Chapter Fourteen

Body size, exploitation and conservation of marine organisms

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Introduction

Aquatic ecologists and conservationists have long been obsessed with trying to understand links between body size, exploitation and conservation (e.g. Adams, 1980; Dickie, Kerr & Schwinghammer, 1987a). There are several reasons for this interest. First, at the individual level, fisheries management for both vertebrate and invertebrate populations tries to minimize the mortality of smaller individuals, in order to increase the probability that individuals have reproduced before they are caught (Jennings, Kaiser & Reynolds, 2001a). Even if other management methods are used, practically every stock assessment that has ever been done on an indeterminately growing species has included size as a key input parameter. Second, at the population level, large-bodied species have life-history traits that lead to slow rates of population turnover, with clear implications for productivity, resilience and recovery potential (Hutchings, 2001; Denney, Jennings & Reynolds, 2002; Reynolds et al., 2005; Goodwin et al., 2006). Third, at the community level, predator-prey relationships are strongly linked to size (Cohen et al., 1993; Woodward & Warren, this volume; Persson & De Roos, this volume), leading to the potential for understanding how fishing mortality may have wider ecosystem impacts through food-web dynamics (Dickie et al., 1987a).

At the population level, studies of the effects of exploitation have long focused on the direct effects of fishing mortality on a single stock, and this is often a pragmatic response to limited information on the indirect effects of mortality on one species affecting other species in the ecosystem (Hilborn & Walters, 1992). However, renewed concerns about the environmental impacts of fishing have encouraged new research on fishing effects on communities and ecosystems, where an understanding of the direct and indirect effects of mortality, and the capacity to partition them, is essential. Since the structure of aquatic food webs is often strongly size based, we hope to show that understanding interactions between body size and exploitation provides the basis for describing and managing the effects of fishing.
In this chapter we consider linkages between body size, exploitation and aquatic conservation at all three scales: individuals, populations and communities. Our aim is to understand, from first principles of metabolic scaling rules and life histories, how population and community dynamics are linked to the sizes of individuals. Although much of the research that has been done in this field has focused on fish as the main animals caught, a nice feature of working with body-size distributions at the community level is their continuity from primary producers to top predators, which often transcend taxonomic boundaries (e.g. Warwick, this volume).

**Setting: the magnitude of fishing effects**

Some brief highlights of the state of aquatic biodiversity can make for depressing reading. The Food and Agriculture Organization of the United Nations (FAO) (2005) report on the state of the world’s fisheries points out that 52% of the world’s stocks are fully exploited, 17% are over exploited, 7% depleted and 1% recovering. The proportion of stocks that are over-exploited, depleted and recovering has increased from 10% in the mid 1970s to 25% in the early 1990s. World marine fisheries catches levelled out in the late 1980s, with fluctuations since then driven by changes in some highly productive areas in the Pacific (Watson & Pauly, 2001; FAO, 2005). This limit to marine catches has occurred in spite of a continuing increase in fishing effort and efficiency.

When we break these global figures down to the level of specific populations, we can identify many reductions in abundance over the past two to three decades. A review of data from 232 exploited fish populations revealed a median maximum rate of decline of 83% from known historical levels (Hutchings & Reynolds, 2004). Over half (58%) the populations declined by more than 80%. Note that these are maximum declines, based on time series of at least ten years, and the time-series usually began well after the onset of fishing. The declines are also much greater than those associated with taking a large sustainable yield from these populations. Even if fishing mortality can be substantially reduced, some stocks, in particular those of bottom dwelling fishes, do not show recovery if they have been pushed to very low abundance (Hutchings, 2001, 2002; Hutchings & Baum, 2005).

There is evidence for extinction of some populations of fishes and other marine species. Dulvy, Sadovy and Reynolds (2003) compiled a list of 133 cases of local, regional or global extinctions of marine species. Of these, 55 cases involved fishes, while the rest included birds, mammals and invertebrates. This is a preliminary assessment: we still know very little about the status of the vast majority of aquatic organisms. Indeed, 80% of the extinctions were discovered through historical comparisons rather than real-time detections, with a median 53-year lag between disappearance and the reporting of
that disappearance. Thus, the near-extinction of the common skate, Dipturus batts, from the Irish Sea was brought to the world’s attention only several decades after the decline had occurred (Brander, 1981).

