Food webs and the transmission of parasites to marine fish

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SUMMARY

Helminth parasites of fish in marine systems are often considered to be generalists, lacking host specificity for both intermediate and definitive hosts. In addition, many parasites in marine waters possess life cycles consisting of long-lived larval stages residing in intermediate and paratenic hosts. These properties are believed to be adaptations to the long food chains and the low densities of organisms distributed over broad spatial scales that are characteristic of open marine systems. Moreover, such properties are predicted to lead to the homogenization of parasite communities among fish species. Yet, these communities can be relatively distinct among marine fishes. For benthos, the heterogeneous horizontal distribution of invertebrates and fish with respect to sediment quality and water depth contributes to the formation of distinct parasite communities. Similarly, for the pelagic realm, vertical partitioning of animals with depth will lead to the segregation of parasites among fish hosts. Within each habitat, resource partitioning in terms of dietary preferences of fish further contributes to the establishment of distinct parasite assemblages. Parasite distributions are predicted to be superimposed on distributional patterns of free-living animals that participate as hosts in parasite life cycles. The purpose of this review is first, to summarize distribution patterns of invertebrates and fish in the marine environment and relate these patterns to helminth transmission. Second, patterns of transmission in marine systems are interpreted in the context of food web structure. Consideration of the structure and dynamics of food webs permits predictions about the distribution and abundance of parasites. Lastly, parasites that influence food web structure by regulating the abundance of dominant host species are briefly considered in addition to the effects of pollution and exploitation on food webs and parasite transmission.

Key words: Marine, transmission, food webs, parasites, fish, zooplankton, benthos.

INTRODUCTION

The marine environment has more higher taxa and twice the number of phyla than tropical rainforests (Suchanek, 1994). Of the 32 phyla occurring in the oceans, 21 are exclusively marine, of which 10 are endemic to the benthos and 1 to the pelagic realm (May, 1994). Generally, species diversity increases along a gradient from boreal estuaries, through boreal shallow marine, with tropical shallow marine and deep-sea benthos being the most diverse (Hessler & Sanders, 1967; Sanders, 1968). Temperate coastal marine communities are among the most productive and diverse ecosystems on earth (Suchanek, 1994) and inshore and shelf habitats possess the most species on a large geographic scale (May, 1994). Species diversity in the deep sea alone may resemble that of tropical rainforests, though most species are rare (Snelgrove & Grassle, 1995). These organisms are integrated together into complex food webs of long average chain lengths (Schoener, 1989). Helminth parasites track these food web interactions in order to propagate and maintain themselves in the marine milieu (Marcogliese & Cone, 1997). The unique fauna found in the oceans, conceivably, should provide new pathways on which parasites may capitalise within food webs, ultimately facilitating parasite diversification.

Numerous characteristics of parasites in marine systems appear at first glance to homogenize their distributions among hosts, leading to undifferentiated communities within regions. Parasites of marine fish tend to be generalists for both intermediate and definitive hosts (Polyanski, 1961; Holmes, 1990); this may be an adaptation to spread the risk among hosts to ensure transmission in a dilute environment (Bush, 1990). Marine parasites tend to be long lived (Campbell, 1983) and many marine parasites indiscriminantly infect paratenic and transport hosts, also possibly as an adaptation to the longer food chains and dilute oceanic environment (Marcogliese, 1995). Among hosts, marine vertebrates tend to be large, extremely vagile and gregarious, with generalized broad diets. This generalized feeding mechanism allows for prey switching and dietary overlap, creating a highly diversified diet in comparison with terrestrial environments. Fish spawning migrations can further obliterate the local character of parasite faunas (Polyanski, 1961). All these factors together would theoretically lead to the homogenization of parasite communities among host species.

Yet, parasite communities differ substantially among fish hosts, even in the same geographic area. The abundant evidence that parasites can be employed as indicators of fish stocks or populations (Williams, MacKenzie & McCarthy, 1992; Arthur, 1997) demonstrates the variability of the marine parasite fauna among host species. Fish and inverte-

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Table 1. Some examples of intermediate hosts of benthically-transmitted parasites in the marine environment. Examples were chosen to represent different trophically-transmitted pathways used by parasites and a diversity of invertebrate intermediate hosts. Where possible, general sources were used as references. Only parasites that require ingestion of intermediate hosts by definitive hosts are included

Parasite	Definitive host	1st intermediate host	2nd host	Reference
Digenea				
Aporocotyle simplex	Flatfishes	Gastropods	Polychaetes	Williams & Jones (1994)
Cryptocotyle lingua	Gulls	Gastropods (*Littorina littorea*)	Teleosts	Køie (1983)
Curtuteria australis	Oystercatchers	Gastropods	Bivalves (*Austrovenus stutchburyi*)	Poulin, Hecker & Thomas (1998)
Derogenes varicus	Teleosts	Gastropods (*Natica* spp.)	Harpacticoid copepods, decapods	Williams & Jones (1994)
Fellodistomum fellis	Wolffish (*Anarhichas lupus*)	Bivalves (*Nucula tenuis*), brittle stars (*Ophiura* spp.)	—	Williams & Jones (1994)
Lecithochirium furcolabiatum	Blennies, gobies	Gastropods (*Gibbula ambilicalis*)	Harpacticoids (*Tigriopus brevicornis*)	Williams & Jones (1994)
Lepidapedon elongatum	Gadids (*Gadus morhua*)	Gastropods (*Onoba aculeus*)	Polychaetes, molluscs	Køie (1985)
Maritrema subdolum	Shorebirds	Gastropods (*Hydrobia* spp.)	Amphipods, isopods, crabs	Kostadinova & Gibson (1994), Gollasch & Zander (1995)
Microphallus pygmaeus	Gulls, eider ducks	Gastropods (*Littorina littorea*)	—	Granovitch & Johannesson (2000)
Microphallus similis	Gulls	Gastropods (*Littorina* spp.)	Shore crab (*Carcinus maenas*)	Granovitch & Johannesson (2000)
Podocotyle reflexa	Teleosts (gadids)	Gastropods (*Buccinum undatum*)	Shrimps (*Crangon crangon*, *Pandalus* spp.), mysids	Williams & Jones (1994)
Proctoeces maculatus	Labrid and sparid fishes	Bivalves (*Mytilus* spp.)	Polychaetes, sea urchins, gastropods, octopods	Williams & Jones (1994)
Ptychogonimus megastomus	Sharks	Scaphopod molluscs (*Antalis* spp.)	Crabs	Williams & Jones (1994)
Renicola roscovita	Gulls	Gastropods (*Littorina* spp.)	Bivalves (*Mytilus* spp.)	Granovitch & Johannesson (2000)
Stephanostomum baccatum	Cottids	Gastropods (*Buccinum undatum*, *Neptunea* spp.)	Flatfishes	Køie (1983)
Zoogonoides viviparus	Flatfishes	Gastropods (*Buccinum undatum*)	Brittle stars (*Ophiura* spp.), plus polychaetes, bivalves, gastropods	Williams & Jones (1994)

