

The significance and prediction of predation in marine fisheries*

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Predation is a pervasive but ephemeral feature of marine fisheries. Losses to predation can exceed losses to fisheries, yet it is often assumed fishing mortality alone is responsible for variation in fish survival. While it may be sufficient to forget predation in short-term prediction and management, this will not further longer-term prediction and management. The predation experienced by a population is influenced by environmental and biological factors that vary spatially, seasonally, annually, and with the abundance of itself, other prey species, and the predator species. Predation can directly regulate prey numbers and indirectly regulate their survival via habitat availability, individual growth, and trophic structure. Despite predation's pervasiveness, its complexity and variability complicate its prediction. Models of predation have shown assumptions made in single-species models to be incorrect, but numerical prediction may be reliable for only the simplest symmetrical predator–prey interactions, where ontogenetic changes in predator diet and prey vulnerability have been accounted for. Knowledge of the effects of predation in marine fisheries will be furthered by an ongoing commitment to test and explore the properties of managed fisheries, while preserving, as necessary, the productivity and buffering capacity of the natural system.

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Introduction

Many of the world's marine ecosystems have undergone major shifts in species composition, which has had severe consequences on their productivity and the derived economic yield (e.g. Sherman, 1992; Wickens *et al.*, 1992; Caddy, 1993; Hylan, 1993). The mechanisms of these shifts are poorly understood because they often have several causes arising from the interaction of species, habitat, and environment (Caddy, 1993). This complexity complicates management measures to reverse the shifts (Wilson *et al.*, 1994, see also Fogarty, 1995; Hilborn and Gunderson, 1996). Measures designed to affect a single species may not be sufficient to prevent or reverse shifts in the ecosystem. Even if a marine ecosystem were stable and had a consistent species composition, a predator–prey system in that ecosystem could not be managed by managing only one

species (May *et al.*, 1979). Although short-term management objectives may be achieved in ignorance of the system to which they apply, longer-term, strategic management that has as its objective maximizing harvest under a set of constraints, requires an understanding of the interactions of species and of fisheries within the context of their physical environment and habitat (Sharp, 1992; Caddy, 1996).

Knowledge of predatory interactions is one source of information for strategic ecosystem management. A species' interaction with other species (and its own) through predation is a source of potential change in the biological environment. Change is direct when a predator kills a prey, and indirect in a multitude of ways, including predation on shared prey resources, effects involving intermediate predators, and predation influencing prey behaviour and resource availability. Recent research on predation in freshwater communities raises the possibility that predation effects may be predictable in closed freshwater lakes (e.g. Carpenter *et al.*, 1985; Mittlebach *et al.*, 1995). This paper assesses the current potential for predicting predation-induced changes in

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marine systems. The review starts with the magnitude and variability of predation in marine systems with emphasis on species of direct interest to commercial fisheries. It continues with the theoretical and biological understanding of predation as a regulatory force and concludes with examples of models that predict predation in marine commercial fisheries.

Magnitude and variability of predation in marine ecosystems

Marine fish are constantly at risk of being attacked and eaten by predators. The risk of predation is a strong selective force over evolutionary time and perhaps even between generations (Reznick *et al.*, 1997). The need to grow and reproduce is also a strong selective force but, on a daily basis, there are few events as unforgiving as the failure to avoid a predator – “being killed greatly decreases future fitness” (Lima and Dill, 1990). Although a fish can be killed and eaten only once, the risk of predation is ever present. A fish will modify its foraging and social behaviour, even its breathing, to reduce its exposure to predation (Lima and Dill, 1990), but there are limits to which it can sacrifice growth and reproduction to avoid being eaten, so its survival is a function of both the presence of suitable predators and its behaviour. The following summary of the magnitude of predation in marine ecosystems is a fraction of available reports but provides a glimpse of predation’s potential to influence ecosystem dynamics directly in practice and indirectly by its threat.

Marine mammals

Whales and seals are major predators of groundfish, herring, capelin, and squid in the Bering Sea (Lowry and Frost, 1985), eating an estimated 10% of all commercial fish stocks annually (humans eat 5%, birds 2%) (US Department of Commerce, 1979; Laevastu and Larkins, 1981). Toothed whales in Icelandic waters are estimated to eat about 850 000 t of fish annually (Sigurjónsson and Víkingsson, 1992). Grey seals in the North Sea were estimated to eat 14.3 million 1 to 4-year-old cod or 4.8% of this size component of the stock annually, imposing a natural mortality in the range of 0.0034–0.1259 (reviewed by Pálsson, 1994). Cape fur seals in southern Africa were estimated to eat around 1 million t of food (mostly fish) per annum, which is equivalent to between a third and all of the commercial catch depending on the extent of the seals’ feeding area relative to the fished area (Shaughnessy, 1985).

A collection of papers on the interactions of marine mammals and fisheries (Beddington *et al.*, 1985) indicates that the amount of commercially important fish eaten by marine mammals is similar to or exceeds that taken by the commercial fishery in at least five areas

(South Georgia, Kerguelen Islands, Southern Africa, North-west Atlantic, Bering Sea). In other areas (locally in the US Pacific North-west coast; Bristol Bay, Alaska), marine mammal predation depletes sessile invertebrates (shellfish, sea urchins) and has prevented development of commercial fisheries (Northridge and Beddington, 1992).

Seabirds

The potential for competitive interactions between seabirds and fisheries is high (see ICES, 1994a for a recent review). Seabirds have both a high metabolic rate and high energy requirements and consequently a high rate of predation. Murres (*Uria* sp.), for example, may eat between 10 and 33% of their body weight each day (reviewed by Vermeer *et al.*, 1987). Therefore, in the Scotia-Weddell Sea, where the average biomass of seabirds is estimated as one-third that of seals and one-sixth that of whales, the daily energy requirements of the birds and mammals are similar (Schalk *et al.*, 1993). Seabird consumption accounts for 22% of fish production off Oregon, USA; 29% of fish production within the 45-km radius of a colony in the Shetland Isles, UK; 24% of the mean catch off South Africa; 21% of total landings from the North Sea (over half from fish discards and waste); 17% of the anchovy off Peru between 1961 and 1965; and 4–7% of the adult herring off the Gulf Islands, Canada (Furness, 1982; Garthe *et al.*, 1996).

Seabirds and commercial pelagic fisheries often target similar sizes of fish, and collapses of fish stocks (and their fisheries) are often associated with breeding failures or population declines of the seabirds (ICES, 1994a). Northern gannets in Newfoundland waters, which harvest the same sizes and species of pelagic prey as the commercial fishery in the area, often harvest more mackerel and squid than the commercial fishery lands (Montevecchi *et al.*, 1988). Between 1977 and 1986 there were four coincidental collapses in the human and avian harvests of squid, and one coincidental collapse in the two harvests for mackerel in these waters. Seabirds usually target the smaller pre-recruit, pelagic life history of demersal fish and links between the size of fish and bird populations and fisheries are less clear; though potentially as important because of the large numbers of small fish eaten. For example, shags and cormorants off Norway ate 144×10^6 0-group and 110×10^6 1-group gadoids per summer between 1985 and 1988, this equates to a similar number to that lost to cannibalism, and over 20% of the (admittedly low) estimate of total annual stock (Barrett *et al.*, 1990). Seabirds can and do deplete the food resources in the waters around their colonies (Furness and Birkhead, 1984; Birt *et al.*, 1987); the number, diet, breeding success, and survival rates in their colonies may indicate the availability and thus, by the use of extrapolation, the abundance of fish prey

(Cairns, 1987; Montevecchi and Myers, 1995; Ainley *et al.*, 1995).

The occurrence of fish in the diet of seabirds does not necessarily imply predation on live fish. Where commercial fisheries operate, a large proportion of seabirds' diet can come from fish discarded from the boats (Hill and Wassenberg, 1990; Garthe *et al.*, 1996). Scavenging seabirds account for between 52 and 66% of the total North Sea avifauna. More than half the fish (and more than 40% of all food) eaten by North Sea seabirds is fishery waste (Garthe *et al.*, 1996). Around the British Isles, seabirds ate 75% of discarded fish, equivalent to 5–10% of the landed catch of gadoids and flatfish (Furness *et al.*, 1988). Feeding on discards can represent a significant shift in trophic specialization: the diet of one Great Barrier Reef bird species, *Sterna bergii*, contained 5% benthic species when no trawlers were operating, but 70% benthic species when they were (Blaber *et al.*, 1995).

The availability of discards can cause major changes in the feeding ecology, breeding success, and the potential population size of seabird species (Furness *et al.*, 1988; Blaber *et al.*, 1995; Oro *et al.*, 1995). Long-term survival of the threatened Audouin's gull, *Larus audouinii*, in north-east Spain may be reduced if a trawling moratorium continues (Oro *et al.*, 1996). The Audouin's gull, which gets 70% of its diet from discards, had decreased clutch size and egg size when the moratorium was early in the breeding season and decreased chick growth and survival when the moratorium was later in the breeding season.

Squid

Squid are abundant, widespread, rapidly growing piscivores. In the Bering Sea, the annual production of Gonatidae (60% of the squid biomass) is estimated at 9.4 million t, which exceeds the combined production of the main families of fish (Radchenko, 1992). Their high turnover rate and the high proportion of juvenile and larval fish in their diet suggest that squid may have a significant impact on marine fish recruitment. Fish were found in more than 80% of non-empty stomachs of two species of the long-finned squid, *Loligo* sp., in the north-east Atlantic, from Scotland to the Azores (Guerra and Rocha, 1994; Pierce *et al.*, 1994). Fish were also the most abundant prey (42% by volume; herring 12% by volume) of short-finned squid, *Illex* sp., sampled off Iceland (Jónsson, 1980). 0-group cod were identified in 8% of the stomachs of short-finned squid caught off Newfoundland (Dawe, 1992).

Off the north-eastern United States, two cephalopod species were estimated to eat between 33 000 and 43 000 t (*Illex illecebrosus*) and between 182 000 and 703 000 t (*Loligo pealei*) of fish per annum. As most of their prey in some seasons were pre-recruits of commer-

cial species, including Atlantic cod, the cephalopods are considered a significant source of pre-recruit mortality (Maurer and Bowman, 1985). In the Gulf of Thailand, Longhurst and Pauly (1987) estimated that cephalopods ate 700 000 t yr⁻¹ of prey in the early 1960s and 500 000 t yr⁻¹ in the early 1980s; the annual fisheries harvest over the same period was approx. 200 000 and 800 000 t, respectively.

Squid are also the prey of fish. The ICES stomach-sampling program found squid to be a small but significant component of the diet of 0-group whitefish (Boyle and Pierce, 1994). There have been several instances of squid biomasses increasing rapidly after the onset of commercial fishing (Gulf of Thailand, Mauritania). It is more likely that this is due to reduced predation by fish on juvenile squid than reduced trophic competition (Longhurst and Pauly, 1987).

Invertebrates (excluding squid)

Fish eggs and larvae are a large component of the diet of many marine invertebrates. Gelatinous zooplankton, copepods, chaetognaths, euphausiids, amphipods, and snails have been recorded as predators of fish eggs or larvae or both (Bailey and Houde, 1989). The relative abundance of these marine invertebrates means that even a small rate of predation can result in a substantial total mortality (Purcell *et al.*, 1994). Exclusion of invertebrate predators from enclosures can increase survival of fish larvae (cod, herring, capelin, and plaice) to metamorphosis by over 50% (Oiestad, 1983). Medusae have been reported to contain up to an average 148 Pacific herring larvae each, and may eat as much as 96% of the local production of herring larvae every day in one site off British Columbia (Purcell and Grover, 1990). Medusae in the Kiel Bight were estimated to eat 2–5% of the total stock of herring larvae daily (Möller, 1980); abundance of herring larvae was low in years when there was a high abundance of medusae (Möller, 1984). Predation by medusae and ctenophores on larval anchovy in Chesapeake Bay was estimated to account for 21% (s.d.=17%) of the total estimated daily mortality (Purcell *et al.*, 1994).

North Sea plaice eggs and larvae, on their way from the spawning grounds to the nursery areas, suffer heavy mortality, some of which is attributable to herring selectively eating the eggs (Daan *et al.*, 1985), but when the larvae reach coastal waters, the late arrivals are subject to high predation by coelenterates that have an explosive increase in numbers at this time. Somewhere between 1 and 2.5% of the *Pleurobrachia pileus* population in the Western Wadden Sea was estimated to have eaten a flatfish larva in the few hours before capture – a predation rate of between 140 and 350 larvae per 1000 m³ every few hours. As the abundance of larvae was estimated to be 230 per 1000 m³, *P. pileus* is thought

to effectively eat all plaice immigrating later to the nursery area and end their recruitment (van der Veer, 1985). The plaice that arrived and settled before the coelenterate increase are preyed upon by brown shrimp, which could remove between 2 and 14% of the population per day (van der Veer and Bergman, 1987). Flounder larvae that migrate to the same nursery areas later in the year, after the coelenterate increase, suffer an even higher mortality than plaice, such that the relative abundance of flounder larvae to plaice larvae drops from 10:1 before settlement, to 1:4 after settlement (van der Veer and Zijlstra, 1982). *Pleurobrachia pileus* was the suspected predator.

Invertebrate reproduction patterns may be linked to the availability of fish eggs and hence exert a density dependent effect on survival of eggs to the larval stage. For example, the amphipod, *Calliopius laeviusculus*, actively preys on the intertidal eggs of capelin (DeBlois and Leggett, 1993). Endogenous reproductive patterns influenced by exogenous seasonal stimuli, together with an overwinter diapause, allow the amphipod to increase in abundance at the same time as the capelin eggs. The success of this linking in any year then provides the basis for a numerical response in a second amphipod cohort produced the same year that is still early enough to predate capelin eggs, and potentially a numerical response in the over-wintering amphipod population in expectation of the availability of capelin eggs the following year.

Fish

Fish are a major predator of other fish, particularly the smaller size classes, in marine ecosystems. Even if a larva escapes its attacker, the stress of being attacked will reduce its future survival probability. Predation of fish eggs and larvae by other fish has been reported by scientists since early this century; for example, Bowman (1922) (in Bailey and Houde, 1989) noted haddock gorged with herring eggs. Based on an average 15 000–20 000 eggs in the stomachs of cod caught near a herring spawning ground in a Norwegian fjord, Johannessen (1980) concluded that predation could remove 40–60% of total egg production in years of low egg deposition. In 1986, Bering Sea yellowfin sole may have eaten 2×10^9 0-group arrowtooth flounder (13 times more than subsequently recruited at age 2) and 80×10^9 0-group Greenland halibut (27 000 times more than subsequently recruited at age 4), but minimal numbers of either fish in 1985 or 1986 (Livingston, 1991; cited by Bailey, 1994). Capelin larvae in mesocosms disappeared rapidly when the herring present started to school; herring predation on capelin might explain the poor recruitment of capelin in the Barents Sea when herring are abundant (Moksness and Oiestad 1987).