As we scale up from populations to communities, the principal effects of fishing on size and species composition are well known. Both spatial comparisons between areas subject to different fishing intensities and temporal comparison within areas where fishing effort has increased over time, indicate broadly predictable effects. As fishing mortality rises, the mean size of individuals in the community falls, and species with larger body sizes form a smaller proportion of community biomass. Since larger species and individuals often, but not exclusively, feed at higher trophic levels, so changes in size structure are often paralleled by a reduction in the trophic level of the community - an effect dubbed ‘fishing down the food web’ by Pauly et al. (1998).

While much of the theory and data on fishing effects refers to target species, we have also learned a great deal in the past 20 years about impacts of fishing gear on the seabed (Kaiser & de Groot, 2000). Impacts on bottom fauna are most severe in habitats that do not naturally receive much disturbance. As we will see below, we can use the same body of theory developed for linking body size, life histories and responses to mortality for predicting the responses of benthic invertebrate species and communities to trawling disturbance.

Size-related responses to exploitation
The responses of populations and communities to human activities depend on interactions between the extrinsic mortality rate and the intrinsic aspects of the species’ biology that affect population growth rates. Body size plays a key role in both elements of vulnerability.

Fisheries are selective, typically targeting the large-bodied, high-value individuals and species that are favoured for consumption and sale. Even when fisheries do not deliberately pursue larger individuals and species, there will still be higher mortality for such animals because they are often caught as by-catch due to their greater likelihood of being retained by gears such as trawls. While there are a few notable exceptions to the rule of larger animals being more vulnerable to capture, such as gill nets and traps that select individuals and species of intermediate size, almost all population-based assessments show that large size classes suffer higher mortality.

There is clear evidence for the size-relatedness of fishing effects in populations and communities. Thus, in one early study, we compared trends in the abundance of populations of the same species that had different maximum sizes, after accounting for differences in fishing mortality. Populations with larger maximum sizes consistently showed greater rates of decline in response
to mortality (Jennings, Reynolds & Mills, 1998). In a second study, using a phylogenetic comparative approach to account for relatedness, we compared trends in pairs of species of different body size. In eight out of nine comparisons, the larger species declined more in abundance during a period of increasing fishing mortality (Jennings, Greenstreet & Reynolds, 1999). There are many other recent examples of trends in abundance that can be related to body size (Reynolds, 2003). The overall trend of targeting large species has had the same impacts on large, profitable prey on land as in the water (Reynolds & Peres, 2006). Thus, we have seen the sequential loss of species from the largest to the smallest, in groups as diverse as whales in the Southern Ocean, abalones along the coasts of western North America, and primates in the Brazilian Amazon.

The effects of fishing on communities are a consequence of interactions between the direct and indirect effects of fishing. The direct effects are due to mortality on component populations and tend to result in a reduction in the mean size of animals in the community. The indirect effects are due to the changes in predator–prey relationships which occur when predator and/or prey abundance changes. Direct and indirect effects usually result in a reduction in the mean body size of animals in the community and a decrease in the proportion of animals with larger body size (Shin et al., 2005). Fishing effects on communities have often been reported in terms of changes to the slope of abundance (y) vs. body mass (x) relationships, otherwise known as size spectra. The slopes of size spectra tend to become steeper with increased fishing (Bianchi et al., 2000; Duplisea & Kerr, 1995; Gislason, 2002; Pope et al., 1988; Rice & Gislason, 1996). Intercepts were often reported to increase as the slope declined, but this could have been a real effect or a statistical artefact resulting from the correlation between intercept and slope. To avoid this, Daan et al. (2005) re-scaled size spectra to the midpoint size class and expressed midpoint heights rather than intercepts. Results suggested that changes in the spectrum can be driven both by the loss of large fish and proliferation of small fish as their larger predators are depleted (Daan et al., 2005).

The physical impacts of fishing gears also cause size-selective mortality. When trawl gears are towed across the seabed they may kill differentially many larger and more fragile animals, as small ones may be pushed aside by the pressure wave in front of the gear (Gilkinson et al., 1998). The larger species are also less able to withstand a given rate of mortality. As a result, benthic communities in trawled areas comprise smaller individuals and species (Kaiser et al., 2000), and the slopes of benthic invertebrate size spectra become steeper in more heavily trawled areas (Jennings et al., 2002; Warwick, this volume).