Cestoda				
Acanthobothrium hispidum	Elasmobranchs	Harpacticoids (*Tigriopus fulvus*)	Teleosts, cephalopods	Williams & Jones (1994)
Bothrimonus sturionis	Teleosts	Gammarid amphipods	—	Williams & Jones (1994)
Grillotia erinaceus	Leopard shark (*Triakis semifasciata*)	Harpacticoids (*Tigriopus californicus*)	—	Williams & Jones (1994)
Lacistorhynchus tenuis	Leopard shark (*Triakis semifasciata*)	Harpacticoids (*Tigriopus californicus*)	—	Williams & Jones (1994)
Nematoda				
Ascarophis morhua	Gadids	Crabs (*Carcinus maenas*), hermit crabs (*Pagurus* spp.)	—	Williams & Jones (1994)
Contracaecum spiculigerum	Cormorants, pelicans	Harpacticoids (*Tigriopus californicus*)	Teleosts	Anderson (1992)
Cucullanus cirratus	Gadids	Gobies, cod fry	—	Køie (2000*a*)
Cucullanus heterochronus	Flatfishes	Polychaetes (*Nereis diversicolor*)	—	Køie (2000*b*)
Hysterothylacium aduncum	Teleosts	Various crustaceans, polychaetes	Many invertebrates and fish	Williams & Jones (1994)
Paracuaria adunca	Piscivorous birds	Amphipods, mysids	Teleosts	Jackson *et al*. (1997)
Pseudanisakis rotunda	Elasmobranchs (*Raja radiata*)	Decapods (*Lithodes* sp.)	Flatfishes, gadids	Williams & Jones (1994)
Pseudoterranova decipiens	Pinnipeds	Harpacticoids, amphipods	Crustaceans, polychaetes, teleosts	Anderson (1992)
Sulcascaris sulcata	Marine turtles	Scallops, gastropods	—	Anderson (1992)
Acanthocephalans				
Corynosoma spp.	Pinnipeds	Amphipods	Teleosts	Valtonen & Niinimaa (1983), Zdzitowiecki (2001)
Echinorhynchus gadi	Teleosts	Gammarid and caprellid amphipods	—	Schmidt (1985)
Echinorhynchus lagenformis	Flatfish (*Platichthyes stellatus*)	Amphipods (*Corophium spinicorne*)	—	Schmidt (1985)
Profilicollis botulus	Eider ducks	Crabs (*Hyas araneus*) hermit crabs (*Pagurus pubescens*)	—	Uspenskaja (1960)

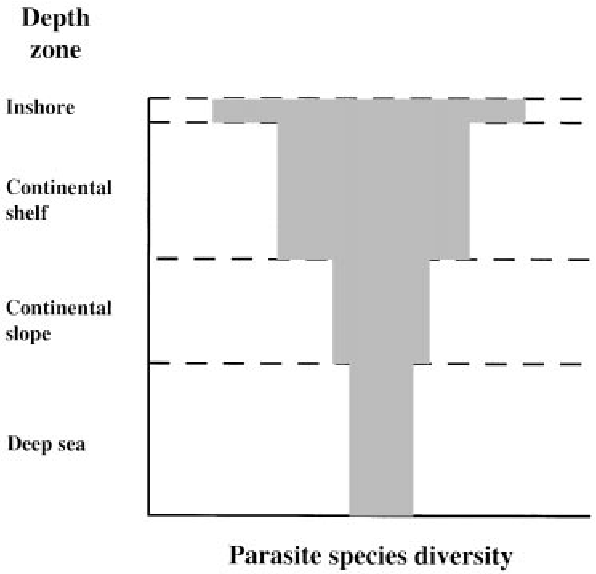

Fig. 1. Theoretical schematic representing relative species diversity of parasites of demersal fish inhabiting different depth zones ranging from inshore to the deep sea. Species diversity decreases with increasing depth.

brates partition the physical habitat and prey resources in space and time. Resource partitioning contributes to the formation of distinct parasite assemblages among host species. Herein, I evaluate patterns of transmission of trophically-transmitted helminth parasites and discuss the relationship with spatial variations in oceanographic conditions that lead to the formation of distinct animal communities. The various roles of community members in the local food web contribute to the development of distinct parasite faunas in marine organisms. Emphasis is placed on research completed in waters off northeastern North America, although other sources are used when pertinent. Lastly, I briefly consider effects of pollution, exploitation and the potential role of keystone parasites on food webs and parasite transmission.

BENTHIC PATTERNS OF DISTRIBUTION

Free-living animals

Marine organisms display horizontal gradients in their patterns of distribution. Proceeding offshore, the composition of the benthic macroinvertebrate fauna (organisms retained by a 500 μm sieve) changes with salinity, substrate, temperature and depth (McLusky & McIntyre, 1988). Particle size diversity of the sediments is a measure of habitat complexity and generally reflects species diversity, with coarse heterogenous sands being more species rich than well-sorted homogenous substrates (Gray, 1974). Continental shelves tend to be impoverished, but slope waters possess high diversity with marked faunal changes at 100–300 m (Sanders, 1968). While community composition is related somewhat to sediment composition, it is also mediated by interactions between organisms and sediments (Gray, 1974).

Numerous studies document the relationship between substrate texture and quality, depth and the type of benthic community that occurs in Atlantic waters off North America (Wigley & McIntyre, 1964; Day, Field & Montgomery, 1971; Maurer & Wigley, 1984; Sherman *et al*. 1988; Weston, 1988), Europe (Basford, Eleftheriou & Raffaeilli, 1989; Eleftheriou & Basford, 1989; Flach & Thomsen, 1998) and elsewhere (Field, 1970). The dominant taxa are often polychaetes or, occasionally, crustaceans. Bivalves and echinoderms are also common on continental shelves and slope waters. Different taxa occur on particular sediment types and their distribution and relative dominance with depth varies accordingly. Species richness of epifaunal organisms, or those living on the sediment surface, tends to be highest on gravel, while infaunal organisms (or those living in the sediments) are most numerous on muddy or silty sand (Rhoads & Young, 1970; Gray, 1974; Eleftheriou & Basford, 1989).

Within the meiofauna (organisms passing through a 500 μm sieve but retained on a 45 μm sieve), nematodes are the most common organisms, with harpacticoid copepods ranking second in most systems (Coull, 1970). Like benthic macrofauna, the composition of copepods and other meiofauna varies with substrate texture and grain size (Coull, 1970). Off northeastern North America, density and diversity of both macro- and meiobenthic organisms decrease with depth (Wigley & McIntyre, 1964; Sherman *et al*. 1988).