Cannibalism is also an important source of egg mortality; adult northern anchovy ate 17% of the anchovy eggs present each day, accounting for 32% of the total egg mortality (Hunter and Kimbrell, 1980), Peruvian anchoveta ate 15% of the eggs produced, accounting for 22% of the total egg mortality (Alheit, 1987; in Bailey and Houde, 1989), and South African anchovy ate 70% of eggs present in the study area (Valdés *et al.*, 1987). This cannibalism may be density dependent, with the observed number of eggs in the stomachs increasing exponentially with egg density in the water (Hunter and Kimbrell, 1980; Valdés *et al.*, 1987), due perhaps to increased intensity of filtering when schools of adult anchovy encounter high densities of eggs (Hunter and Kimbrell, 1980). At other times adults at the front of a school bite on larger items, while at the back of the school smaller items are filtered; thus, the degree of cannibalism is dependent on the abundance of eggs, the abundance of adults and their patchiness.

The predation by fish on later life stages of fish is not as large (in terms of numbers per fish) as predation on eggs and larvae, however, it may occur after recruitment levels for that year are determined and thus, its influence on the adult population and hence on the yield of commercial fisheries may be more direct. Cannibalism by cod in the Baltic Sea varied between less than 1% and over 30% of the catch (in weight) between 1977 and 1992 (Sparholt, 1994). An analysis of the sources of fish mortality in six different exploited marine ecosystems (Bax, 1991), showed that the main source of mortality of fish beyond the larval and early juvenile stage in these ecosystems is predation by fish (Table 1). Predation by fish appears to range from 2 to 35 times the loss to commercial fisheries. However, the main causes of mortality will vary between species. For example, fishing is more likely to have the greater impact on larger specimens of commercial species, whereas predation is more likely to have the greater impact on smaller specimens and smaller non-commercial species.

Differences between the sizes of fish taken by fisheries and fish predation can indicate quite different impacts of the mortality. For example, although it was estimated that 25–35% of primary production on continental shelves was necessary to account for the recorded catches and discards (Pauly and Christensen, 1995), the same data indicate that the biomass lost to predation by fish is between 3 and 25 times larger than that to the commercial catch (Table 2; Christensen and Pauly, 1993). This is only possible because the predation removes lower trophic levels than the fishing and with the commonly assumed 10% transfer efficiency between trophic levels there is an order of magnitude greater biomass at each lower trophic level. Trophic position and life history stage are as important as species in describing the effects of predation in marine systems.

Table 1. Annual loss of fish to predators in six marine ecosystems (from Bax, 1991).

Ecosystem	Annual fish loss (t km ⁻²)				Fish/ Fishery
	Birds	Mammals	Fish	Fishery	
Benguela Current	0.3	2.6	56.5	1.6	35
Georges Bank	2.0	5.4	42.5	6.1	7
Balsfjord	0.0	0.0	14.1	1.5	9
East Bering Sea	0.2	1.5	11.0	1.4	8
North Sea	0.6	0.1	7.0	4.4	2
Barents Sea	0.0	3.0	5.1	1.8	3

Original data sources provided in Bax (1991).

Table 2. Annual biomass of fish lost to fish predators and the fishery in four continental shelf ecosystems (data from Christiansen and Pauly, 1993). Note g dw=grams of dry weight.

Location (reference)	Area (km ²)	Units	Biomass lost to		Fish/ Fishery
			Fishery	Fish	
Yucatan, Mexico (1)	100 000	gdwm ⁻² yr ⁻¹	0.09	2.12	25
Gulf of Mexico (2)		gdwm ⁻² yr ⁻¹	2.40*	8.24	3
Venezuela (3)	30 000	t km ⁻² yr ⁻¹	5.20	32.02	6
Brunei Darussalam (4)	7 396	t km ⁻² yr ⁻¹	0.70	15.06	20

(1) Arreguin-Sanchez *et al.* (1993); (2) Browder (1993); (3) Mendoza (1993); (4) Silvestre *et al.* (1993).

*Includes large bycatch of shrimp fishery.

Prey selection

Predation studies focus mainly on the predator and rates of predation. However, the selectivity of predation requires comparable attention. Size is the most obvious aspect of selectivity. Different size classes of a species exploit different sizes and species of prey allowing different size classes to use different ecological niches (Polis, 1984); there is often greater diet overlap between similar sized individuals of different species than different sized individuals of the same species. The size range of prey available to a predator increases as the predator's gape and pursuit speed increases (Okada and Taniguchi, 1974; Last, 1980; Robb and Hislop, 1980; Langton, 1981; Armstrong, 1982); the frequently observed increase in average prey size with predator size may result from active selection or be a passive process mediated by differential size-based capture success (Juanes, 1994). The diet of larger fish often still includes smaller prey items (reviewed by Juanes, 1994), which may be due to a lack of suitable larger prey items (Armstrong, 1982), or capture success. In freshwater communities (at least) this can lead to "species stacking" and a bimodal length distribution, where smaller individuals stay at the lower modal size until sufficient larger prey items become available (Griffiths, 1986). When other factors are confounded with increased size, selectivity may be stage-dependent instead of just size-based. For example, increased pigmentation and visibility of

growing Baltic cod eggs may increase their susceptibility to predation by herring (Wieland and Koster, 1996).

Once an individual reaches a particular size (or stage) it may reach a refuge from predation (sometimes resulting from metamorphosis) by the common predatory fish in the area (Cushing, 1975; Ellis and Gibson, 1995), although for larval fish, medium sizes may be preferred (or encounter rates increased) over both smaller and larger individuals, leading to a dome shaped selectivity function and potentially negating the advantages of a rapid growth rate (Cowan and Houde, 1993; Leggett and DeBlois, 1994; though see Meekan and Fortier, 1996). Indeed laboratory and enclosure studies of predation by crustaceans, ctenophores, medusae, and fish on ichthyoplankton suggests that maximal vulnerability occurs when the prey is 10% of predator size, regardless of predator type (Paradis *et al.*, 1996). Because mean predator size varies with predator type, small fish have to grow and survive through a series of predators' niches and final predation rate may be determined more by the spatial and temporal overlap of predator and prey than absolute size of the prey. The value of an individual to the future of the population also varies with the size of that individual; an individual that has outgrown predation threats to reach maturity ready to pass gametes on to the next generation is more valuable than a freshly spawned individual that has a small likelihood of surviving to the size of maturity (Paine, 1976). This is especially the case for teleost fish,

which usually produce thousands of eggs or larvae during their lifespan, only two of which need to survive and successfully spawn for the population to be maintained at the same level.

The pronounced selectivity of predation is only just beginning to be integrated into ecological models, with the understanding that modelling the “average” response of a cohort may obscure the trend for only the exceptional individuals to survive to maturity (e.g. Beyer and Laurence, 1981; West, 1988; Rice *et al.*, 1993). Individual differences tend to be stabilizing (at least in models) because individuals or classes of individuals with less vulnerability to predators provide a refuge from predation for the species, and refuges are in general stabilizing (Smith and Mead, 1974) although individual differences in predators may be destabilizing (Chesson, 1984). Similarly the impacts of selective predation (in this case selection of larger individuals by the fishing industry) are essentially unknown or unaccounted for (although see Reznick, 1991; Hylan, 1993; Gislason and Rice, 1996; Rochet, 1996). Potential detrimental effects on inherent fish size (Ricker, 1980; Ricker and Wickett, 1980), genetic diversity (Smith *et al.*, 1990; though see Ward and Elliott, 1993), time of spawning (Pedersen, 1984), and the resistance of a population to successive recruitment failures (Murphy, 1967) have been suggested.

Variability

Predation can be highly variable between years (e.g. Möhler, 1984; Mehl, 1989; Livingston, 1991; Sparholt, 1994). In 1984, Barents Sea cod ate 0.4 times their own biomass of capelin (Mehl, 1989). In 1985, they ate three times as many including an estimated 85% of the numbers of 3- and 4-group capelin. The increase is attributed to a strong year class of cod growing big enough to take larger capelin, and a greater geographic overlap between the two species in early 1985. In the Baltic Sea, cannibalism by cod varied between 100 000 t in 1979 and 1980 to around 1000 t in recent years, or between 30 and less than 1% of the commercial catch (Sparholt, 1994). The large decrease reflects both the overall decline in the cod stock and a series of poor year classes of cod in later years. Increased predation by cod on capelin, which occupy a similar ecological niche to herring, may have contributed to the recovery of the Norwegian herring following the strong 1983 year class (Hylan, 1993). Ten years earlier, when cod stocks were at a low level, the strong 1973 herring class did not result in a recovery of the Norwegian herring.

Predation on fish eggs and larvae may be especially variable. Bering Sea yellowfin sole were estimated to have eaten 4058 t (s.e. 4006) or up to 27 000 times the number of Greenland halibut that recruited to the fishery in 1 year, but minimal numbers in other years (Livingston, 1991). Abundance of medusae and their

predation on herring larvae off British Columbia was estimated to vary by two orders of magnitude over a 3 year study (Purcell and Grover, 1990). Norwegian spring spawning herring eggs may suffer losses to predation of up to 40% in years of light spawn, but only minor amounts in years of moderate or heavy spawn (Johannessen, 1980), which contrasts with anchovy where predation rates increase as egg density increases (Hunter and Kimbrell, 1980; Valdés *et al.*, 1987). High predation variability is facilitated by the frequently extreme patchiness of fish eggs, so that at low densities predators adopt searching and feeding strategies that maximise their feeding but at high densities may result in a predators capacity for feeding being exceeded once a patch is found. Good survival of herring eggs and larvae may require a widespread distribution, a long spawning period, and a rapid advection from the spawning grounds, concomitantly these mechanisms reduce their susceptibility to congregated predator species (Dragesund and Nakken, 1973). The variability of predation has led to alternate life history mechanisms in the North Sea herring to balance the dangers of starvation and predation of the larvae: large numbers of small eggs in the summer when predation is high, but smaller numbers of larger eggs in the winter when the risk of starvation is high (Hempel, 1965). Hatching of eggs occurs over a short period of time for many species so that the feeding capacity of local predators is exceeded and there is insufficient time for an aggregative response of more distant predators. The synchronized hatching event may be linked to periods of low light, favourable currents, abundant food, and few predators (see review by Fuiman and Magurran, 1994).

The extent of predation on a fish species is susceptible to changes in the predator population, perhaps in response to their own predators (May *et al.*, 1979). This may happen at many trophic levels within an ecosystem. For example, the scyphomedusan, *Chrysaora quinquecirrha*, consumes *Mnemiopsis leidyi* ctenophores, whole or in part, the latter reducing ctenophore fecundity (Purcell and Cowan, 1995). Both the scyphomedusan and the ctenophore are important predators of bay anchovy – the dominant ichthyoplankton in Chesapeake Bay (Purcell *et al.*, 1994). Peak abundance of the ctenophore occurs before the peak abundance of the scyphomedusae that may result in its elimination from areas of the Bay (Cowan and Houde, 1993; Purcell and Cowan, 1995). Peak spawning of the bay anchovy occurs after the peak abundance of the ctenophores and as the abundance of medusae is increasing. Interannual variation in the abundance of gelatinous zooplankton and their temporal succession (some years ctenophore abundance remains high and/or medusae abundance is low during peak spawning time for herring) will impact the total predation on bay anchovy and may affect their eventual recruitment (Cowan and Houde, 1993).

Large-scale oceanographic variability is an integral component of the dynamics of individual marine populations and affects their interaction through predation and competition (Dragesund and Nakken, 1973; Croxall *et al.*, 1988; Ainley *et al.*, 1995). One example is the annually variable geographic overlap between Barents Sea cod and capelin populations that determines the vulnerability of capelin to predation by cod (Mehl, 1989). A second example occurs off the east coast of Tasmania, Australia, where the warm filaments and eddies of the East Australia Current meet cold subantarctic waters creating the broad subtropical convergence (temperature gradient of ~ 2 to 4°C) that varies in latitudinal position seasonally and annually (Harris *et al.*, 1987; Young *et al.*, 1993). The convergence drives more productive slope waters on to the shelf. These waters mix with nutrient-rich west coast river run-off and cause increased production of krill and gelatinous zooplankton that are the food of small pelagics such as jack mackerel (target of a local reduction fishery), which in turn are a main prey of the southern bluefin tuna (target of a widespread fishery) (Young *et al.*, 1996). The position of the convergence and hence the potential to drive productive waters on to the shelf varies annually, perhaps linked to the strength of prevailing westerly winds and anti-ENSO (*La Niña*) events (Harris *et al.*, 1992; Pook, 1992). For example, in the summer of 1988/1989, when the sub-antarctic convergence was further south, the shelf was washed with nutrient-poor East Australian Current waters, krill stocks were absent, the jack mackerel fishery collapsed, which in turn reduced the tuna fishery (Young *et al.*, 1993).

Predation as a regulatory process

Hardy's classic diagram of the details of the "simple" trophic chain (herring eat copepods, copepods eat algae) demonstrates that predation in marine systems is a complicated affair (Hardy, 1924; Fig. 1). The level of detail in predation interactions rapidly becomes overwhelming, and the potential interactions in even comparatively simple seven-compartment models make prediction highly uncertain (Gomes, 1993). This is in marked contrast to freshwater systems with fewer fish species, where there can be a domino effect down a single food chain and the abundance of predators can be adjusted to control biomass at different trophic levels (Carpenter *et al.*, 1985; Mittlebach *et al.*, 1995), although marine intertidal studies including invertebrates with restricted range have shown similar properties (Simenstad *et al.*, 1978; Duggins, 1980; Estes and VanBlaricom, 1985; Kneib, 1988).

Predation does not always have a regulatory effect on a population; the mortality rate from predation can be either independent of the prey animal's density (density-independent) or dependent on this density (density-

dependent). Whether predation is a density-dependent or density-independent influence on populations is a key component of the 50-year ecological debate concerning how populations are regulated (see Wu and Loucks, 1995 for a summary of this debate). Many fish are general predators, and early researchers suggested that such predators are stabilizing (density-dependent) forces on populations because they eat a variety of prey, targeting the most abundant species until its abundance is reduced relative to other suitable prey (e.g. Elton, 1927 in Murdoch, 1969). Since those early days, there has been considerable effort to try and understand exactly how different types of predator impact their prey populations and in particular whether generalist or specific predators are more likely to exert a density-dependent effect on prey populations. It is illuminating to follow the course of this research, as it provides a framework for how we think about predation, its regulatory impact and its operation in the complex systems that are natural communities.

Theoretical basis of population regulation by predation

Predators' responses to prey can be divided into the numerical response (where predator numbers changes with prey density) and the functional response (where the numbers of prey eaten per predator per unit time changes with prey density) (Solomon, 1949 in Murdoch, 1969). The numerical response can be further divided into an intragenerational aggregative response to prey patchiness and a development response (birth, death, and growth rates) that has inter- and intragenerational components, although small-scale aggregative responses to prey patchiness are often included in the functional response (Murdoch and Oaten, 1975). A further interaction of predators and their prey derives from the response of each predator to other predators, which might be a more important source of stability than the response of each predator to prey density (Holling, 1959; Hassel and May, 1973).