**Linking body size, life histories and population dynamics**

Rates of metabolism, the biological processing of energy and materials, are systematically related to body size and ultimately correlate with the life histories
of animals and their responses to exploitation. Relationships between metabolism and size are further modified by chemical composition and temperature (Brown et al., 2004). These factors consequently drive most other biological rates and timings, such as lifespans and growth (Gillooly, 2000; Gillooly et al., 2001, 2002; Brown, Allen & Gillooly, this volume; Atkinson & Hirst, this volume).

The combined effect of body size and temperature on individual whole-organism metabolic rate has been approximated as:

$$ I = i_0M^{0.75}e^{-E/RT} $$  \hspace{1cm} (14.1)

Where $I$ is individual metabolic rate, $i_0$ is a normalization constant, $M$ is body mass, $T$ is temperature (Kelvin), $E$ is the activation energy of metabolism and $k$ is Boltzmann's constant. Since the mass-specific rate of metabolism ($R$) is $1/M$, $R$ will scale with $M$ as

$$ R \propto M^{-0.25}e^{-E/RT} $$  \hspace{1cm} (14.2)

This demonstrates that large organisms must require more resources and flux them more slowly than smaller ones (Brown et al., 2004). Not surprisingly, intrinsic rates of increase and production scale similarly, and turnover time as the inverse of production; approximately $W^{0.25}$. Changes in resource requirements with size will limit the resources available for allocation to life histories, and species have evolved many ways of allocating these limited resources to maximize reproductive output.

In a former British Ecological Society symposium, Law (1979) described the Darwinian demon, an organism in which all the problems of maximizing reproductive output had been solved. This animal began reproducing immediately after birth, producing large numbers at frequent intervals as it got older. It experienced no mortality and its capacity for dispersal and finding mates knew no bounds. Of course, as Law pointed out, no such animal exists because of trade-offs. Thus, species have followed a wide diversity of paths through these trade-offs in arriving at the combinations of life-history traits that we see today and which maximize individual fitness (Atkinson & Hirst, this volume). Relationships among traits can be described with invariants, which reflect general life-history patterns among species after removing the dimensions of mass and time (Charnov, 1993). Examples of invariants are relationships between size at maturity and maximum size, lifespan and age at maturity, natural mortality and growth rate (Beverton, 1992).

Two aspects of life histories, which result from trade-offs, are critical in determining the response of a population to additional mortality: the intrinsic rate of increase and the strength of compensation. The intrinsic rate of natural increase is often denoted $r_{max}$, to make it clear that this is the maximum rate that populations could achieve in the absence of density dependence, which we can usually expect to apply to small populations that are far from their carrying
capacity. There is a strong theoretical literature that links body size to \( r_{\text{max}} \) through links with key components of \( r_{\text{max}} \) such as age at maturity and natural lifespan (Roff, 1992). The strength of compensation, or density dependence, indicates how the production of recruits (juvenile fish at a specified age) per spawner changes with the abundance of spawners. Since the abundance of recruits can be measured at different ages for different populations, estimates of population-specific mortality in subsequent years can be used to express recruits per spawner in a consistent way for comparative purposes: as spawners per spawner (Myers, Mertz & Fowlow, 1997).

