see* Chapter 6.13) by primary consumers, but also owe their trophic structuring to the overwhelming influence of these compartments.

In comparison to the other systems, coastal sandy ecosystems (*see* Chapter 6.10) are often typified by a low biomass of both producers and consumers, with the structuring displaying many of the characteristics of an immature system – external subsidy, open cycles, and small individual body size. The other systems have much higher biomass, although for the oyster/mussel systems this high biomass is confined to the consumer levels. Again, there is some level of external subsidy to them all, and Heip et al. (1995) in their review considered that estuaries as a whole had a tendency to be heterotrophic systems. Both mangrove and salt-marsh systems have a primary production greatly in excess of the herbivorous components on their respective systems, and the remainder, in excess of that which cannot be recycled within the system via the decomposers, is exported. This export effectively subsidizes the neighboring waters, leading Odum (1980) to put forward his 'outwelling' hypothesis (but see also Odum (2002)).

6.01.3 Conclusions

One of the salient points to come out of these chapters is the degree of similarity among the systems in the various habitats, in that, on a purely conceptual, nonquantitative level, all could be fitted into a simple food-chain, and even food-web model. From that starting point, there are the subtle differences in bottom-up (inputs) and top-down controls (e.g., trophic cascades), which give each its distinctive character. In fact, there is a good case to be made that there can be more difference between two systems within the same habitat category than between two from different habitats. It all depends on the controls in the system, and this is where lies a major challenge for future research: until there is sufficient understanding as to how estuarine and shallow coastal systems respond to environmental and anthropogenic pressures, their preservation, let alone their sustainability and not to mention sustainable development, may be a dangerous lottery.

We are planning future editions of the treatise and will take the opportunity to fill any gaps, which are identified in the present edition. We invite readers to help us identify any additions for future editions.

References

Heip, C., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology Annual Review 33, 1–149.

Odum, E.P., 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling and detritus-based food chains. In: Kennedy, V. (Ed.), Estuarine perspectives. Academic Press, New York, pp. 485–495.

Odum, E.P., 2002. Tidal marshes as outwelling/pulsing systems. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology, Part 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 3–7.

Ventner, C., Remington, K., Heidelberg, J.F., Halpern, A.L., Rusch, D., Eisen, J.A., Wu, D., Paulsen, I., Nelson, K.E., Nelson, W., Fouts, D., Levy, S., Knap, L., Lomas, M.W., Nealson, K., White, O., Petersen, J., Hoffman, J., Parsons, R., Baden-Tillson, H., Pfannkoch, C., Rogers, Y.-H., Smith, H.O., 2004. Environmental genome shotgun sequencing of the Sargasso Sea. Science 304 (5667), 66–74.

Wood, E.J.F., 1965. Marine Microbial Ecology. Chapman and Hall, London, 243 pp.

Relevant Websites

http://www.//eunis.eea.europa.eu – The European Environment Agency: EUNIS habitat types.