The predators' functional response to prey has, until recently, received the most attention and this probably reflects its amenability to investigation in the laboratory and controlled field situations. Murdoch (1969) coined the phrase "switching" to describe the response of individual predators to changing prey densities. The functional response defines the degree of switching from one prey to another. The earliest experiments that demonstrate switching may be those of Popham (1941 in Murdoch and Oaten, 1975) for rudd. Timing and degree of switching are crucial to the stabilizing effect of the general predator, because for switching to produce stability, it must result in an increasing proportion of a prey population being eaten as the prey population

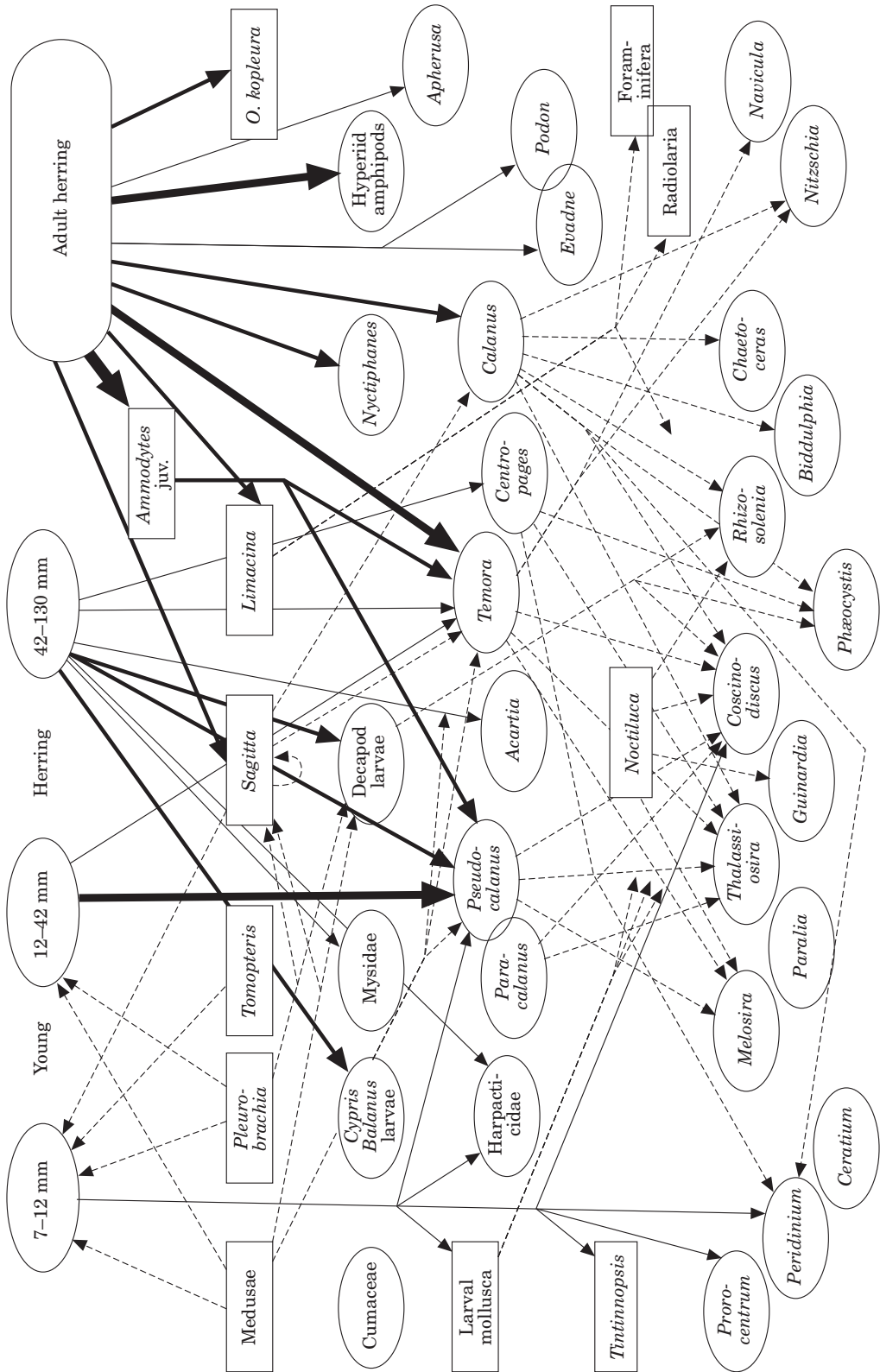


Figure 1. The food web representing the food sources that North Sea herring depends on during its life cycle as described by Hardy (1924).

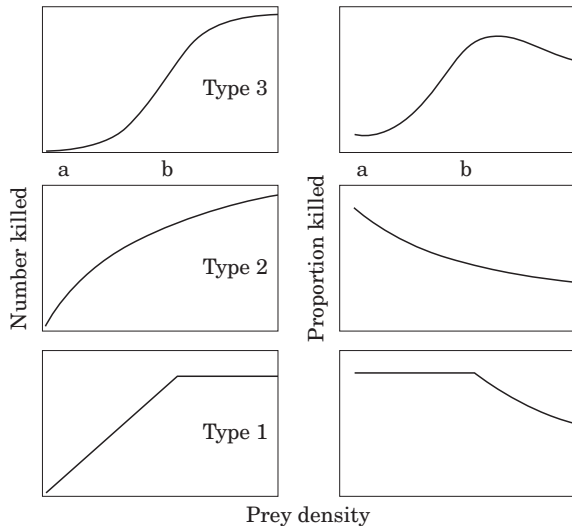


Figure 2. Three types of relationships between prey density and the attack rate of a single predator (the functional response). Only type 3 yields density dependent mortality, in the interval a–b (redrawn from Murdoch, 1973).

increases in size (Murdoch, 1969). Holling (1959) recognized three main types of functional response and their impact on prey killed per unit time (Fig. 2). Only the sigmoid curve (type 3) produces density-dependent mortality and would be stabilizing for the prey population. The type 1 functional response is the most commonly observed functional response in laboratory experiments with single prey species. It is density independent over the lower range of densities and inversely density dependent after that (Murdoch, 1969). Type 2 functional responses have been widely observed in laboratory experiments for many phyla including fish (summarized by Murdoch and Oaten, 1975). It produces inverse density dependence over the entire range of prey density because, although a predator eats more prey as prey density increases, the proportion of the prey population eaten is still less, perhaps because handling time is limiting or because the predator becomes satiated. Only type 3 functional responses would result in density dependent mortality and therefore be stabilizing for the prey population. But type 3 functional responses have rarely been observed in a laboratory with only one prey species (Murdoch and Oaten, 1975); some exceptions are protozoan predators, parasitic insects, and native fish. However, some factors that would cause the predation rate to decrease when prey was low – which is necessary for the type 3 functional response – may be missing in laboratory experiments. Examples include decreased predation with decreased stimulus from encounters with prey, development of an alternate search image, decreased probability of encountering prey patches, or a

change in behaviour of the prey species with changes in its density.

Density-dependent responses are more likely when more than one prey species is present, but they are not a necessary characteristic of multispecies systems and are frequently not stabilizing for the less preferred species (May, 1973). Stabilizing predation by switching between prey species is most likely to occur for predators with weak and variable prey preferences, i.e. general predators. Switching may not be sufficient unless the prey is patchily distributed, and the predator targets the most abundant prey (cf. search image), or remains in patches where the prey are most abundant. In such cases prey switching causes density-dependent mortality in the prey species, and is more efficient for the predator (Murdoch *et al.*, 1975). The form of the functional response of predator to prey is only one component of the predator–prey interaction; in Hassel and May (1973) it is suggested that it may be less important than interactions among predators (interference and aggregation) for population regulation. Furthermore, even if a stabilizing functional response were present for individual predators, there is no reason to expect that the same functional response would operate at the population level unless all predators were identical (Chesson, 1984). Negative switching (ratio of prey species in diet changes more slowly than their ratio changes in the environment) is the most likely result of individual differences in predators, and it would be destabilizing.

Real systems are much more complex than the direct interaction of predator and prey. These complexities can be stabilizing or destabilizing. Stabilizing predator–prey features include: refuges, invulnerable classes of prey, resource limitation for the prey, and spatial heterogeneity (Murdoch and Oaten, 1975). Destabilizing features include time lags and trophic complexity. Because predators are typically larger than their prey, they often also have a longer generation time. Any developmental response by the predator to prey density would therefore operate on a longer time scale than the dynamics of the prey population – there would be a time lag in the response.

Time lags are also destabilizing at the system level, where lags greater than a system's natural time scale (reciprocal of intrinsic growth rate) are destabilizing even if there is a potentially stabilizing negative feedback mechanism (May, 1972). Because a system's natural time scale increases with additional trophic levels, this is one example where increased trophic complexity can enhance stability. Generally, however, theoretical studies indicate that increased trophic complexity is associated with greater instability (May, 1973), although this may only apply at the individual species level and not at the community level (King and Pimm, 1983). The perceived wisdom is that complex systems are more stable than simpler systems, but this may reflect the

greater opportunities in a stable environment for complexity to develop and fully exploit resources, rather than increased stability due to increased complexity (May, 1973). Complexity is not as destabilizing when interactions are concentrated in small blocks (cf. the hierarchical concept of ecosystems – May, 1973; O'Neill *et al.*, 1986), and strong predator–prey interactions (i.e. highly specific predators) that reduce connectance overall also serve to reduce complexity and increase stability (May, 1973). Thus, although in laboratory situations generalist predators were considered to be a stabilizing influence, at the system level they are destabilizing.

Much of the literature of the 1970s and 1980s emphasized that predators can stabilize prey populations, but it appears that aquatic predators (and especially predators in fresh water) are more likely to be destabilizing than stabilizing (Murdoch and Bence, 1987). These authors found only one example in fish of a short-term type 3 functional response that could be attributed to switching, and even in this instance mortality at the population level remained inversely density-dependent. Overall, fish predators (in fresh water) are considered to be forces for instability, because they respond to prey density with a time lag (they have longer generation times), tend to continue eating a preferred prey even as its density decreases (may lead to local extinction), and satiation and handling time are constant constraints on switching even if preference does change with prey density (Murdoch and Bence, 1987). The presence of refuges may produce type 3 functional responses, but then this is a function of the refuge and not the response of the predator.

More recent work has placed greater emphasis on the role of spatial heterogeneity in promoting stability with the thought that aggregating non-equilibrium dynamics at the local population level may produce equilibrium dynamics at the metapopulation level. Local extinction may favour overall system persistence and, paradoxically, generalist predators may be forces for stability by causing local extinction. However, Murdoch (1994) points out that metapopulation models, where a population in a patch can go extinct and be recolonized, are analogues of single population models where each patch is equivalent to an individual. The stabilizing dynamics have been transferred to inter-patch dynamics and stabilizing forces are still required. This does, however, increase the range of possible stabilizing mechanisms. For example, limited mobility of adults and local spawning can lead to overall stability in a population through asynchrony of predator–prey dynamics in different patches (McCauley *et al.*, 1996). The scale of the regions of stability and instability depend on the degree of dispersal of offspring. Some difficulties identifying regulatory mechanisms for populations, even though their presence is required to explain the long-term persistence of many populations in nature, may derive

from looking at the wrong scale. This could explain why, despite the emphasis on population regulation by ecologists over the last 50 years, we are still no closer to a general solution (Murdoch and Bence, 1987). However, emphasis over the years has changed from a concern with equilibrium, homogeneity, determinism, and local or single-level properties of systems to non-equilibrium, heterogeneity, stochasticity, and hierarchical properties of ecological systems (Wu and Loucks, 1995). Future discoveries in population dynamics may come from considering the richness of natural communities.

Biological basis for population regulation by predation

“... an abstract population may be conceived when a real population is contemplated but certain of its qualities are arbitrarily abstracted from it so that they can be ignored. ... the abstraction make(s) analysis simpler. But simplicity may be dearly bought because the price is measured in departure from reality. This debt must be repaid before a realistic knowledge of the natural population can be claimed.” (Andrewartha and Birch, 1984, p. 16)

Given the demonstrated high levels of predation in marine ecosystems and its potential for selectively changing marine ecosystems, it might be expected that the importance of predation in regulating those systems would be as easily demonstrated, even if the theoretical basis for its regulatory effect is not defined. This has not proved to be the case. The potential for predation regulating recruitment and the potential for marine mammal predation regulating exploited fish species are two specific areas that have generated many studies. The indirect effects of predation and the impacts of predation on determining overall productivity and system structure have been less studied in marine ecosystems (cf. Kitchell *et al.*, 1994 for freshwater ecosystems).

Predation and recruitment

Much research has been conducted worldwide to determine whether starvation (derived from Hjort's 1914 critical period concept) or predation determine year-class strength in commercial fish stocks, but little evidence has been found to support the critical period concept (May, 1974; Bailey and Houde, 1989; although see Thresher *et al.*, 1989). The general absence of large numbers of starving larvae in the sea, the higher mortality of egg and pre-feeding larvae with plentiful yolk reserves than of larvae at yolk absorption (the critical period), and the high survival rates of several

commercial species raised in enclosures in the absence of predators all indicate that starvation may not be the primary determinant of year-class strength (Bailey and Houde, 1989). However, with few exceptions, it has also not been possible to demonstrate that predation determines year-class strength. The effects of predation are intertwined with those of food availability: starvation leads to an increased susceptibility to predation (Ricker, 1954; Bailey, 1984; Rice *et al.*, 1987). Generalist predators, such as jellyfish, can impact the year class of species such as herring first through direct predation, second through competition for food (which would slow growth rates), and thereby, third, increasing the prey's vulnerability to direct predation (Purcell *et al.*, 1987). However at present, there is no unequivocal proof that slower growth, caused by reduced food supplies, leads to more deaths from predators (Leggett and DeBlois, 1994). Reduced food supplies can, however, lead to increased exposure to predators (Gilliam and Fraser, 1987; Bailey, 1989; Gotceitas and Brown, 1993; Sogard and Olla, 1993; Hixon and Beets, 1994; Gotceitas *et al.*, 1995; Jordan *et al.*, 1996). This is well illustrated by the Japanese flounder, which moves up off the bottom two days after settlement unless it finds sufficient food (Tanaka *et al.*, 1989). Once off the bottom it becomes once again more susceptible to predators, including larger juveniles that settled earlier.

Although predation on the eggs, larvae and juveniles of fish is high, it has been difficult to define a relationship between abundance at these stages and recruitment to the mature stock (Sissenwine, 1984; though see Hylan and Dragesund, 1973; Myers and Barrowman, 1996). One problem is that eggs and larvae are often only one of several available food sources, predation on them is adventitious. Another is that in a flexible multispecies community, high mortality due to predation can happen locally over a short time and as consequence of independent events. This makes it very difficult to define regulatory processes that may depend on as much on the abundance and distribution of predators (and other suitable prey items) as on the abundance and distribution of the particular fish larvae.