Thus, based on the spatial distribution of both meiofauna and macrofauna, we can expect the parasites transmitted in a habitat to vary with substrate texture and depth according to their life histories and benthic invertebrate species composition.

Parasites

Benthic invertebrates act as intermediate hosts for digeneans, nematodes, acanthocephalans and, to a lesser extent, cestodes. Crustaceans are the most common intermediate hosts in parasite life cycles, but it must be noted that digeneans require molluscs as obligate first intermediate hosts. Polychaetes and echinoderms participate in a limited number of helminth life cycles. A summary of life cycle patterns and types of intermediate hosts for parasites infecting benthic marine invertebrates is found in Table 1.

Horizontal variations in abiotic parameters and the biota are important in determining the distribution of parasites. A wider range of intermediate hosts occurs in shallow waters. Flatfish, for example, inhabiting deeper waters have fewer parasites than those species in shallow waters (Scott & Bray, 1989; Lile, 1998). Variation among local habitats also affects parasite species composition (Polyanski, 1961; Thoney, 1991). Thus, it can be expected that the variation in spatial distribution of the different benthic invertebrate taxa will reflect the distribution of parasites that use them as intermediate hosts.

For instance, Campbell, Haedrich & Munroe (1980) examined 52 deep-sea benthic fishes at depths from 50–5000 m off the New York Bight. The species composition of their parasite fauna reflect dietary differences. The abundance and prevalence of parasites with complex life cycles depend directly on the abundance of free-living fauna, and parasite species richness declines with depth (Fig. 1) (Campbell *et al*. 1980; Campbell, 1983). The parasite fauna in certain benthic fish suggest that prey fish migrate from midwater to the bottom, implying that some parasites pass between habitats or communities as they complete their life cycles (Fig. 2).

Perhaps the most extensive examination of marine parasitic fauna ever undertaken is the benthic survey of Uspenskaja (1960) in the Barents Sea from 1949–54. A total of 10 species of digenean, 6 cestodes, 6 nematodes and 2 acanthocephalans, all larval forms, were found in 31 species of crustaceans. Similarly, Gollasch & Zander (1995) examined for helminths over 36000 crustaceans from the Schlei fjord in the Baltic Sea, in which were found 4 digenean, 1 cestode, 1 nematode and 1 acanthocephalan species. These studies illustrate the complex web of parasite transmission that occurs through the crustaceans alone in benthic communities.

PELAGIC PATTERNS OF DISTRIBUTION

Free-living animals

In the open ocean, the water column is divided into the epipelagic zone, the mesopelagic zone below the thermocline between 200–1000 m, and the bathypelagic zone below 1000 m (Madin & Madin, 1995). The bathypelagic zone comprises 88% of the total global oceanic area, and is characterized by the absence of light and a constant temperature of 4 °C. Its inhabitants tend to display different, sluggish lifestyles compared to other pelagic animals. While a few species are common, over 80% are considered rare (Madin & Madin, 1995).

Within the pelagic zone, zooplankton consist of primarily calanoid copepods, but also other crustaceans including euphausiids, cyclopoid copepods and hyperiid amphipods. Soft-bodied zooplankters are typically predators on other zooplankton and fish larvae, and include chaetognaths, coelenterates and ctenophores (Marcogliese, 1995).

The bottom waters 1 m above the sediments are referred to as the hyperbenthos (or suprabenthos or nektobenthos) (Hamerlynck & Mees, 1991). This fauna has often been neglected because of the difficulty of quantitative sampling (Hamerlynck & Mees, 1991). Its main constituents are decapod larvae, mysids and other crustaceans, fish eggs and larvae, but also include amphipods, isopods and chaetognaths (Hamerlynck & Mees, 1991; Mees, DeWicke & Hamerlynck, 1993). Bottom waters and the sediment surface also are termed the benthic boundary layer (Wildish, Wilson & Frost, 1992). Within this layer, organisms segregate vertically by depth, with densities increasing towards the bottom (Oug, 1977; Chevrier, Brunel & Wildish, 1991). Mysids, amphipods, isopods and chaetognaths are found year-round in the hyperbenthos, with mysids the most abundant (Mees *et al*. 1993). These organisms are an important source of nutrition for fish and this has important ramifications for parasite transmission.

Certain benthic organisms such as harpacticoid copepods, amphipods and cumaceans as well as planktonic copepods migrate in abundance into the hyperbenthos at night (Oug, 1977; Sibert, 1981; Kaartvedt, 1986; Chevrier *et al*. 1991). In addition, mysids can migrate into the zooplankton. These vertical movements create trophic linkages between zones and opportunities for parasites to traverse habitats (Fig. 2).

In addition, surface and subsurface habitats are linked. Epifaunal predation on infaunal organisms is more important than infaunal predation (Virnstein, 1977; Ambrose, 1991), though polychaetes are common infaunal predators in many systems (Wilson, 1991). Benthic copepods dominate the diets of predators, especially juvenile fishes, even though they comprise only 2–20% of meiofauna (Virnstein, 1977; Coull, 1990). Mysids such as *Neomysis integer* also consume meiobenthos, in particular harpacticoid copepods (Johnston & Lasenby, 1982). Thus, the benthic boundary layer provides ample opportunities for pelagic-benthic coupling and cycling of parasites (Fig. 2).

Parasites

Transmission of parasites from zooplankton to fish was reviewed by Marcogliese (1995). Diversity of helminths using zooplankton as intermediate hosts is relatively high in marine systems, mainly due to the presence of hemiuroid, lepocreadoid and didymozooid trematodes, in addition to trypanorhynch and tetraphyllidean cestodes (Marcogliese, 1995). However, infection rates are extremely low owing to the dilute nature of the pelagic realm. The addition of an extra trophic level of planktonic predators and the capacity of many marine helminths to use organisms as paratenic hosts serves to promote transmission and maintain parasites in the environment even at low densities (Marcogliese, 1995). For

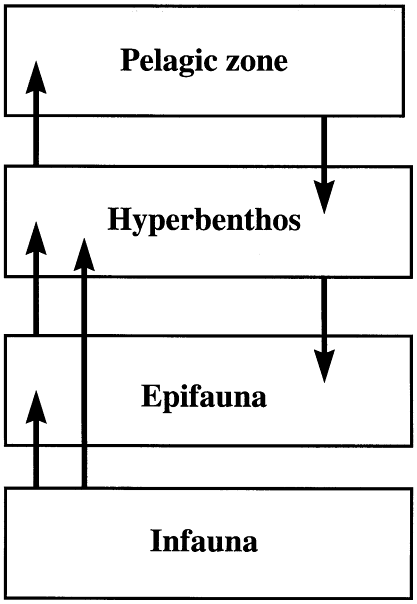

Fig. 2. Theoretical schematic representing vertical flow of parasites among different depth strata based on presumed trophic interactions. Vertical exchange may also occur within the layers that constitute the pelagic zone.

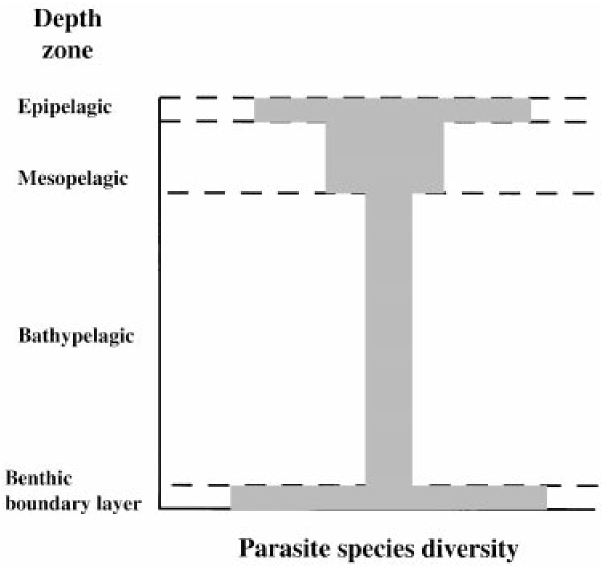

Fig. 3. Theoretical schematic representing relative species diversity of parasites of pelagic fish inhabiting different depth zones in the water column. Species diversity decreases with depth to a minimum in the bathypelagic zone, and then increases in the benthic boundary layer.

examples of zooplankton intermediate hosts used by marine helminths, consult Table 1 in Marcogliese (1995).

Zonation with depth into littoral, sublittoral, pelagic and bathypelagic habitats is an important determinant of the parasite fauna of fish (Polyanski, 1961). With depth there occurs a corresponding change in the intermediate host fauna. Plankton-feeding fishes do not usually acquire parasites from benthic invertebrates. Their parasite fauna, acquired mainly from copepods and chaetognaths, is distinct and impoverished (Polyanski, 1961), in accordance with the low infection rates in intermediate hosts in dilute waters. Similarly, mesopelagic and bathypelagic fish possess poor parasite faunas consisting of few adult forms, few digeneans, and mainly juvenile nematodes and cestodes (Campbell, 1983; Gartner & Zwerner, 1989). Away from the continental shelf slope waters, parasite diversity generally decreases with depth (Campbell *et al.* 1980; Campbell, 1983; Gartner & Zwerner, 1989). Biomass also decreases with depth in the pelagic zone; thus, there are fewer prey to serve as intermediate hosts for parasites of bathypelagic fish, accounting for the relatively impoverished nature of their parasite fauna (Campbell *et al.* 1980; Campbell, 1983; Gartner & Zwerner, 1989). Species richness and intensity of infection are highest in epipelagic and benthic zones, decrease in vertically-migrating mesopelagics and are lowest in deep nonmigratory mesopelagic and bathypelagic fishes (Fig. 3). Mesopelagic and bathypelagic fishes possess impoverished parasite communities compared to those of benthic fishes, which possess more diverse adult and larval helminths (Campbell *et al.* 1980; Campbell, 1983). The high diversity, density and longevity of benthic invertebrates compared to pelagic ones promote parasite transmission (Campbell *et al.* 1980; Campbell, 1983). These factors account for the relative high diversity of parasites in benthic fishes compared to those found higher in the water column (Fig. 3).

Though cycling of helminths is primarily within the benthic boundary layer in deep-sea fishes (Campbell *et al.* 1980), the temporary spatial overlap of vertically-migrating organisms and trophic interactions between predators and prey in the water column, hyperbenthos, epifauna and infauna would be expected to promote some exchange of parasites between zones and permit their movement vertically within marine systems (Fig. 2).

DISTRIBUTION AND DIETS OF FISHES

Like benthic communities (Sanders, 1968; Gray, 1974), fish communities vary along a gradient with depth (Markle, Dadswell & Halliday, 1988). However, seasonal inshore-offshore migrations link food webs across depths (Ojeda & Dearborn, 1990). This has implications for parasite transmission, potentially linking parasite faunas from different areas, but tends to blur the distinctiveness of parasite communities.

On the Scotian Shelf off Nova Scotia there are five different bottom types based on grain size that are correlated with water depth and fish distributions (Scott, 1982*a*). Coarse sands are shallow and fine sands deeper, with the different bottom types having characteristic invertebrate communities that support a distinct fish fauna. The highest fish diversity occurs on mixed sediment types. Generally, the most widespread predators possess the highest dietary diversity (Richards, 1963; Hacunda, 1981).

Much diet overlap occurs among fishes off northeastern North America and elsewhere (Langton & Bowman, 1980; Langton, 1982; Martell & McClelland, 1994). Dietary overlap is frequently higher between species than between size classes of the same species (Garrison & Link, 2000), as diet shifts are common with age and are virtually ubiquitous (Tyler, 1972; Braber & de Groot, 1973; Langton, 1982; Gibson & Ezzi, 1987). Much of the overlap results from similarities in mouth morphology and gape size, even among unrelated species (Hacunda, 1981; Gibson & Ezzi, 1987). A large portion of this overlap is due to the prominence of crustaceans in fish diets. Crustaceans and epifauna are often over-represented in fish diets, while taxa such as polychaetes and members of the infauna are under-represented (Richards, 1963; Hacunda, 1981; Langton, 1982; Macdonald & Green, 1986).

Despite this overlap in diet, resource partitioning has been repeatedly demonstrated in marine fish off North America and Europe (Tyler, 1972; Langton & Bowman, 1980; Hacunda, 1981; Gibson & Ezzi, 1987; Langton & Watling, 1990; Martell & McClelland, 1994). Diets may vary seasonally, geographically and with depth (Richards, 1963; Langton & Bowman, 1980; Hacunda, 1981; Langton & Watling, 1990). Feeding guilds may be derived from fish diets and dividing prey into functional groups according to lifestyles, sediment preferences and depth off bottom. Guilds may include piscivores, mixed feeders on crustaceans and fish, mesoplankton and macroplankton feeders, nekton feeders and those feeding on benthic and/or hyperbenthic prey (Langton & Bowman, 1980; Mattson, 1981; Vinogradov, 1984; Gibson & Ezzi, 1987; Langton & Watling, 1990; Garrison & Link, 2000). The partitioning of prey should promote segregation of parasites among guilds of hosts, countering the homogenizing influences that were discussed earlier. As a consequence, guilds of parasites may result that are transmitted by suites of invertebrates characteristic of particular habitats to suites of fish in those habitats (Zander *et al*. 2000; Zander, 2001). For example, local differences in ecology are reflected in parasite species composition in the Barents Sea, where parasites are divided into broad host categories (littoral and coastal species, planktivores, benthophagous fish and migratory species) and the Bering Sea (planktivores, piscivores-planktivores and piscivore-benthivores) (Polyanski, 1961). Most parasites are associated with a specific ecological niche and diet.