Despite the opportunistic feeding behaviours of predators of egg and larvae, the high specificity of predation to time and place and the multiplicity of predators provide many opportunities for population regulation. This has been best documented in the southern North Sea plaice, where the total number of recruits appears to be determined during the pelagic egg and larval stage, when plaice suffer heavy mortality from selective predation by herring in open waters (Daan *et al.*, 1985), followed by coelenterates in coastal waters (van der Veer, 1986). At this point the coefficient of variation of year-class strength is 62%. The post-settlement and density-dependent predation by shrimp (more brown shrimp move into the area and include a

higher proportion of plaice in their diets as the number of plaice increase; van der Veer and Bergman, 1987) is the final regulator of year-class strength, reducing the coefficient of variation to 30%, which is close to that of 2-year-old plaice recruiting to the fishery. Beverton and Iles (1992) concluded that the mortality of North Sea plaice in the pelagic larval stage was density-independent and caused high variability in year-class strength, but that post-settlement mortality was density-dependent (perhaps operating through three sequential stages) and was sufficient to cause the low year-class variability characteristic of North Sea plaice (Fig. 3). Stock recruitment data for 69 out of 72 flatfish stocks are consistent with density dependent mortality occurring in the juvenile stages (Beverton, 1995). The conclusion that density-independent annual variability in population size is determined in the larval stage, but that density-dependent mortality in the juvenile stage attenuates this variability has been extended to 13 other North Atlantic demersal species (Myers and Cadigan, 1993).

Although predation has a large role in regulating fish recruitment in North Sea plaice, it may not be the general mechanism determining recruitment. There are other instances, including Pacific salmon migrating to sea and passing a relatively fixed gauntlet of predators, and herring eggs in Norwegian fjords having a relatively fixed amount of predation where predation will be inversely density-dependent taking a higher proportion of the eggs or juveniles in low recruitment years than in years of high recruitment (Neave, 1953; Johannessen, 1980; Peterman, 1982). Indeed, there is unlikely to be a single mechanism, rather a suite of factors affecting different life-history stages and where effects are enhanced or diminished by environmental variability. The impact of large-scale climate variability on local recruitment events (Sharp, 1992) indicates the ability of the environment to modify recruitment success, while the comprehensive demonstration by Myers and Barrowman (1996) of the positive relationship between spawner abundance and subsequent recruitment for almost all of 364 spawner-recruitment time series investigated shows that spawner abundance cannot be neglected. Interestingly, Myers and Barrowman's analyses found that of the six fish orders for which they had data, it was the flatfish that showed the weakest relationship between spawner abundance and subsequent recruitment.

Predation and marine mammals

Marine mammals are major predators of fish, including commercially fished populations, and generally concentrate on recruited fish. It might be expected that determining the effect of their predation on the size of fish populations would be relatively straightforward, however, it has once again been difficult to demonstrate that

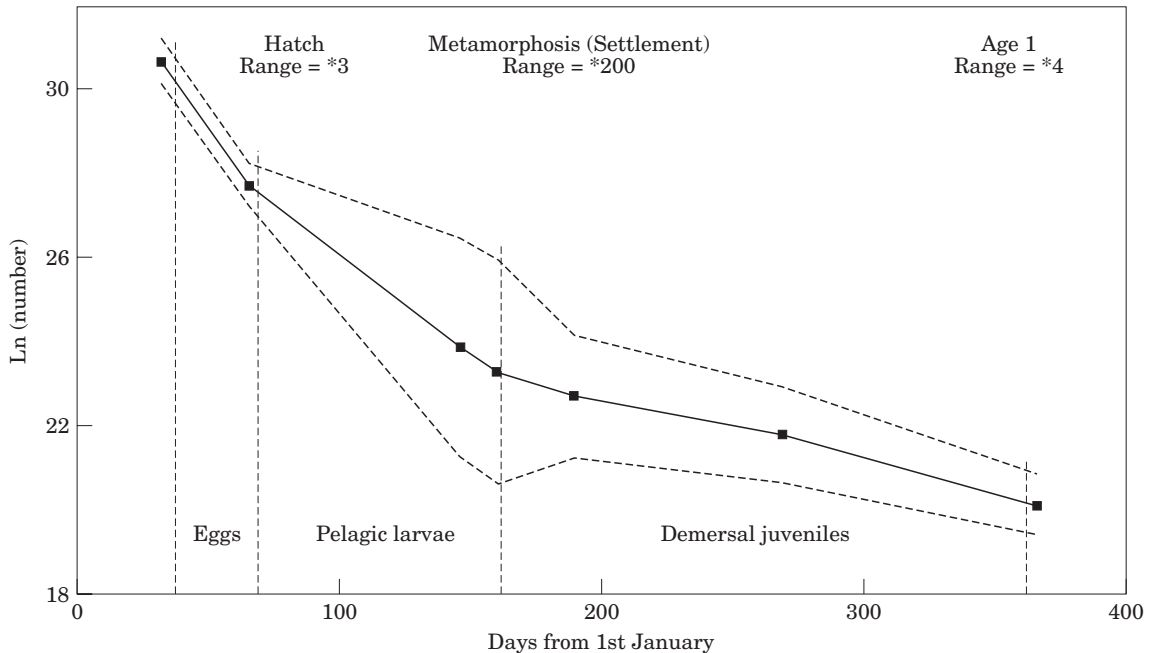


Figure 3. Survival curve for North Sea plaice from parents to the end of the first year, showing maximum ratios of year-class strength at intermediate ages. The expansion of the ratios at about 150 days expresses the possibility of very high variability (200-fold) during the pelagic larval stage, which is then progressively “damped” by density-dependent mortality to the observed 4-fold range at recruitment at age 1 (redrawn from Beverton, 1995).

predation has a regulatory impact. Even when predation by marine mammals may be equal to, or more than, commercial catches, there is insufficient evidence to conclude that this predation drives the changes in the fish populations (reviewed by Beverton, 1985). Only in an isolated freshwater lake, where there were few alternative food resources, was there good evidence that seals reduced fish abundance (Power and Gregoire, 1978). In this instance, the susceptible species (lake trout) had fewer larger-size classes, faster growth rates, greater fecundity, and an earlier age of maturity than in lakes without seals. The non-susceptible species (brook trout) were more abundant than in lakes without seals, as a result of decreased competition (for habitat) – an indirect effect of mammal predation.

Marine mammals have been shown to regulate populations over several trophic levels in the marine intertidal (Simenstad *et al.*, 1978; Duggins, 1980; Estes and VanBlaricom, 1985). Duggins (1980) showed that, within a year of removing sea urchins (a favourite food of sea otters) a kelp association of high biomass and diversity developed; in the second year both declined as a single kelp species became dominant. A similar trend in kelp biomass and diversity was observed when contrasting Torch bay (which has no sea otters) with Deer Harbor (which has had sea otters for less than 2 years) and Surge Bay (which has had them for 15 years) (Fig. 4).

Population regulation by marine mammals appears to occur (or is detected) primarily where their diet is specialized. Northridge and Beddington (1992) contrast the recognizable impacts of marine mammals with specialized diets, with the undetectable impact of marine mammals with more generalized feeding habits. Specialized predators like gray whales, which feed by sucking sediment into their mouths and extracting food items, create pits that may cover more than 30% of the sea bed in places. Dense tube mats of ampeliscid and other amphipod crustaceans are destroyed in the feeding process and replaced by other scavenging invertebrates (Oliver and Slattery, 1985). Similarly, areas of high walrus density in Alaskan waters are associated with relatively low bivalve mollusc densities (Fay *et al.*, 1977; in Northridge and Beddington, 1992), and walrus in Bristol Bay appear to eat more surf clams than the population can sustain (Fay and Lowry, 1981; in Northridge and Beddington, 1992). Conversely, grey seals in the North Sea, which feed on a variety of mobile fish species, are not considered to be a major factor influencing community dynamics, because the mortality they cause is generally one or two orders of magnitude less than that caused by fishing, and is not limited to one or two species (Harwood and Croxall, 1988). In this instance, fisheries interests held the view that the seals should be culled, mainly because, in

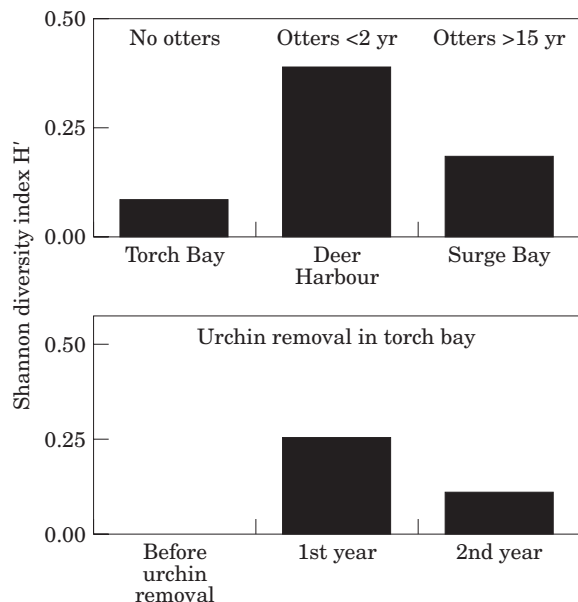


Figure 4. Species diversity of kelps in areas with otters present for different time periods (top) and in one experimental area after sea urchins were removed (bottom). There was no growth of macroscopic algae in removal areas before the experiments began (redrawn from Duggins, 1980).

1976, they ate about 112 000 t of commercially exploitable fish; if fishers could catch half of this amount, the extra harvest would be worth 15–20 million pounds sterling.

Indirect effects of predation

Indirect effects of predation can be divided into two general mechanisms: an interaction chain where a predator changes the abundance of an intermediary species (or resource) and this affects another predator on the same intermediary species; and an interaction modification, where a predator changes the use of a prey species (or resource) by another predator (Wootton, 1994). Interaction chains can be predicted readily, but interaction modifications are very difficult to predict (Wootton, 1994; though see Beverton, 1985). Typically, predictive models for predation consider only interaction chains, while many of the biological observations focus on interaction modification.

The threat of predation complicates the determination of its impact on the ecosystem as one consequence of the threat of direct predation is to change resources use by the potential prey, i.e. an interaction modification. For example, the threat of predation may result in (or be determined by) slower individual growth due to restricting potential prey to less preferred habitats (Gotceitas and Brown, 1993; Walters and Juanes, 1993; Crowder

et al., 1994; Gotceitas *et al.*, 1995; Jordan *et al.*, 1996), altered individual morphology to increase predator handling times (Nilsson *et al.*, 1995; though see Holopainen *et al.*, 1997), altered behaviour (reviewed by Lima and Dill, 1990; Burrows *et al.*, 1994), altered reproductive behaviour (reviewed by Sih, 1994), and an altered population growth rate due to selective predation of one size component of a year class (e.g. Bundgaard and Sparholt, 1992; Rice *et al.*, 1993; Gislason and Rice, 1996). Because fish accumulate large reserves of key nutrients (nitrogen and phosphorus) and are relatively mobile, they are important vectors of nutrients. Predator–prey interactions in lakes can change nutrient recycling rates and accelerate the exchange of nutrients between habitats (Kitchell *et al.*, 1994). Impacts of predation can be mediated through other limiting resources, for example habitat. Recruitment success of cunner, *Tautogalabrus adspersus*, that settled at similar rates in four different habitats (rocky reef, cobble, seagrass, and sand), was positively related to habitat complexity, while predation risk was negatively correlated with habitat complexity (Tupper and Boutlier, 1997). These examples are all phenotypic changes within a generation, but in a study of guppies transferred from a stream section with high natural predation to one with low natural predation, Reznick *et al.* (1997) found that the transferred guppies showed genotypic changes in age and size maturity within just a few generations (7 for males and 13 for females).

The indirect effects of predation are well illustrated in freshwater communities where predation that changes the habitat occupancy and foraging success of individual fish can lead to slower individual growth (Werner *et al.*, 1983; Werner and Hall, 1988; Tonn *et al.*, 1992) and fewer over-winter survivors (Post and Evans, 1989; Tonn *et al.*, 1992), which increases the prey's period of susceptibility to size-selective predation. Size-selective predation can therefore change the population growth rates, and species-selective predation can change both the community structure and the nutrient recycling in marine and fresh water (Vanni, 1987; Hanson and Chouinard, 1992; He and Wright, 1992; Hixon and Beets, 1993; Beyer and Lassen, 1994; Kitchell *et al.*, 1994; Gislason and Rice, 1996). The effects of predation on the feeding behaviour of the prey in freshwater ecosystems is often driven by small-scale patchiness in the environment, a feature often neglected in less easily studied marine ecosystems. However, recent *in situ* observations of microscale fish distribution show the association of individual fish on the continental shelf and upper slope with microhabitat including shells, small depressions, and depressions left by larger fish (Auster *et al.*, 1995). This may decrease detectability by other predators, while increasing opportunities for ambushing prey. Laboratory studies show that substrate choice by juvenile Atlantic cod varies in the presence of

predation threat (Gotceitas and Brown, 1993) and that avoidance of non-vegetated areas by pinfish and juvenile pollock results from presence of piscivore predators (Sogard and Olla, 1993; Jordan *et al.*, 1996). Trade-offs between predation risk and feeding opportunities may be as common a feature of marine ecosystems as they are for freshwater ecosystems. A particularly elegant example is the study of seabird community structure along a productivity gradient in the oceanic eastern tropical Pacific, where it was found that competition structured the community in areas of high productivity (flocks of Boobies competitively displaced flocks of smaller sooty terns), but energetic constraints structured the community in areas of lower productivity (sooty terns with relatively low flight costs were the only birds able to profit from the patchily distributed resources, Ballance *et al.*, 1997).

Both freshwater and marine fish will respond to the threat of predation by staying in the habitat where the risk of mortality, or the mortality risk per unit growth, is lowest (Gilliam, 1982; Gilliam and Fraser, 1987; Bailey, 1989; Tanaka *et al.*, 1989; Gotceitas and Brown, 1993; Sogard and Olla, 1993; Burrows *et al.*, 1994; Hixon and Beets, 1994; Kennedy *et al.*, 1994; Gotceitas *et al.*, 1995; Jordan *et al.*, 1996). When habitat is limiting this can lead to density-dependent regulation of the population, for which there is evidence in many flatfish stocks (Beverton, 1995). Habitat includes bottom features and water column properties. For example, Rose and Leggett (1990) report that although cod and capelin aggregate in the same local area, capelin concentrate in waters with temperatures outside the range preferred by cod. Avoidance of predation by vertical migration is often associated with diel feeding patterns (see review by Neilson and Perry, 1990); the onset of vertical migration can be delayed by the threat of predation (Burrows *et al.*, 1994). However, predation is not the only factor influencing habitat choice during vertical migration; energetic advantages and food availability can override predator avoidance. Juvenile pollock are found closer to the bottom, where there is a high risk of cannibalism, when food for the juveniles is limiting and lower temperature bottom waters would reduce metabolic demands (Bailey, 1989). The relation between predation and habitat may therefore be a major determinant of predation impact. Of the factors that influence habitat quality of flatfish (habitat quality is defined as the product of habitat structure, salinity, oxygen, water depth, hydrodynamics, food, predators, and temperature) the last three are considered to be the main ones (Gibson, 1994). Thus habitat quality in marine ecosystems will vary with environmental conditions on a diel basis, seasonally, and between years (Croxall *et al.*, 1988; Bailey, 1989; Mehl, 1989; Young *et al.*, 1993). Cold winters in the southern North Sea may limit the spread of brown shrimp in plaice nursery areas, reducing

predation on the recently settled larvae and leading to a strong year class (van der Veer and Bergman, 1987); however, no single event determines year-class strength – the strong year class of plaice in 1981 settled during a warm winter (Neill *et al.*, 1994).