In a number of demersal fish off Nova Scotia, many species displayed modifications in diet with growth that were accompanied by a change in the parasite fauna (Scott, 1975, 1981, 1982*b*, 1985; Scott & Bray, 1989; see also Thoney, 1991, 1993). For example, American plaice shifted from small crustaceans to echinoderms (Scott, 1975), haddock from plankton to benthos (Scott, 1981), pollock from crustaceans to fish (Scott, 1985), and Atlantic and Greenland halibuts to increasing amounts of fish (Scott & Bray, 1989).

Among related species such as flatfish, there exists some host specificity, but evidence suggests that factors controlling species composition of parasites are ecological, not physiological or phylogenetic (Polyanski, 1961; Scott, 1982*b*; Lile, 1998). However, Pacific halibut (*Hippoglossus stenolepis*) are unusual for temperate marine fish in that their parasite fauna is extremely speciose (Blaylock, Holmes & Margolis, 1998). Most of their parasites are generalists, but these authors were able to detect a phylogenetic component to parasite species composition. As in other species and studies, the parasite fauna changed with age corresponding to a shift from shallow inshore habitats and invertebrate diet to deeper offshore habitats and piscivorous diet. Clearly, the invertebrate and fish fauna that in turn reflect habitat characteristics are important factors in dictating the local composition of the parasite fauna.

PATTERNS IN MARINE FOOD WEBS

Food web structure varies among ecosystems in different parts of the world. Thus, it is worthwhile to briefly consider some of the variations in structure as these differences will impact on the flow of parasites along food chains in these ecosystems.

In marine waters, there are basically three types of production: temperate seas, upwelling areas and oligotrophic oceans (Cushing, 1988). The pelagic realm is divided on the basis of topography, hydrography and latitude, such that distinct ecosystems are formed (Smetacek, 1988). Continental shelves are the most productive of the extensive areas in the oceans. Diversity is highest on the boreal continental shelf in summers, with high copepod production, and high abundance of invertebrate planktonic predators like chaetognaths, ctenophores and coelenterates (Smetacek, 1988). In shelf waters, Atlantic cod and herring are at the top of the demersal and pelagic food chains respectively, but cod also eat herring (Cushing, 1988), thus integrating pelagic and benthic food webs. Copepods are the most important taxa in terms of biomass in the water column (Smetacek, 1988).

Tropical waters have continuously high diversity and possess complex ecosystems. Food chains differ in strong versus weak upwellings. In weak ones, anchoveta and zooplankton both consume phytoplankton and are in turn ingested by carnivores. In strong upwellings, anchoveta eat zooplankton and are then eaten by carnivores (Cushing, 1988).

Productivity in polar systems can rival the tropics, but it is limited seasonally. In the Antarctic, food chains are short, euphausiids being primary consumers and whales, secondary consumers. Seabirds dominate northern food webs such as at Svalbard, Spitzbergen (Weslawski & Kwasniewski, 1990). Small fish are common and abundant, as are seals. Predaceous hyperiid amphipods are potentially important links in parasite transmission, especially in the Arctic where they are among the most common prey of fish and birds (Weslawski & Kwasniewski, 1990).

Interestingly, and perhaps counter-intuitively, benthic production is highest at high latitudes. The productivity ratio of plankton : benthos is 6 : 1 in the Indian Ocean, 3 : 1 in the North Sea, and 1 : 1 off Greenland (McLuskey & McIntyre, 1988). Pelagic organisms are more important in tropical fisheries and demersal ones in the subarctic (Petersen & Curtis, 1980). In tropical waters, zooplankton are a dominant trophic link to pelagic fish. In contrast, on northern continental shelves, 80 % of animal species are benthic, with the remainder being pelagic zooplankton (Curtis, 1975). Marine mammals and birds that prey almost exclusively on benthos occur in subarctic and Arctic waters, but not in the tropics (Petersen & Curtis, 1980). Thus, the basic structure of oceanic food webs varies with latitude. Pelagic parasites are probably more common in subtropical and tropical waters, whereas benthic parasites are more important at higher latitudes.

In northern Norway, there are two fundamentally different pathways within the food web. The first is short. In pelagic waters, euphausiids are the primary consumers and are eaten by Atlantic cod. A similar near-bottom food chain exists where prawns, mysids and other crustaceans are the primary consumers, and demersal Atlantic cod their main predators. However, the most important pathway consists of copepods and euphausiids as primary consumers, capelin (*Mallotus villosus*) as secondary consumers and Atlantic cod as the apex predator (Falk-Petersen, Hopkins & Sargent, 1990). In contrast, in the Barents Sea, ctenophores are important copepod predators and they almost act as a trophic dead end, although they can be ingested by *Beroe* sp., another ctenophore that is then preyed upon by Atlantic cod. Ctenophores actually consume much of the copepod production on the continental shelf. This may limit parasite transfer from copepods to fish compared to Spitzbergen, where capelin is the most important copepod predator, although some are also eaten by chaetognaths. These in turn may act as paratenic hosts for numerous parasites, thus facilitiating transmission.

Primary production on the shallow and cold continental shelf off Nova Scotia is less than that on the slope waters, which are deeper, warmer and more nutrient-rich. However, demersal fish production is highest on the shelf but declines further offshore, whereas pelagic fish production is highest on the slope waters and declines inshore (Mills & Fournier, 1979). The fish community on the Scotian Shelf is composed largely of cod, haddock, pollock and flatfish, whereas hake, redfish, grenadiers and argentines are more common on the slope (Mills & Fournier, 1979). Thus, not only is there a transition in the fish fauna at the shelf-slope interface, but there should be a transition in the parasite fauna as well. Pelagic parasites are predicted to be more common in slope waters, and benthic parasites on the shelf (Mills & Fournier, 1979). These authors further suggest that there are fundamental differences in the food chains between Nova Scotian waters and those of the North Sea, with the pelagic web being more important in the latter. This implies that pelagically-transmitted parasites that use zooplankton as intermediate hosts (such as cestodes) are predicted to be more prevalent in the North Sea, whereas abundance of parasites transmitted via the benthos should be similar as demersal catches are similar between the two areas.

More generally, Hairston & Hairston (1993) suggest that trophic structure controls energy flow within food webs. Using freshwater systems as an example, they note that pelagic food webs possess 1–2 extra trophic levels compared to terrestrial webs. In freshwater pelagic systems, there are 2 distinct levels of predation, those being zooplanktivorous fish and piscivorous fish, both gape-limited, whereas in terrestrial systems there is only 1 trophic level of carnivores that is functionally significant (Hairston & Hairston, 1993). In some freshwater systems and most marine systems, there exists an additional level of predatory zooplankton (Marcogliese, 1995). Coastal systems differ from open ocean systems in that they possess shorter food chains (Hairston & Hairston, 1993). The least restricted webs are those of the marine pelagic. They are expanded 3-dimensionally in space and contain the longest number (5) of food chain lengths. Marine benthic webs possess slightly shorter chain lengths (4) on average, and are more spatially restricted. Estuarine webs are the most constrained and possess short food chain lengths (3) (Schoener, 1989). These generalizations must be interpreted with caution. For example, well-studied speciose estuarine webs such as the Ythan possess distinctly longer webs (Hall & Raffaelli, 1991; Huxham, Raffaelli & Pike, 1995). A major problem in food-web construction is whether to draw a link between 2 components (Schoener, 1989). Parasites may help verify links, and possibly could help determine the strength of the linkage (Marcogliese & Cone, 1997). Indeed, one model of the Ythan food web postulates links between predators and prey based on parasites present in the system and their life cycles, in the absence of diet data (Huxham *et al.* 1995).

PARASITES IN THE FOOD WEB

The different organisms that occur in or on a particular habitat are integrated together into food webs through trophic interactions. The webs found across different habitats blend together gradually much like the distribution of their component organisms in the seas, with gradients in diversity and interactions. Numerous studies suggest that parasite diversity is related to the diversity of free-living organisms or diversity of the host's diet (Campbell *et al*. 1980; Scott, 1981; Campbell, 1983; Lile, 1998). For example, the White Sea is oceanographically similar to the Barents Sea, but its fish possess fewer parasite due to a reduction in its free-living fauna that act as intermediate hosts (Polyanski, 1961).

An examination of the parasite fauna of Atlantic cod illustrates the diversity of parasitism and the role of cod within the food web (Hemmingsen & MacKenzie, 2001). A total of 107 species of parasites have been reported in cod, of which only 7 are species specific, and another 17 specific to gadids. The remaining 83 are generalists. Atlantic cod acts as intermediate, paratenic or definitive host to these parasites. Eight species mature in marine mammals and another 12 in large piscivorous fish, showing that cod can be an important link to top predators in the food chain. In contrast, only 5, of which 2 are rare, mature in birds, effectively demonstrating that avian predation on cod is limited on a global scale. The fact that Atlantic cod is definitive host to many species of parasites indicates that cod is a major predator on many taxa including fish, crustaceans, polychaetes, coelenterates and chaetognaths.

Within a fish species, parasites will vary between inshore and offshore stocks (Polyanski, 1961; Thoney, 1993; Hemmingsen & MacKenzie, 2001), reflecting differences in the respective food webs. Parasites transmitted by intertidal snails, such as *Cryptocotyle lingua*, and those infecting pinnipeds, such as *Pseudoterranova decipiens*, will be more common in inshore fish. Those using whales as definitive hosts, such as *Anisakis simplex*, will be more abundant in offshore fish. Inshore-offshore differences also occur in parasites of seabirds. Those feeding inshore acquire the acanthocephalan *Corynosoma* spp. from feeding littorally on small to medium nototheniid fishes or amphipods. This parasite does not occur in zooplanktivorous seabirds offshore that prey primarily on euphausiids (Hoberg, 1985, 1986).

Long-term changes in the prevalence and abundance of parasites indicate the variations in density of animals that serve as intermediate or definitive hosts, and/or changes in environmental conditions that subsequently affect food webs (Hemmingsen & MacKenzie, 2001). For example, an increase in *Anisakis simplex* may reflect more predation on capelin, while a decrease in *Contracaecum osculatum* may indicate reduced seal predation on cod. Long-term changes in the food chain have lead to shifts in the helminth fauna of seabirds in the Seven Islands archipelago of the Barents Sea. Between 1940–41 and 1991–93 the species richness of digeneans declined drastically in common gulls, herring gulls and great black-backed gulls. This decline is attributed to a decrease of molluscs in the birds' diets (Galaktionov, 1995). The species composition of cestodes also changed, reflecting a diet shift from fish to crustaceans as a result of the collapse of the herring and capelin populations (Galaktionov, 1995).

Few studies have incorporated parasites into food webs (Marcogliese & Cone, 1997). In an open water pelagic example, two species of short-finned squid (*Illex coindetii* and *Todaropsis eblanae*) are sympatric off the coast of Spain. Their parasites suggest that they serve as prey for large predators. The squid *I. coindetii* is infected by tetraphyllideans and trypanorhynchs, obtained from feeding on planktonic invertebrates, suggestive that sharks are one of its important predators. In contrast, *T. eblanae* is infected with anisakid nematodes, implying that it feeds on micronekton (small fish and squid) and that it in turn is preyed upon by marine mammals (Pascual *et al*. 1996). Curiously, these squid are not infected with didymozoid digeneans. Normally, squid are important in the diet of top carnivorous teleosts such as swordfish, but the absence of these parasites indicate that tuna, sailfish and swordfish are absent from these waters (Pascual *et al*. 1996). Thus, in this case parasites provide information about the role of squid in the food web, and about the structure of the web itself.

Two species of *Contracaecum* follow distinct pathways to the same seal hosts in Antarctic food webs. Both *C. radiatum* and *C. osculatum* infect Weddell seals (*Leptonychotes weddellii*) as definitive host, but *C. radiatum* is transmitted via a pelagic pathway while *C. osculatum* uses a benthic food chain. The two pathways are integrated through the diet of piscivorous bentho-pelagic channichthyids, which are the seal's main prey (Klöser *et al*. 1992).

Extensive studies by Zander and colleagues have documented patterns of transmission in the inshore brackish waters of the Baltic Sea, and elaborated parasite transmission pathways in food webs (Zander, 1992/93, 1998). Within the parasite communities of small fish (gobies, sprat, sand eels, sticklebacks) in the middle of the food web, over 50% of parasite specimens were larvae, small fish being important in the transfer of parasites from the first intermediate host to the definitive host (Zander, 1998). High prevalences of microphallid digeneans in snails and benthic crustaceans indicates that seabirds are common in the food web (Zander *et al*. 2000). Shallow inshore areas provide more opportunities for birds to feed, thus promoting allogenic life cycles (Campbell, 1983; Zander, Reimer & Barz, 1999). The different species of fish partition planktonic and benthic prey resources, as indicated by their parasite fauna (Zander, Strohbach & Groenewold, 1993; Zander, Groenewold & Strohbach, 1994; Zander *et al*. 2000). Conditions in the Wadden Sea are optimal for 2–3 host life cycles: there is a high density of intermediate hosts, short infection pathways and infection times, and high encounter rates between intermediate and definitive hosts (Groenewold, Berghahn & Zander, 1996). As a result, paratenic hosts are less important and less common in this type of habitat and parasite life cycles are thus shorter than in open marine waters. This host–parasite system reflects the conjecture that coastal systems have short food chains (Schoener, 1989; Hairston & Hairston, 1993).