Limits to habitat availability will vary with environmental factors and with population density (MacCall, 1990; Beverton, 1995). As the size of a population increases there will be less favourable habitat available and some individuals will be restricted to less favourable (greater predation risk or lesser food) habitats. Models including this trade-off have stock and recruitment dynamics similar to the classic Beverton-Holt and Ricker forms (Walters and Juanes, 1993).

Predation and ecosystem function

Just as there have been attempts to determine whether starvation or predation determine the survival rate of fish larvae and juveniles, so have there been attempts to determine whether predation (top-down) or food availability and competition (bottom-up) control the overall dynamics of aquatic ecosystems. Despite divisive early stances that either predation or competition was of greatest importance, both processes have been shown to be of varying importance in different studies and in different ecosystems (see reviews by: McQueen *et al.*, 1989; Hunter and Price, 1992; Sherman, 1992; Power, 1993; Polis, 1994; Brett and Goldman, 1997). This result was presaged by May (1972), whose model results supported by some observational data suggested that in a three level (vegetation–herbivore–predator) trophic system, herbivore population numbers would be set by neither predators nor vegetation alone, but by “an explicit interplay” between them. Theoretical studies suggest that top-down processes control the upper trophic levels, while production controls abundance in the lower trophic levels, the ultimate productivity of the system and the number of trophic levels (Leibold, 1989). An alternative, and not necessarily contradictory, view developed through extensive observation and manipulation of freshwater lake ecosystems is that potential productivity at all levels is set by nutrient supply, while actual productivity is determined by the recycling of nutrients by different populations (Carpenter *et al.*, 1985).

Factors, in addition to bottom-up production and top-down predation are important in determining trophic functioning. For example, not all production may be suitable for the next trophic level (Brett and Goldman, 1997), or potential prey species at the lower trophic levels just may not interact with predators at the higher levels (Rudstam *et al.*, 1994). Because different trophic levels operate at different space and time scales, high planktivore abundance may be sufficient to change zooplankton community structure for a decade, but

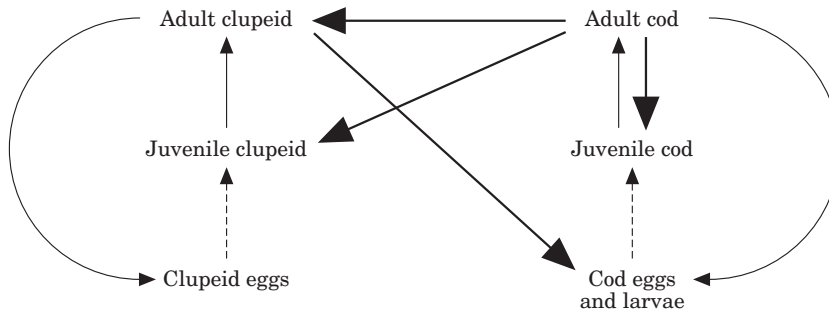


Figure 5. Conceptual model structure of the predatory interactions in the cod-clupeid system in the Baltic Sea. Top-down control through predation is marked by the thick arrows. Thin arrows represent the life-cycle progression of the two species; solid thin lines are well established relationships and dashed thin lines are relationships strongly affected by hydrographical conditions (redrawn from Rudstam *et al.*, 1994).

be insufficient to impact peak zooplankton abundance that develops rapidly due to parthenogenetically reproducing zooplankton (Rudstam *et al.*, 1993). Top-down processes may have a direct nutrient-mediated impact on lower trophic levels in addition to the one occurring due to predation on intermediate trophic levels (Vanni and Layne, 1997). In one of the few marine studies, Caddy (1993) concluded that in enclosed and semi-enclosed marine ecosystems, nutrient enrichment and fishing acted in synchrony to change the trophic structure, a conclusion also reached by Rudstam *et al.* (1994) for the Baltic Sea.

Although predation can significantly alter the community composition of an ecosystem, this may not alter ecosystem-level properties such as abundance, production and species diversity. There may be considerable “biological redundancy” in aquatic ecosystems (Schindler *et al.*, 1985), although this biological redundancy confers resilience to further external stress on an ecosystem (King and Pimm, 1983; Folke *et al.*, 1996). In the case of Schindler *et al.*'s (1985) studies where successively greater chemical treatments were applied to freshwater lakes, dominant species became rare and rare species dominant, but ecosystem-level properties did not change as they were set by the environment in which the lakes were set. One of the dangers of managing natural systems for consistent harvests, is that ecosystems may evolve to be more spatially uniform, less functionally diverse and more sensitive to disturbances that otherwise could have been absorbed – they have lost resilience (Folke *et al.*, 1996). In the Baltic Sea, where two competing top-down control processes have been observed (Fig. 5 from Rudstam *et al.*, 1994), the fishery has contributed to dominance of the planktivores (clupeids) by depleting the economically more valuable piscivores (cod). Planktivore dominance may prevent cod recruitment and the Baltic move to a clupeid-dominated system.

Examples of predation's impact

A good test of the role of predation in structuring marine ecosystems is the response to its removal. When sea otters were hunted to near-extinction in the North Pacific earlier this century, the abundance of sea urchins increased and kelp beds disappeared along large stretches of North Pacific coastline. However, sea otter populations are now increasing, which is reducing grazing by urchins and promoting growth of dense kelp beds (Estes and VanBlaricom, 1985). The renewed kelp forests provide refuge for kelp-bed fish, providing food for the otters, which have increased in abundance above the levels attained when invertebrates were the primary food resource. In this instance, the effects of predator removal were reversible; this may not always be the case. For example, an intertidal community on the west coast of South Africa is normally dominated by the rock lobster, which eats other benthic components, especially whelks, reducing their abundance but increasing the relative abundance of one whelk species covered by an unpalatable commensal bryozoan (Barkai and McQuaid, 1988). However, on one island, from which lobsters disappeared for unknown reasons within the last 20 years, several whelk species are abundant and there are extensive beds of black mussels, holothurians and sea urchins not found in areas where rock lobsters are present. This indicates the effects of predator removal on the benthic community, but what is more interesting is that, when externally sourced rock lobsters were released in the whelk-dominated habitat they were killed within 15 min (on average) of reintroduction as a result of approximately 300 whelks attaching themselves to the lobster. In this instance, the community has entered a new stable state where the former dominant predator (when artificially introduced from outside) can no longer survive, let alone structure the community (Fig. 6).

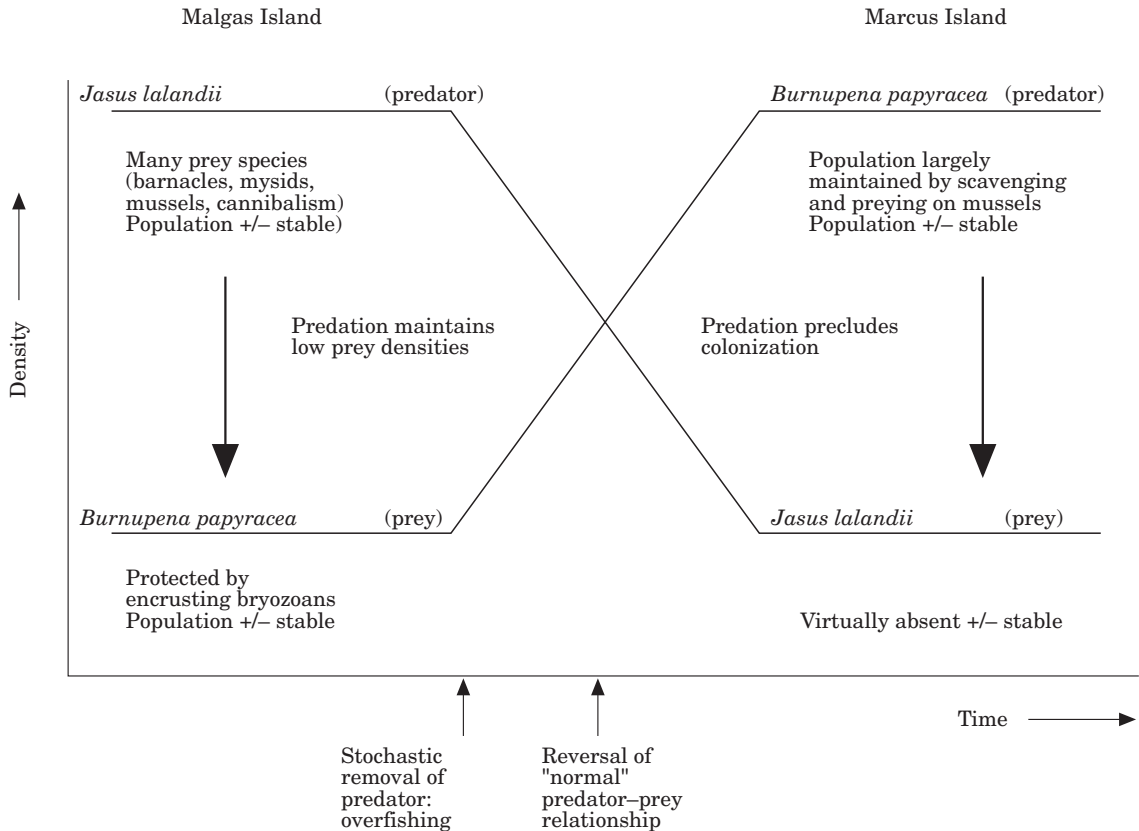


Figure 6. Schematic portraying the reversal of roles as predator and prey for rock lobster (*Jasus lalandii*) and the whelk (*Burnupena papyracea*) at Marcus and Malgas islands. The population have been monitored and found to be stable for more than 4 years (reprinted with permission from Barkai and McQuaid, 1988, Predator-prey role reversal in a marine benthic ecosystem, Science, volume 242, pp. 62–46. Copyright 1988 American Association for the Advancement of Science).

The United States north-east shelf ecosystem provides a large-scale (in geographic and economic terms) example of the selective removal of higher-valued, demersal predatory fish (e.g. cod, haddock, and flounders) through intensive fishing leading to an ecosystem dominated by lower-valued predatory fish (dogfish and skates constituted over 70% of the demersal biomass in 1986, and about 25% in 1963). This led to changes in consumption and predation throughout the ecosystem (Overholtz and Nicholas, 1979; Powers and Brown, 1987; Payne *et al.*, 1990). Despite reduced fishing effort this pattern has not changed (Sherman, 1992). It is not known whether this ecosystem has reached an alternate stable state that will require concerted management action to correct, or whether in time it will return to a state closer resembling its original condition.

Intensive fishing does not necessarily change an ecosystem to an alternate stable state. The North Sea has been intensively fished for decades as indicated by the decreased proportion of large fish in catches compared to catches from comparable areas including Georges Bank (Pope, 1989; Pope and Knights, 1982; ICES,

1994c). There have also been substantial changes in the abundances of individual species and the size of the overall catch. Yet, the community composition of demersal fish in the North-west North Sea between 1929–1953 and 1980–1993 remained relatively constant with only small and subtle changes in the relative abundance of rarer species (Greenstreet and Hall, 1996). Along with this, whilst the length composition of the whole demersal fish assemblage shifted towards smaller fish over this period, length frequency distributions of the non-target component remained relatively unchanged despite a century of intensive fishing. Ecosystem functioning (at least for the fish) may have been similarly unaffected – the mean trophic level of 34 fish species remained constant from 1947 to 1977, despite a doubling of catch (Yang, 1982). One reason for the species shifts on Georges Bank and the lack of species shifts in the North Sea may be the selective removal of only preferred species from particular length groups on Georges Bank, which are then replaced by those species which are only lightly fished (Pope, 1989), or have a high survival rate when discarded.

Modelling predation

Models are “. . . a marvelous crutch to the imagination, expanding awareness of subtle interactions that on first acquaintance are called ‘counterintuitive results’.” (Larkin, 1978)

An ultimate objective of modelling predation interactions in marine fisheries is to predict the results of selectively fishing different species thus reducing predation losses of desired species and increasing economic returns. Although selective fishing to reduce predation losses has been suggested (e.g. Gulland, 1982), the uncertainties involved in forecasting predation interactions and future recruitments make it a very risky proposition. Currently, in most fisheries management analyses, the rate of predation is assumed constant, which seems unreasonable (because losses due to predation usually equal or exceed those due to fishing), but has been shown to be reasonable in some instances (Punt and Hilborn, 1994). Even in models where most predatory interactions are included, the chosen stock and recruitment relationship remains of paramount importance (Shepherd, 1988). However, it is possible to model likely predation interactions and resulting abundance changes for a set of varied recruitments (Gislason, 1993) to determine whether a particular model prediction is robust to changes in recruitment of other species.

The level of aggregation of modelled subsystems, time, and geographic scales determine the questions that are suitable to be addressed with a particular model (Larkin and Gazey, 1982). They must be chosen appropriately or, and preferably, the sensitivity of predictions to a range of scales and levels of aggregation explored. The danger in modelling marine systems at only one scale is not just that important effects may be omitted, but also that the chosen units (e.g. stocks, species, or fisheries) reflect more the interests and judgment of the researcher than the actual structure of the system (Silvert and Dickie, 1982). Hierarchical modelling promotes the use of different scales in a hierarchy of models and provides a method for dealing with several levels of scale, while restricting complexity to achievable levels at each scale (May, 1973; O'Neill *et al.*, 1986). At least three levels need to be modelled: the focal level, a higher level to provide context and top-down constraints, and a lower level to provide mechanisms and impose bottom-up constraints. It may often be necessary to model one part of the whole interconnected assemblage in sufficient detail to be revealing while the remainder is treated as either constant or is relatively simplistically approximated. As Larkin and Gazey (1982) conclude: “Those with greater pretension will more often fail; those with [lesser] pretension will more often be irrelevant.” Whether a modelling approach is likely to have predictive power will depend on the complexity of

the system and the complexity of the questions to be asked. For example, when it is not possible to predict the dynamics of individual species, it may be possible to predict the dynamics of trophodynamic guilds (Tyler *et al.*, 1982; Sainsbury, 1988).

Because it is not possible to look at all predation processes in a fishery ecosystem, one must concentrate on those of greatest importance, being always aware that the excluded aspects may attain greater importance when there is a change in the context (*sensu* Sharp, 1992) of the predation processes. The simplest, and most common, assumption is that predation on a stock from all sources imposes a constant rate of mortality and therefore the stock can be assessed in isolation from its environment. For a fished population, which is fished at a commonly accepted sustainable level ($F_{0.1}$), this implies that half of the mortality (that due to natural causes) is considered constant, while the other half (that due to fishing) is considered to cause any variability in fish survival (Deriso, 1987). One step removed from this extreme is to concentrate only on direct (linear) predation interactions; for example if seals eat cod, it is assumed that reducing the number of seals reduces the consumption of cod, so the numbers of cod would increase. The next step is to consider first-order indirect (triangular) interactions, which have the potential to reverse the effects of direct interactions (e.g. May *et al.*, 1979; Butterworth *et al.*, 1988), and may confer stability on marine ecosystems (Ursin, 1982; Jones and Henderson, 1987; Fig. 7). For example, increased cod abundance increases predation on whiting and reduces the whiting abundance. Decreased whiting abundance reduces predation on Norway pout and the individual size and abundance of Norway pout increases. The larger, more abundant Norway pout are then a suitable prey for cod and predation on Norway pout increases. Thus if fishing pressure on cod in the North Sea were reduced such that the consumption of fish by cod doubled, more than half the increased consumption would be provided by fish that would not have been available to cod, if cod had not first consumed their other predators (Ursin, 1982).