Information from littoral communities at higher latitudes suggests that shorter life cycles are favoured in harsh environments. Fourteen species of digeneans are found in *Littorina* spp. and other snails on the Norwegian and Russian coasts, all but one of which use birds as definitive hosts. The parasites can be divided into 2 groups, those that employ a single intermediate host without any free-living stages (microphallids), and those that have free-living infective stages and more than 1 intermediate host (Galaktionov & Bustnes, 1999). The former tend to occur along the Russian coast, which has a harsher climate, while the latter are more common in Norway. The authors postulate that parasites with free-living stages might not be favoured in harsher climates, whereas longer life cycles may proceed to completion more successfully in milder climates. The dichotomy might also represent differences in food chain lengths between the two environments, with shorter food chains in harsher littoral habitats. There is a tendency to shorten life cycles in brackish waters as well (Kesting, Gollasch & Zander, 1996).

Among the most detailed studies of parasitism in relation to the ecosystem and food web structure are those of deep-sea mesopelagic and bathypelagic fishes off North America by Campbell and colleagues. They found that parasites are appropriate indicators of community interactions and host biology in that parasitic helminths use the food chain and reflect the diversity of the host's diet (Campbell *et al*. 1980; Campbell, 1983). Effectively, the composition of the helminth fauna in a host indicates that host's role in the food web. This information was corroborated with diet data and stomach content analysis. Parasites, for example, clearly demonstrate a shift from benthic invertebrates to more pelagic cephalopods and fish with depth (Campbell *et al*. 1980). Prevalence of infection and species richness are higher in those deep-sea fishes that feed on benthos compared to those foraging on pelagic or planktonic prey (Zubchenko, 1981; Houston & Haedrich, 1986). In a comparable study, Gollasch & Zander (1995) and Kesting *et al*. (1996) demonstrate the flow of parasites through benthic, hyperbenthic and planktonic intermediate hosts into small brackish fish and other vertebrates in the Schlei fjord of the Baltic Sea.

Given that cestodes, nematodes and acanthocephalans rely exclusively on trophic transmission (George-Nascimento, 1987; Zander, 1992/93), George-Nascimento (1987) suggests that parasites may be useful indicators of persistent food web interactions. He further notes that in fish, larvae typically have a greater host range than adult parasites in the marine environment. The highest species richness should be found at intermediate trophic levels where fish can serve as intermediate, paratenic or definitive hosts, with the proportion of adult digeneans increasing with trophic level.

Marine fish parasites tend to be generalists, as an adaptation for completing their life cycles in a dilute open system (Bush, 1990). Often the most common parasites in fish are juveniles which often are generalists and are commonly transferred trophically from one fish to another via predation. Thus, fish are important and frequently used as intermediate or paratenic hosts (Marcogliese, 1995; Blaylock *et al*. 1998). Many marine parasites possess the ability to maintain themselves without development in paratenic hosts be they invertebrates or fish (Marcogliese, 1995). This too is considered an adaptation to survival in a dilute environment where intermediate hosts such as copepods are relatively short-lived and encounter rates between definitive host predators and intermediate host prey are limited. Colonization success is enhanced and local extinction reduced if a resting stage is present in a parasite's life cycle (Kennedy, 1994).

The large invertebrate predators that commonly occur in marine systems offer unique opportunities for parasites to be transmitted in packets (Bush, Heard & Overstreet, 1993; Lotz, Bush & Font, 1995). Intertidal and salt marsh crabs may be infected with up to 6 species of microphallid digeneans that can be transmitted together as 'source' communities to birds and mammals (Bush *et al*. 1993; Lotz *et al*. 1995). Similarly, co-occurring anisakid nematodes may be transferred simultaneously from fish to fish or from fish to pinnipeds (Marcogliese, 2001*a*). While not as species rich, numerous co-occurring parasites can be transmitted together from infected planktonic invertebrates such as ctenophores infected with *Scolex pleuronectis* and *Opechoena bacillaris* to pelagic fish (Yip, 1984).

For marine mammals, which are apex predators in food webs, parasite species richness is less than that of their piscine prey. Their parasite faunas are considered impoverished compared to those of their terrestrial ancestors, probably because many ancestral helminth species failed to adapt to the marine habitat during the evolution of marine mammals, and to their isolation from existing mammal parasites (George-Nascimento, 1987; Balbuena & Raga, 1993;

Aznar, Balbuena & Raga, 1994). Thus, they are poor integrators of parasites and food web processes. Marine mammal parasite communities are impoverished despite the fact that they possess many of the criteria hypothesized to lead to species rich assemblages (endothermy, large size, longevity, gut complexity, vagility, catholic diet) (Kennedy, Bush & Aho, 1986).

Observations in fresh waters may also be applied to marine systems. For example, planktivores are typically dominated by cestodes and benthivores by digeneans (Dogiel, 1961). Among tropical freshwater fish, herbivores, algal feeders and zooplanktivores have more impoverished enteric helminth communities than do piscivorous and benthophagous fish (Choudhury & Dick, 2000). The richest communities are associated with fish possessing a mixed carnivorous diet of invertebrates and fish. This is similar to the conclusion of George-Nascimento (1987) that small fish in the middle of the food web will have the most speciose parasite communities.

POLLUTION, FOOD WEBS AND PARASITISM

Contamination in the marine environment has an impact on the species composition of benthic macroinvertebrates (Warwick & Clarke, 1995). Annelids tend to be more tolerant of polluted or stressed conditions than are echinoderms, molluscs or crustaceans (Warwick, 1988; Warwick & Clarke, 1993). In the Gulf of Mexico estuaries, sediment contamination with trace metals or organic chemicals decreases taxonomic and trophic diversity, affecting macrobenthic community structure and function (Rakocinski *et al.* 1997). Shrimps and amphipods appear sensitive to contaminants, while certain ophiuroids and crustaceans are more tolerant. Such overall changes in species composition and abundance will, no doubt, affect parasite transmission dynamics.

Indeed, parasites have been proposed as effective indicators of marine pollution (MacKenzie *et al.* 1995; MacKenzie, 1999). Parasites with complex life cycles can be affected at any stage in their life history. As a general rule of thumb, infections with endoparasites decrease and those of ectoparasites increase with pollution (MacKenzie, 1999).

The Baltic Sea has become increasingly eutrophic over the last 40 years, resulting in more parasites with short life cycles involving no or a single intermediate host (Reimer, 1995). Among 4 species of goby, there is a balance between benthic-transmitted and pelagic-transmitted parasites under normal conditions (Zander & Kesting, 1996). In stressed areas, the marine fauna becomes impoverished, with subsequent effects on the parasite fauna. Among parasites, stress leads to fewer specialists, more autogenic parasites and a dominance of plankton-transmitted species (Zander & Kesting, 1996).