However, it can be difficult, or impossible to predict the effects of fishing or culling on even these fairly simple triangular representations of predation processes. Impacts of fishing on these triangular interactions are symmetrical if the fishery and predator exploit the same prey, but asymmetrical if the fishery and predator exploit different (interacting) prey species (Beverton, 1985). Beverton concludes that the likely impact of a change in abundance of the predator (e.g. marine mammals) on the abundance of the commercially exploited fish may be qualitatively predictable for symmetrical interactions, but that even the direction of change in the abundance of the commercial fish following a change in abundance of the predator is indeterminate for

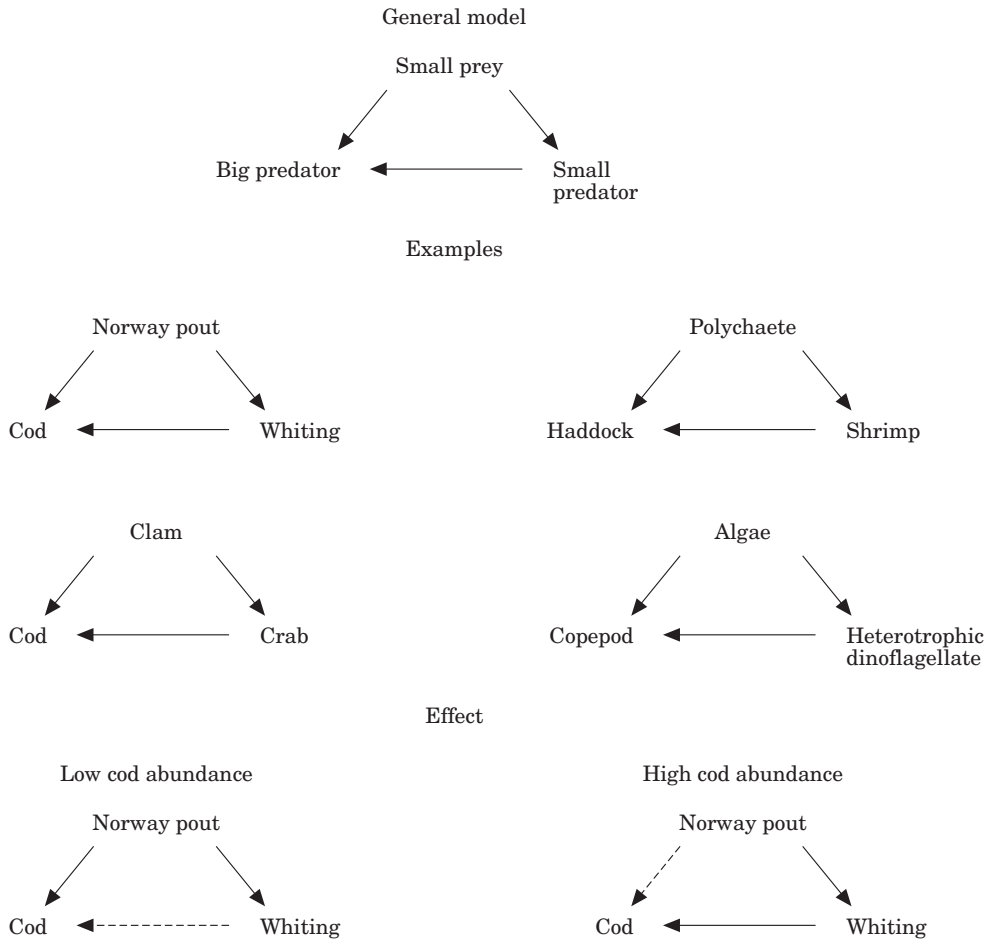


Figure 7. Triangular food web (top) proposed by Ursin (1982) as a mechanism of stability in marine ecosystems, some examples of triangular food webs (middle) and an illustration of how the interactions change to confer stability on a plankton community (redrawn from Ursin, 1982).

asymmetrical interactions. Beyond this level of abstraction the predation interactions, and especially interactions that modify resource use (Wootton, 1994), become more complicated and the results dependent on the model's specifications (Gomes, 1993). It is at this level that general regulatory patterns are unknown and much work remains to be done, although there have been advances in freshwater ecosystems (e.g. Kitchell *et al.*, 1994; Mittlebach *et al.*, 1995).

Available models

"All models are wrong, but some are useful" (Chatfield, 1995)

Models of fish predation in marine ecosystems vary from whole-ecosystem simulation (e.g. Andersen and Ursin, 1977; Laevastu *et al.*, 1982) and the more simplified box models (e.g. Polovina, 1984; Christensen and Pauly,

1992) that simulate predation and energy flow through the ecosystem, to highly idealized models derived from theoretical ecology (e.g. May *et al.*, 1979) and intermediate models that retrospectively analyse the catch data of a limited number of species while accounting for predation (e.g. Helgason and Gislason, 1979; Pope, 1979).

Whole-ecosystem models provide a comprehensive representation of predation in the ecosystem and can be used to isolate dominant interactions, but require extensive data input and are unable to provide precise estimates. This lack of precision has restricted their general acceptance, but they have stimulated the development of conceptually simpler, but more precise models (Sissenwine and Daan, 1991). Features of these earlier models (especially spatial structure) will continue to be added to the more precise models as new modelling approaches and additional data increase the level of realism that can be modelled precisely. However, the relative importance of realism in model structure vs.

precision in model output remains a vexing question in modelling predation interactions. There is little justification for increasing realism without a clearly demonstrated need yet, as the importance of modelling predation interactions in the marine ecosystems is to provide long-term forecasts for events outside those observed previously, it would be short-sighted to unnecessarily restrict the parameter space that could be explored. Simplicity may be dearly bought because the price is measured in departure from reality – a debt that must be repaid before a realistic knowledge of the natural population can be claimed (Andrewartha and Birch, 1984). Complex natural communities exist as the result of intricate evolutionary processes, and their stability may depend on a relatively tiny and mathematically atypical region of parameter space (May, 1973).

One strength of the whole-ecosystem models is that they can give alternate estimates of marine resource abundance, which is especially valuable for stocks and areas where standard techniques cannot be used or where there may be a systematic bias in more standard abundance estimators (Laevastu and Larkins, 1981; Bax and Eliassen, 1990). These models, and the more tractable box models that incorporate inverse analysis to provide fits to undetermined systems (Christensen and Pauly, 1992) are useful in deciding which species should be incorporated or aggregated in reduced and more rigorous models. The weakness of these models is that they require extensive information on the diet of all included species (groups) and there is little possibility of examining the accuracy of this information (or the aggregation procedure) unless independent estimates of biomass are available (e.g. Bax and Eliassen, 1990). Detailed analysis of these models, especially the simplified box models, though mathematically attractive, will suffer from many of the same limitations as analysis of food webs, where incomplete sampling or the aggregation of trophic entities can strongly bias estimates of food web properties (e.g. Paine, 1988; Peters, 1988; Polis, 1994; Goldwasser and Roughgarden, 1997; though see Pimm and Kitching, 1988). This may be especially true for aquatic food webs, where ontogenetic shifts in diet are common (Fuiman, 1994), but species are rarely broken down into size, age or life history stages that would represent distinct trophic components.

Simpler theoretical models, often extensions of the classical Lotka–Volterra equations to include harvesting, provide a means of exploring the interactions of predator and prey. They cannot capture the complexity of natural systems, but they are a valuable means of understanding the relevance of particular ecological processes and their mathematical representation to system properties such as stability, extinction, sustainable yields and predation interactions (e.g. May *et al.*, 1979; Yodzis, 1994; see review by Sainsbury, 1988). Some of the constraints in the theoretical models based on

Lotka–Volterra equations are (Beverton, 1985): impacts of predation are mediated through changes to the logistic growth dynamics of the prey (an abstract formulation); the amount of predation is usually considered a constant proportion of the predator's biomass and independent of prey abundance; predator biomass is usually assumed to depend only on prey abundance (no allowance for limited resources other than prey or for changes in resource availability); and, interactions are usually specified as independent of the size composition of predator and prey species.

Multispecies extensions to retrospective catch models provide the possibility of incorporating the interactions of the species that are either of interest to, or susceptible to, management intervention. Considerable effort has been expended on them. Forward projections from these retrospective analyses, using a multispecies extension to age-structured yield-per-recruit models have clearly indicated that predatory interactions could influence standard fisheries prognoses in the North Sea (Fig. 8) and Irish Sea (Macer and Shepherd, 1987; Brander, 1988). The ICES Multispecies virtual population analysis (MSVPA; Helgason and Gislason, 1979; Gislason and Helgason, 1985; Gislason, 1993) is the most thoroughly researched model (see Magnússon, 1995) but other models have been used to explore the interactions of marine mammals and fisheries (e.g. Leonart *et al.*, 1985; Punt, 1994) and several of the available catch-at-age analyses can be configured to examine the implications of direct predation, including cannibalism.

It is usual when modelling predation to assume that the main properties of interspecies predation can be described by a function with parameters that remain constant over the period of analysis or prediction. Without this assumption, extensive collections of stomachs would be necessary over all scales of variability. This assumption replaces the assumption common to single-species models that all mortality except that due to fishing is constant over the period of interest. It is not known whether interspecies predation in marine fisheries can be described by this assumption, which is the key assumption in moving from single species to multispecies prediction. The ICES multispecies assessment of North Sea fisheries provides one of the first tests of the validity of this assumption and the results are considered below.

The ICES MSVPA generalizes single-species VPA (a retrospective examination of catch data) so that natural mortality is no longer a constant value but consists of a fixed component, which represents non-predation natural mortality and predation by species not included in the model, and a variable component that is a function of the estimated consumption of the modelled fish and the suitability (edibility) of other fish and age classes. The variable component of mortality is estimated within the model and depends on the assumption

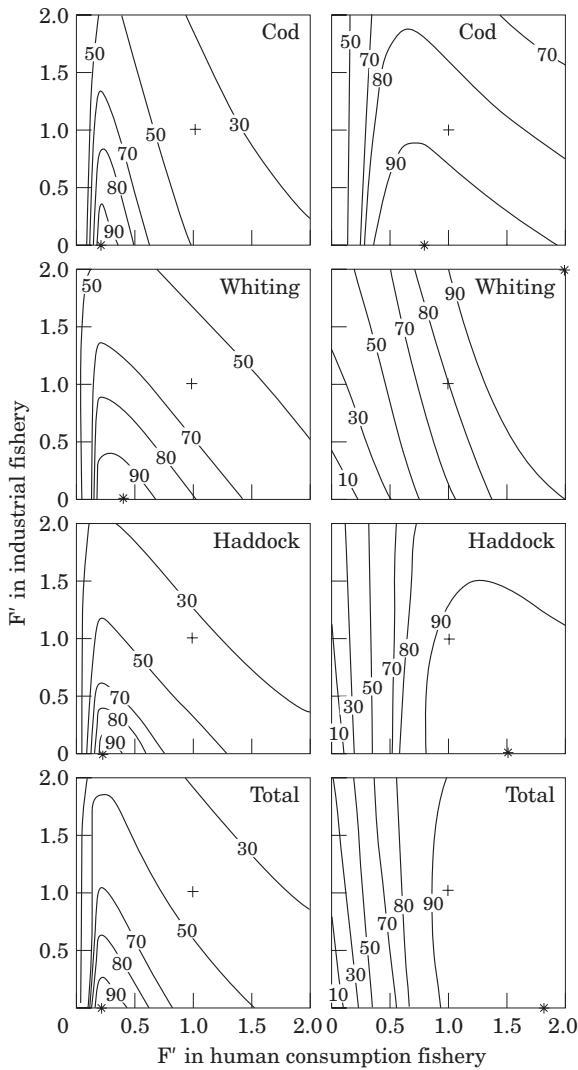


Figure 8. Yield-per-recruit isopleths expressed as percentages of maximum yield-per-recruit (*) for given levels of fishing mortality in the industrial fishery (targeting small fish) and the human consumption fishery (targeting larger fish) for North Sea cod, whiting, haddock, and the combined species. Isoleth graphs in the left-hand column exclude predation effects; isopleth graphs in the right-hand column include predation effects for these three species. Fishing mortality is expressed relative to the current situation (+) (reprinted from Fisheries Research, Volume 5, Macer and Shepherd, The effect of species and fisheries interactions on the assessment of some North Sea Gadoids, pp. 303–317, 1987, with permission from Elsevier Science).

that the suitability of a prey item for a predator remains constant over time and that the biomass of other prey (species not explicitly modelled) remains constant (Gislason, 1993); this leads to a type II functional relationship (Magnússon, 1995). These assumptions were tested by configuring MSVPA with data from the

stomach collections from 1981 (55 166 fish) and 1991 (92 894 fish) in a “key run”, and using the constant suitabilities generated by the model to predict stomach contents in 1981 and 1991 (ICES, 1994b). Eleven species (and other prey) were included in the model: two species were predators, three species were predator and prey, four species were prey only, and two species did not interact with other species. The model does not include predation on eggs, larvae or small juveniles.

In Figure 9, the model’s prediction of the relative consumption of the five predators in 1981 and 1991 is compared with their estimated actual consumption (computed from the stomach contents) in the 2 years. Further details and analyses are provided in ICES (1994b). The model predicted that the relative consumption of Norway pout by all predators should be at similar levels for each year, however, the estimated actual consumption was higher in 1991 than in 1981 (Fig. 9). The same prediction was made for relative consumption sprat by all predators but estimated consumption declined between 1981 and 1991. Generally, the relative consumption of prey species predicted by the key run for 1981 and 1991 were closer to each other than to the estimated consumption for those years. When a prey selection model was fitted to the estimated suitabilities from 1981 and 1991, approximately 50% of the variation was explained (ICES, 1994b). A further 5–10% of the variation was explained by including year effects in the model. A very small proportion of the unexplained variability could be explained by suitability changing with prey biomass, but this was not a strong effect (ICES, 1994b). The remainder of the unexplained variability may result from changes in spatial overlap of the species (no spatial structure is included in the North Sea MSVPA), other aspects of predator–prey interactions that have not been modelled, and sampling variability.

That the suitability does not seem to change very much over the 10 year period is a significant achievement. The North Sea MSVPA integrates predator–prey interactions over many spatial scales and has a coarse time step relative to many of the interactions that will have occurred. The results suggest that some features of predator–prey interactions could be reasonably modelled at the ecosystem level without explicitly representing their finer-scale attributes. The drawback is that the North Sea MSVPA has required a tremendous amount of field collections, data analysis and modelling; few other marine ecosystems are likely to be so thoroughly studied.

The models described so far consider the ecosystem as a collection of interacting species. The complex interactions of species in a natural ecosystem cannot be represented in their entirety, and no model describes the interactions of the egg, larvae, and early juvenile stages, although this may be where year-class strength is

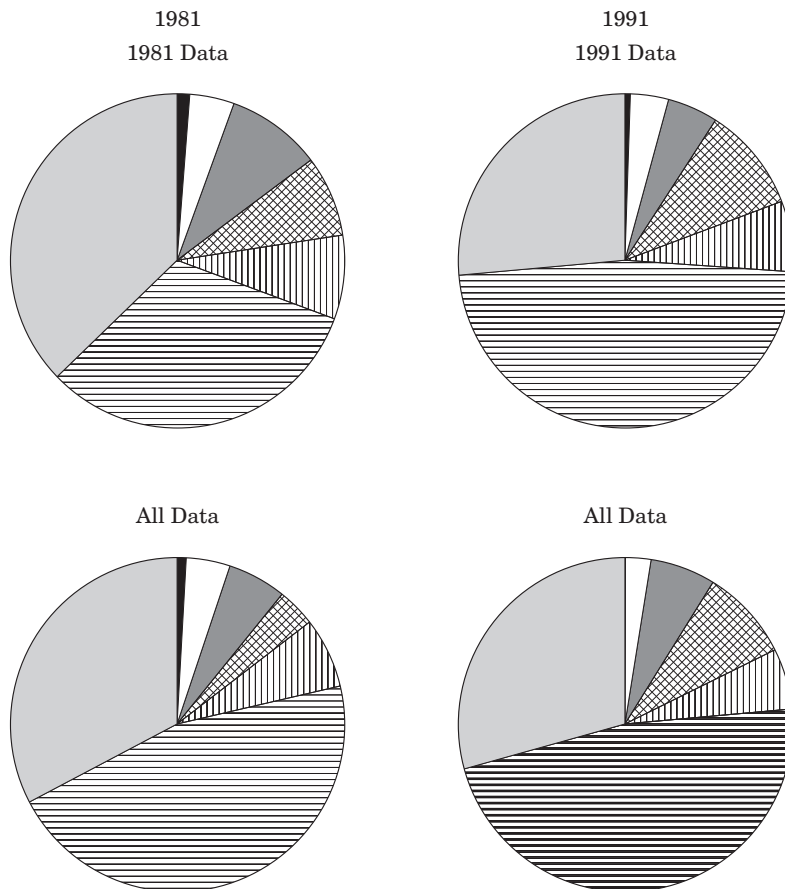


Figure 9. Relative consumption by all North Sea MSVPA predators in 1981 and 1991 estimated from the data collected in those years, compared with that estimated by the MSVPA model keyrun, which uses all data (redrawn from ICES, 1994b). Cod (■); Whiting (□); Haddock (▨); Herring (▧); Sprat (▩); Norway pout (▪); Sand eel (▬).

determined for many species (Myers and Cadigan, 1993).

Many attributes of species interactions in marine communities can be explained on the basis of individual size (e.g. Gomes, 1993; Paradis *et al.*, 1996; though see Fuiman, 1994) and most models that aim to describe system properties at levels higher than species have been particle-size spectrum models (e.g. Sheldon *et al.*, 1977; Platt, 1985; see Mann, 1988 for review). These models assume (based on considerable observation) that the frequency distribution of particles is represented by an orderly decline with increasing size; the biomass of one sector of the community (large fish for example) should, therefore, be deducible from another sector (phytoplankton, for example) where the steepness of the slope is a measure of the effectiveness of transferring energy from small to large organisms. This approach was used by Maloney and Fields (1985) to estimate potential pelagic fish yields off southern Benguela and Namibia, and estimated yields in the same range as recorded catches. Pope and Knights (1982) and Ursin (1982)

demonstrated that the size-spectrum of groundfish taken in a North Sea survey was uniform in different years and in periods of different fish composition, although it has changed since then (ICES, 1994c). Pope (1989) compared the slopes for North Sea and Georges Bank fish over the range of 10–110 cm. The steeper slope for the North Sea fish indicates the proportion of smaller fish is larger than on Georges Bank, and is the expected result of the higher fishing pressure in the North Sea (Fig. 10). Both single species and multispecies models predict that the slope of the size spectrum will steepen in direct proportion to an increase in fishing pressure (Gislason and Rice, 1996). Pope concluded that much of the management emphasis for North Sea fish over the next 100 years will be in defining and managing for the optimum size composition of the fish assemblage. These models provide an alternative approach to assessing and managing marine ecosystems. Their advantage is that they start to look at the properties of the system rather than at those of individual species or a select group of interacting species (Mann, 1988). Their disadvantage is

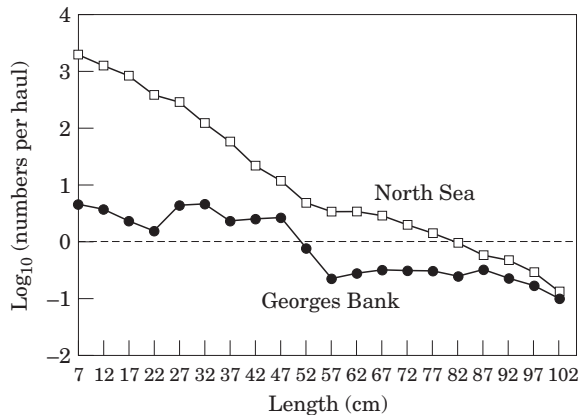


Figure 10. Comparison of the total finfish catch-at-length per trawl haul on Georges Bank and in the North Sea (from Pope, 1989).

that they look at total biomass without discrimination by species. This limits their direct utility to managers and omits important population level attributes that may change while system properties remain relatively constant. They will need to be integrated with other properties of ecosystem functioning if they are to become of more relevance to management.

Examples

Given the uncertainties and variability of predation in marine ecosystems, the necessity of modelling it must be questioned. Punt and Hilborn (1994) make the case that including predation (cannibalism in this instance) in stock assessment models does not necessarily improve their performance, but a distinction must be drawn between short-term tactical and medium- to long-term strategic forecasting. In tactical management it may be reasonable to assume that natural mortality remains fixed except on important prey species that are also commercially fished, e.g. Barents Sea capelin. The effect of changes in the survival of the recruits, who suffer most from predation, will only affect a small part of the exploitable biomass in the short term. In effect, there is no need to predict outside of the current small parameter space. However, over the time periods of interest in strategic management, year-class strengths will depend on the relative abundance of predator and prey species, predation parameters can no longer be considered constant, and predictions outside of a small current parameter space will be required. Three examples – models of interactions of seal and hake off South Africa, the ICES MSVPA and MSFOR, and an approach to distinguishing competing models of species interaction on the North-west Shelf of Australia will be discussed here.

ICES MSVPA and MSFOR

The ICES MSVPA and MSFOR models are extensions of earlier single species catch at age models that have incorporated predation interactions. Explicit age structure and seasonal resolution have resulted in extensive data requirements met only by coordinated international sampling programmes. Commercial species are the focus of these models; the potential for non-commercial species to cause novel or to modify existing predation interactions is unknown.

Results from the ICES MSVPA have had a marked effect on the scientific advice provided to managers. Quite early in its development, it became apparent that the convenient assumption that juvenile fish suffered the same instantaneous mortality rate as adult fish was incorrect. An incorrect schedule of mortality rates would substantially alter the scientific advice provided to managers on mesh selectivity, for example. As Gislason and Helgason (1985) concluded “a changed exploitation pattern and a higher natural mortality for the younger age-groups will change both the yield-per-recruit and the mesh-size assessments. It thus seems likely that much of the current advice, which is based on calculations where the same natural mortality has been applied to all ages, is wrong.” Updated mortality rates developed in the MSVPA are now included in single-species assessments of North Sea fish.

An example of the value of strategic modelling is provided by the application of a forecasting model, MSFOR (which followed on from the ICES MSVPA) to examine the likely impact of an increased mesh size in the North Sea fishery (ICES, 1989). It was expected from single-species analyses that increasing the mesh size would increase yield-per-recruit of the main commercial fish because more of the younger smaller fish would survive to a larger size. However, when multispecies interactions were included, it was found that yields would decrease for almost all commercial species. ICES (1992) concluded that the quantitative results from predictions with this multispecies model underscore an earlier warning that “intuition and qualitative models can mislead when used to evaluate indirect effects of fishing . . . Even the directions of responses are indeterminate and magnitude of responses differ greatly in response to a fixed change in harvest.” (ICES, 1992, p. 37.)

The ICES MSVPA and MSFOR models have had an impact not because of individual predictions but because they have been able to demonstrate that (then) accepted ideas of population dynamics used in single species models were either wrong or, by failing to consider indirect effects of predation, overly simplistic. It is recognized that some predictions from MSFOR are not robust to recruitment variability (Gislason, 1993), and that this constrains the direct application of such results.

Seals and hake

The generalist diet of predatory marine mammals makes it very difficult to determine their impact on a prey species or on the ecosystem, because several species other than the commercial species of interest could be affected and these fish species might be competitors or predators (e.g. Northridge and Beddington, 1992). Bowen (1985) concluded from a review of the interactions of seals and fisheries in the North-west Atlantic that “we simply cannot say what effect an increase or decrease in the harp seal populations will have on fish catches over the long term”, because the generalist diets of the remaining seals and the presence of other predators (whales, seabirds, and cod), that also eat juvenile fish, make it likely that any reduction in predation on the various commercial fish populations would be compensated by predation from other sources. The Royal Commission (1986) on seals and sealing in Canada concluded that, although there was strong evidence that seals could affect the abundance of fish stocks, it was “not aware of any instance in which known and measured change in the abundance of seals has had a measurable effect on fish catches”. Butterworth *et al.* (1988), investigating the scientific basis for reducing the South African seal population, could find no “proven link between seal population reduction and a consequential increase in yield to any fishery world-wide”.

Despite these cautions, there has been interest in the north- and south-east Atlantic in reducing the population of seals to increase returns to the commercial fisheries. The Fisheries Resource Conservation Council, an independent advisory body set up in 1993 to make formal public recommendations to the Minister of Fisheries and Oceans Canada, reaffirmed the appropriateness of the “ecological approach”, and concluded (among other things) that early action should be taken to significantly reduce the populations of seals to help recovery of the groundfish stocks (FRCC, 1994). Interestingly, the Council concluded that good decisions can be made on the basis of common sense, even though the complex interactions operating in the ecosystem are not formally understood. However, more detailed analysis showed first that cod were a relatively small component of the three major seal species in the region and second, while the three seal species consumed cod less than age 3, recruitment at age 3 was only below normal for one of the six Canadian stocks 3 during the cod collapse, thus indicating that it was increased mortality on cod no longer susceptible to seals that led to the collapse (Myers *et al.*, 1997).

Another example of where common sense might not prevail is provided by modelling of the hake and seal interaction off Southern Africa. The Cape fur seal (which has tripled in numbers since the introduction of

legal controls in 1893), are now estimated to eat as much hake as the fishery catches, and are likely to increase further because resources are not yet limited (Wickens *et al.*, 1992). A model developed by Wickens *et al.* (1992) represents a single unstructured population of seals from which (among many other things) the annual consumption of fish is estimated under various harvest strategies. The structure of this model is represented in Figure 11. The model was designed to test different management hypotheses against their success in “efficiently: (1) culling to reduce seal population growth rate, (2) culling to reduce fish consumption, and (3) harvesting to maximize number of seals removed over a period of time.” Simulation model runs indicated that reduction of fish consumption was achieved under any scenario that reduced seal population growth rate (Fig. 12). No attempt was made to define the species composition of fish eaten, which is an important distinction from the next model.

A second model, developed by Punt (1994), is a “minimal realistic” model that only incorporates predation on hake by seals and other hake species and cannibalism. This model (see Fig. 13) could be configured to include one or two hake species. When configured to include only one hake species, it consistently predicted that a cull of seals would lead to slightly increased average catches, catch rates and profits, balanced by a decreased consumption of hake by seals. However, when configured to include two morphologically different hake species interacting through predation, the opposite was predicted: seal culling would lead to reduced average catches, catch rates and profits (Fig. 14). The reason for this reversal is that only one of the two hake species is vulnerable to predation by seals, and adults of this species eat the juveniles of the other species. If the seal population were reduced, the numbers of the predatory hake would increase, while the numbers of the predated hake would decline, resulting in an overall decline in catch rates.

The predictability of these results conforms with Beverton’s (1985) overview of interactions between marine mammals and fisheries. Results of a change in predation are only predictable by common sense when the predator and the fishery target the same prey species (the interaction is symmetrical). When the fishery and the predator target different prey species (or the prey comprises several species not all of which are targeted by both fishery and predator), then the results of a change in predation are unpredictable (the interaction is asymmetrical), without a detailed knowledge of the interactions between predator, fishery and prey species.

Predation interactions may appear symmetrical when information is lacking. In the above examples the interaction between Cape fur seals and the two species of hake appeared symmetrical when the several prey species were aggregated as fish (Wickens *et al.*, 1992) or

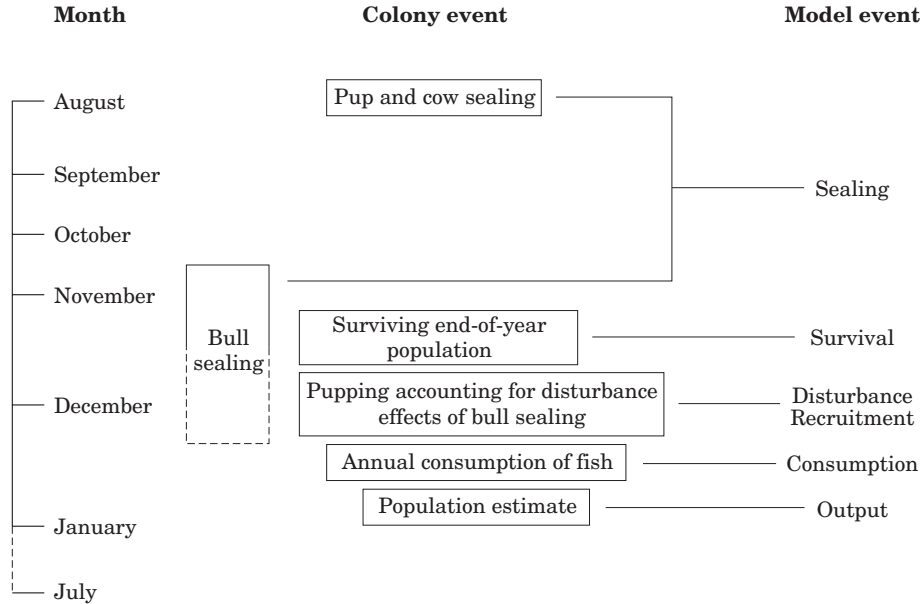


Figure 11. Schematic showing the temporal sequence of events at a South African fur seal colony and the corresponding sequence in the simulation model (from Wickens *et al.*, 1992).

a single hake species (one-species model of Punt, 1994). When the several prey species were recognized as interacting species subject to different exploitation (two-species model of Punt, 1994), the asymmetric interactions were evident.

The asymmetry of predation interactions is often not recognized until ontogenetic predation changes are recognized. In an earlier model of the Cape fur seal and hake interaction (Bax and Crawford: unpublished data)

the two interacting hake species were specified as one cannibalistic species separated into juveniles and adults. The predicted impact of seal culling on the adult hake exploited by the fishery was again negative, mediated by the cannibalism of adult hake on juvenile hake, and by increased predation of predatory fish (including squid) on juvenile hake; abundance of predatory fish increased because of reduced predation by fur seals.