Parasites benefit from eutrophication at first, as it promotes plant growth and herbivores and detritivores, such as snails and crustaceans that act as intermediate hosts for parasites (Zander *et al.* 1999; Zander *et al.* 2000; Marcogliese, 2001*b*). These areas are also attractive to fish and birds, and a balance exists between parasites with pelagic and benthic life cycles (Zander *et al.* 2000). As it proceeds further, eutrophication affects invertebrate intermediate hosts through oxygen depletion (Zander, 1998; Marcogliese, 2001*b*). Eutrophication favours generalist parasites (Zander & Kesting, 1998), and promotes 1–2 host life cycles compared to longer ones. A comparison of parasite faunas over 18 years in a region subject to eutrophication indicates a reduction in parasite species richness, a preponderance of simple parasite life cycles, and an increase of planktonic and hyperbenthic intermediate hosts over benthic hosts (Kesting & Zander, 2000). Comparable results were obtained for flounder (*Platichthys flesus*) and eelpout (*Zoarces viviparus*) in areas of the southeastern Baltic polluted with industrial sewage and experiencing eutrophication (Sulgostowska, Banaczyk & Grabda-Kazuska, 1987; Sulgostowska, Jerzewska & Wicikowski, 1990).

EFFECTS OF EXPLOITATION ON FOOD WEBS AND PARASITES

Commercial fishing may have profound impacts on community structure and food web organization. A meta-analysis comparing fishing methods from 56 international studies suggests that intertidal dredging and scallop dredging have the largest impact (Collie *et al.* 2000). Overall conclusions demonstrate that reductions of 27% in species number have occurred, with anthozoans and malacostracans the most affected. Other results indicate that holothurians and ophiuroids are the most sensitive of the echinoderms, gastropods are more sensitive than bivalves and oligochaetes are more vulnerable than polychaetes, the least impacted of all taxa. It is noteworthy to point out that no taxa increased in abundance (Collie *et al.* 2000).

In heavily-trawled areas such as the Gulf of Maine, Georges and the Grand Banks, benthic food webs are altered due to excessive removal of Atlantic cod and flatfish, resulting in increased numbers of skates, rays and longhorn sculpin (Smith *et al.* 2000). Changes have propagated through benthic invertebrates, with the macrofauna changing from echinoids and large clams to opportunistic brittle stars and polychaetes. Biomass of large epibenthic organisms including decapods and echinoderms was reduced by otter trawling on the Grand Banks, Newfoundland (Prena *et al.* 1999). Presumably, alterations of this magnitude on the food web will affect parasite transmission, abundance and diversity. Reduction of benthos should impede transmission of parasites that use benthic intermediate hosts, in particular those found in echinoderms. A long-term study on Georges Bank documents drastic changes in fish abundance by species, with a shift in dominance from demersal to pelagic species (Garrison & Link, 2000). Weakly exploited species such as spiny dogfish (*Squalus acanthus*) and skates increased in range and spatial and dietary overlap. Thus, we might expect significant changes to the parasite fauna as a result of changes in species composition, including an increase in parasites of elasmobranchs.

On a global scale, commercial fishing has affected the structure of entire food webs. As a result of depletion of the top piscivores, the preferred catch in many fisheries, the species now targeted are smaller and the mean trophic level fished has shifted downwards (Pauly *et al*. 2000). Fishing down food webs conceivably will reduce or eliminate top piscivorous fish that serve as definitive hosts for numerous parasites, and their incidence is predicted to decrease. Increasing the relative abundance of pelagic fish, as observed in the northwestern Atlantic, may also shift the parasite fauna from a speciose assemblage of benthic-transmitted forms to a more impoverished pelagic parasite fauna. These ideas can be tested in areas where historic data sets on parasites exist, as in parts of North America and Europe.

KEYSTONE PARASITES IN THE MARINE ENVIRONMENT

A keystone parasite basically has an impact on an entire community through regulation of an important predator or prey species (Minchella & Scott, 1991). Most keystone parasites have been documented for terrestrial systems (Dobson & Hudson, 1986; Marcogliese & Cone, 1997). However, populations of the green sea urchin (*Strongylocentrotus droebachiensis*) are controlled locally by outbreaks of parasites on both sides of the Atlantic Ocean by, curiously, two completely different parasitic organisms. This sea urchin decimates kelp beds and creates barrens, thus completely altering coastal ecosystems. In Norwegian waters, populations of sea urchins are reduced by a nematode (*Echinomermella matsi*), while in Nova Scotia they are limited by a protozoan parasite (*Paramoeba invadens*) (Hagen, 1992, 1996; Scheibling, Hennigar & Balch, 1999). The outbreak of disease is the only known mechanism to cause a large-scale shift from urchin-dominated barrens to lush, species-rich kelp forests (Scheibling *et al*. 1999). Productivity of vegetated habitats is greater than in adjacent areas, and the physical structure provided by macrophytes further influences the food web by increasing habitat complexity and enhancing diversity (Snelgrove *et al*. 2000). Thus, parasites may be important in regulating coastal ecosystem functions. Indeed, parasites may be the cause of trophic cascades (Skorping & Högstedt, 2001).

The ingestion of larval parasites during predatory interactions is a frequent event that aids in the comprehension of foraging dynamics and food web structure due to the ubiquity of trophically-transmitted parasites (Lafferty & Morris, 1986). Without consuming much host energy, parasites greatly increase predation rates on their hosts. This may reduce the density of the intermediate host and actually permit the persistence of a predator that otherwise could not support itself, thus affecting the structure of the entire food web (Lafferty & Morris, 1996).

CONCLUSIONS

Consideration of parasites in food web studies leads to alterations in food web properties and dynamics (Huxham *et al*. 1995; Huxham, Beaney & Raffaelli, 1996). Marcogliese & Cone (1997) suggested that the incorporation of parasitological information would assist in the construction and resolution of food webs and they provided justifications to that end. Herein I propose the reverse: that consideration of the structure and dynamics of food webs permits predictions about the distribution and abundance of parasites. Although this review deals exclusively with marine systems, this generalization also applies to fresh waters. Numerous testable hypotheses based on this generalization result from ideas and concepts discussed here. They include: (1) parasite species composition in local demersal fish varies with substrate quality, benthic invertebrate community structure and local food web patterns; (2) the benthic boundary layer is a focal point for parasite exchange among faunas inhabiting different vertical zones in marine habitats; (3) parasite species composition changes in heavily exploited areas to reflect modifications in fish and invertebrate communities; and more specifically, based on ecosystem information; (4) pelagic parasites are more common in slope waters and benthic parasites in shelf waters off Nova Scotia; and (5) pelagic parasites are more common in the North Sea than off Nova Scotia.

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