It is the potential for ontogenetic changes in diet and susceptibility to potential predators that causes one of the main uncertainties in predicting predation interactions (Fuiman, 1994, see Fig. 5 from Rudstam *et al.*, 1994). Predation interactions that appear symmetrical when considering only adult fish (often the fish exploited by a fishery) may be asymmetrical once the predation interactions of the juveniles are understood. Asymmetry may result from increased predation on the juveniles or through increased competition. A model of a north Norwegian fjord ecosystem (Bax and Eliassen, 1990) demonstrated that although increasing herring abundance would at first directly benefit the cod population, the competition for food between adult herring and juvenile cod would result in higher juvenile cod mortality and a subsequent overall decline in the cod population.

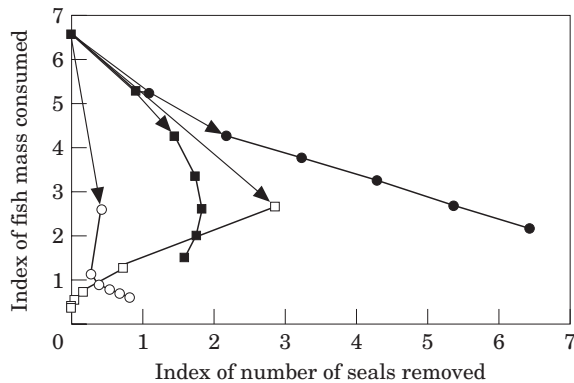


Figure 12. Index of fish consumption by the South African fur seal for different levels and different selectivities of seal culling, from a simulation model. Each line represents increases in the cull rate from 0 to 60% in steps of 10% in the direction of the arrows. Culling is simulated for pups (solid squares), cows (open squares), bulls excluding disturbance (solid circles) and bulls including disturbance (open circles) (from Wickens *et al.*, 1992).

It is clear that reducing the numbers of a particular predator is unlikely to lead to a proportional reduction in the predation on a targeted prey species; the remaining predators (of the same or different species) will increase their predation as the abundance of the targeted prey species increases. Ontogenetic changes in diet may

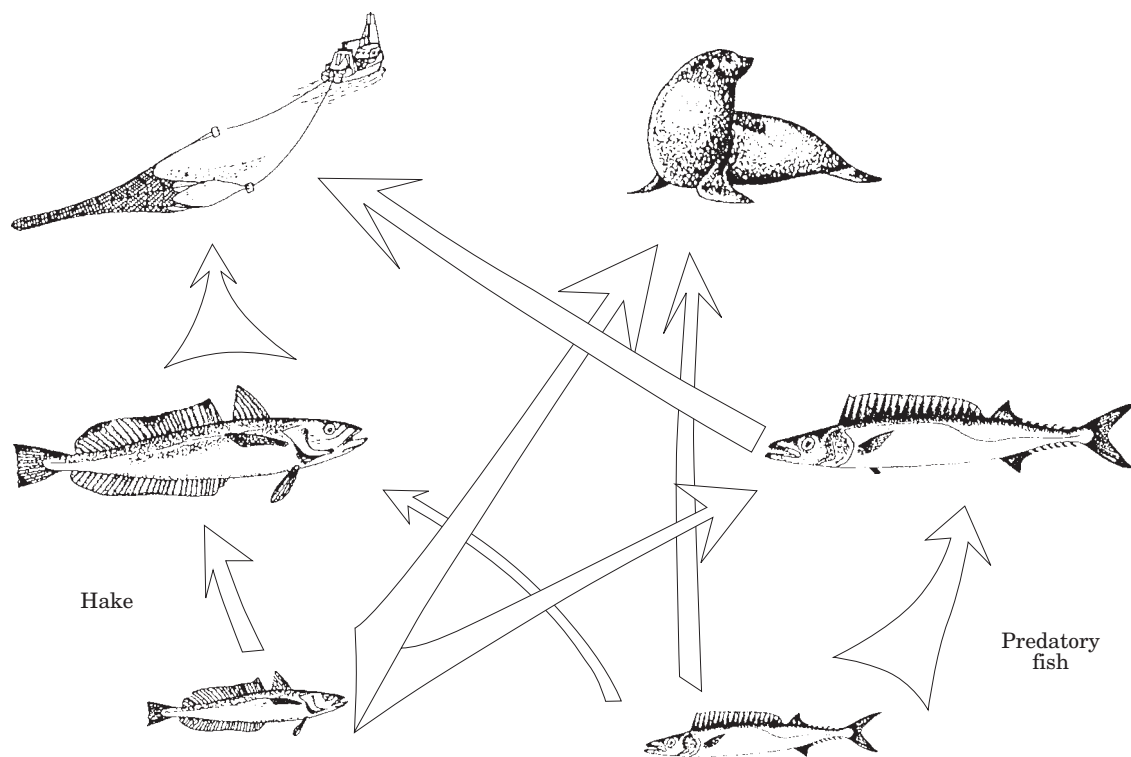


Figure 13. Schematic showing the trophic groups and their interactions in the minimal realistic model of Cape fur seal and Cape hake interactions off South Africa (from Punt, 1994).

serve to further compensate (or even reverse) any reduced predation. Given the many potential pathways connecting marine predators and their prey, it would currently take a bold scientist to claim accurate prediction of the direction and magnitude of predation-driven changes in marine fishery ecosystems.

Discriminating species interaction models for the Australian North-west Shelf

The tropical fish community of the North-west Shelf has highly uncertain dynamics, and has been exploited by a sequence of fisheries: a Japanese trawl fishery (1959–1963) that targeted higher-valued, long-lived species (Lethrinidae) associated with sponge and gorgonian-dominated habitat (total effort of 7600 h trawling); a Taiwanese pair trawl fishery (1972–1991) that took many species including lesser-valued, shorter-lived species (Nemipteridae and *Saurida*) associated with mud and sand substrates (maximum effort 80 000 h trawling); and a small Australian trap fishery (1984 to present) that targets the higher-valued, long-lived species, including Lethrinidae and Lutjanidae in areas that have been subjected to little trawling. During the course of the trawl fisheries, the relative and absolute abundances of Lethrinidae and Lutjanidae have

declined, while the relative abundances of Nemipteridae and *Saurida* have increased. At the same time, the demersal habitat has changed with loss of large epibenthos, sponge, and gorgonian corals. Lethrinidae and Lutjanidae have a greater probability of being associated with habitat containing large epibenthos; Nemipteridae and *Saurida* have a greater probability of being associated with open sand habitat.

Further development of the Australian Lethrinidae and Lutjanidae fishery requires the historical species composition to be recovered and the key ecological question to be addressed is how are the different populations regulated. Since the early 1980s, the North-west shelf has been the subject of an actively adaptive management experiment to formally evaluate a range of alternative ecological models that describe the species interactions and the performance of prospective management actions across these models (Sainsbury, 1991; Sainsbury, *et al.*, 1997). Four ecological models are compared:

- Model 1. All species are controlled by “intraspecific” processes – i.e. a single species assessment approach.
- Model 2. Lethrinidae and Lutjanidae are controlled by intraspecific processes, but have a negative impact on Nemipteridae and *Saurida* – i.e. predation is a significant factor.

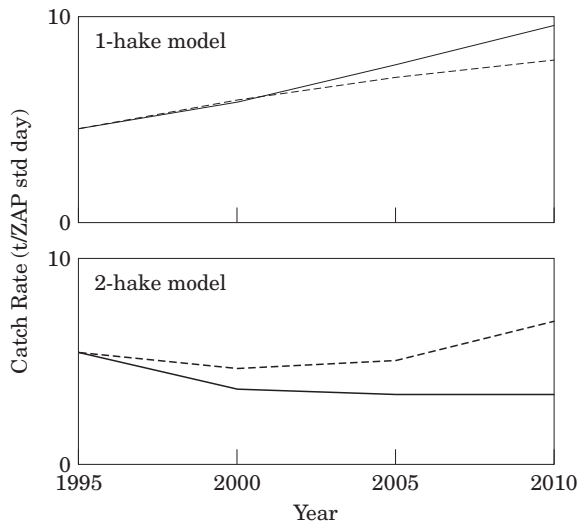


Figure 14. Comparison of the effects on future commercial hake catches of increased seal removals (broken lines) against no seal removals (solid lines) for a minimal realistic model of seal and hake interaction configured so that either it aggregates (1-hake model) or separates (2-hake model) and two hake species (redrawn from Punt, 1994).

Model 3. Nemipteridae and *Saurida* are controlled by intraspecific processes, but have a negative impact on Lethrinidae and Lutjanidae – i.e. competition is a significant factor.

Model 4. The carrying capacity of all groups is determined by the amount of suitable habitat and habitat is altered by the physical effects of trawling.

The performance of different short (a learning period of up to 20 years) and long-term fishing regimes has been assessed as a function of the estimated economic benefits to each fishery, prior probabilities of each model being correct, and the predicted value of reduced uncertainty through experimental management (areas closed to trawling and annual research surveys) (Sainsbury, 1991). Surveys following experimental closures have been used to update probabilities of each model being correct.

Actual management of the North-west Shelf has not precisely followed the adaptive management approach, at least in part because an Australian trawl fishery was developed in 1988, but management has included areas closed to trawling and this, together with infrequent research surveys, has allowed the probabilities of the different ecological models to be updated (Table 3). Each model was assigned equal probability before the first survey. After the first surveys, but before the closures began, the probability of each model was updated using the abundance information collected from research surveys. At this time there was little to distinguish models 2 and 4, which were clearly superior

to models 1 and 3. However model 2 (species regulation driven by predation) has quite different management implications from model 4 (species regulation driven by habitat). A further research survey, 5 years after closures were instituted, provided data favouring model 4 and over model 2. Future, biennial surveys will continue to improve discrimination between the models.

The adaptive management approach used on the North-west Shelf is not strictly an example of the success of modelling predation in marine systems. It is instead an exploration and testing of the hypothesis that predation (among other hypotheses) is the principal factor regulating the population dynamics of selected species. The models used were very simplistic, the level of aggregation high, and they represented only a fraction of available models. However, in the absence of suitable data to develop more complex process-driven models, they have served the purpose of directly evaluating alternative options for managing a difficult community level management problem, where conflicting hypotheses of population regulation could not be resolved at the time of decision making (Sainsbury, 1991). The approach is an example of how to achieve the precision necessary to distinguish alternate hypotheses while modelling a complex system. Delaying choice of alternate models incorporates uncertainty in model specification through to predictive strategy development. Neglecting uncertainty in model structure is recognized as leading to unrealistically low estimates of uncertainty and is considered a shortcoming of much current ecological modelling (Reichert and Omlin, 1997).

Summary and conclusions

“Knowledge increases not by the matching of images with the real world . . . , that is, not by the direct perception of truth but by . . . the perception of error.”
(Boulding, 1980.)

The variety of predator–prey interactions in aquatic systems is truly amazing. It is a variety based on small scale-spatial patterns, temporal synchrony and the individual responses of prey to highly selective predators. At a community level, this variety is increased by the wealth of direct and indirect interactions. There is a growing consensus among population ecologists and fisheries scientists that it is not possible to numerically predict any but the simplest (symmetrical) predation interactions in marine ecosystems. Yet at the same time there is a growing recognition – perhaps demand – from managers and the public that fisheries be managed as a component of marine ecosystems.

Proven techniques are available for the tactical management of marine fisheries, although lack of data often limits their reliability. However, they are only

Table 3. Probabilities of four ecological models describing the interactions of commercial fish groups on the North-west Shelf of Australia (data from Sainsbury, *et al.* 1997).

Model	Probability		
	Prior to survey	Prior to experiment	After 5 years of experiment
Intraspecific control	0.25	0.01	0.02
Predation control of L&L on N&S	0.25	0.52	0.33
Resource control of N&S on L&L	0.25	0.01	0.03
Habitat and intraspecific control	0.25	0.46	0.62

L&L, *Lethrinus* and *Lutjanus* (high valued fish); N&S, *Nemipterus* and *Saurida* (lower valued fish).

slowly being developed for strategic management, and numerical prediction may rarely be viable, except where large-scale experimentation is possible. Even qualitative prediction is suspect when predictive models cannot represent the small-scale, seemingly insignificant events or species that may determine community structure. Management by intuition seems doomed to failure given the importance of indirect predator-prey interactions in determining system response to an intervention.

Fishery science has developed around highly developed, high yield fisheries. Landed, sorted, catches have provided the major source of biological information, and it is only comparatively recently that the complexity of fishing operations and the diversity of landed catches and bycatch in most fisheries has been recognized (e.g. Alverson *et al.*, 1994). The emphasis has been on managing individual species or, more recently, individual species linked by predation interactions. Unfortunately, the species sought by many fisheries, and especially those on the continental shelf, do not exist in isolation or as a part of limited number of interacting species, but as a component of a larger assemblage. One approach to managing these assemblages is the extension of single species modelling techniques to include predation interactions. Data requirements would be immense and it would be impractical to manage the varied species of the continental shelf on a species-by-species basis (Larkin, 1977).

An alternative is to manage groups of trophically coupled, resident species as operational units while still managing the migratory species as separate components (Tyler *et al.*, 1982). Component species would be selected by their temporal and geographical attributes to make it possible to manage each unit as an entity. The operational units would be managed adaptively to determine the fishing effort that each unit could sustain. Adaptive management of species assemblages of the North-west Shelf of Australia has been shown, over the last 10 years, to be a scientifically and economically viable approach to resolve management uncertainties

(Sainsbury *et al.*, 1997). The approach of comparing alternative process models provides a method for incorporating ecological complexity in the modelling process, while maintaining simplicity (and therefore precision) in the actual models.

Management and conservation of the production bases for fishery ecosystems – habitat, pre-recruits and forage fish – may provide a useful supplement to single-species management, especially for systems characterized by complex dynamics (Wilson *et al.*, 1994; Walsh *et al.*, 1995). Managing habitat to preserve sufficient complex habitat to provide refuge from predation may be similarly useful. There will be times when knowledge of a marine system is considered too slight, or the costs of obtaining further knowledge too great (see Punt and Butterworth, 1991), that the most practical approach might be to conserve the production basis instead of assuming that managing species as though they were independent can provide the basis for strategic management.

Just as it is clear that no single model is appropriate for the study of multispecies interactions (Larkin and Gazey, 1982; Starfield *et al.*, 1988; Reichert and Omlin, 1997), it is clear that no single management policy is appropriate for the management of multispecies fisheries. Analytical and management techniques suitable for tactical management and those suitable for strategic management must be carefully distinguished. A single survey, or a single adaptive management experiment may meet tactical management needs, but strategic management needs will only be met through an ongoing commitment to exploring the properties of the managed system. New experimental and management techniques are required that utilize the diversity of marine ecosystems to gain information in a non-disruptive manner, while at the same time preserving the system's productivity. This will require the cooperation of resource users, scientists and managers, but it has the best potential for furthering an understanding of the role of predation in marine ecosystems and the consequences of any modifications.

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This review has developed from discussions over the years with many researchers interested in providing the means to manage marine fisheries as more than the sum of their individual parts. Taivo Laevastu was particularly influential in first making it look simple and later making the complexity manageable. The content and presentation were improved following comments from Tony Koslow, Jock Young, Vivienne Mawson and two anonymous reviewers.

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