Population dynamics and responses to mortality

**Intrinsic rates of increase**

Species with high \( r_{\text{max}} \) will have fast population turnover, and should therefore be better able to compensate for increased mortality due to fishing. This has been suggested by a variety of theoretical analyses, which have focused on body size as well as its correlated life-history traits, such as age at maturity and natural lifespan (Adams, 1980; Stokes, McGlade & Law, 1993). The prediction that large-bodied species should decline more quickly when exposed to a given rate of fishing mortality has been upheld in many studies of marine fishes in both tropical and temperate waters (reviewed by Reynolds, 2003). Many of these studies have included comparisons between closely related species, to avoid ‘apples and oranges’ comparisons between species that differ greatly in other aspects of behaviour or life histories (Harvey & Pagel, 1991). The prediction that large-bodied species should have lower recovery potential has also been upheld in comparative studies of marine invertebrates (Fenchel, 1974) and fishes (Denney et al., 2002). For example, Denney et al. (2002) measured the slope at the origin of recruitment plotted against adult stock size for fish populations in the northeast Atlantic. This provided a practical metric for \( r_{\text{max}} \), the number of spawners produced per spawner in the absence of density dependence (Myers et al., 1997), which could be plotted against various life-history traits. Body size was negatively related to \( r_{\text{max}} \), the implication being that, all else being equal, small-bodied species should be able to bounce back from small population size faster than larger ones. When the length-based measures of body size reported by Denney et al. (2002) are converted to mass (Maxwell & Jennings, 2005), it is notable that the slope of the relationship between \( \log_{10} \) spawner per spawner and \( \log_{10} \) maximum body mass does not significantly differ from the \( M^{-0.25} \) scaling of intrinsic rate and body mass predicted from theory (Eq. (14.2); Savage et al., 2004).

**Density dependence**

The strength of density dependence is critical for determining the ability of populations to compensate for increased mortality. Yet, by definition, \( r_{\text{max}} \) and
the surrogates used to measure it, such as the slope at the origin of a spawner-recruitment relationship, apply to small populations in the absence of density dependence. For example, if the population follows a logistic growth pattern, the rate of change in number of individuals per unit time, \( \frac{dN}{dt} \), will depend on population growth rate \( r \) and the carrying capacity, \( K \).

\[
\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right)
\]  

(14.3)

Only at the smallest population size will \( r = r_{\text{max}} \). Cynics might argue that this is the case for the majority of fisheries today, so we need go no further! Even in heavily fished populations, however, we cannot completely ignore density-dependent interactions between individuals, predator-prey relationships and other aspects of ecology and behaviour that may determine intrinsic aspects of vulnerability. These features of biology translate the conceptually simple \( r_{\text{max}} \) into realized population growth rates.

Recently, Goodwin et al. (2006) have examined relationships between density dependence and life history. They used stock-recruitment curves to measure the compensation ratio of a population (Fig. 14.1). The compensation ratio (CR; Goodyear, 1977) was defined as:

\[
CR = \frac{\text{Maximum recruit survival(\( \alpha \))}}{\text{Recruit survival at SSB}_{F-0}}
\]  

(14.4)

Where \( \alpha \) is the slope at the origin of a spawner-recruit relationship and \( \text{SSB}_{F-0} \) is the spawning stock biomass at equilibrium in the absence of fishing. Goodwin et al. (2006) demonstrated that large-bodied species with low maximum rates of increase and long generation times tended to have strong compensation. Their results help us to understand how populations respond to fishing. Those populations with small body size and low spawners per recruit in the absence of fishing \( \text{SSB}_{F-0} \) have weak density-dependence and high annual production. At the outset

Figure 14.1 A spawner-recruit relationship where \( \alpha \) is the maximum recruits per spawner at low population size and \( S_{F-0} \) is equilibrium spawner abundance in the absence of fishing. The relationship between maximum recruits per spawner and recruit survival at \( S_{F-0} \) defines the compensation ratio. After Goodwin et al. (2006).
of fishing even low fishing mortality could rapidly deplete these populations since they would show little compensatory response. However, they would show high resilience to extinction at very low abundance. Conversely, populations with strong density-dependence have a greater initial compensatory reserve, but can collapse owing to low resilience once they reach low abundance.

Communities and their responses to mortality
Size-based structuring of marine communities
To understand and predict how fishing affects communities, it is necessary to know how communities are structured in the absence of fishing. Strong size-based structuring is ubiquitous in marine ecosystems (Sheldon, Prakash & Sutcliffe, 1972) and trophic level increases more or less continuously with body size (Fry & Quinones, 1994). Why food webs of this type have evolved in aquatic environments when many terrestrial webs have clear trophic levels is not clear. Loeuille and Loreau (2005) recently explored one possibility, based on a model where food webs evolve from a single ancestor and assuming that adaptation acts on body size, which has a well-established impact on metabolism and interactions between organisms. Based on parameters defined at the organism scale, the model predicts emergent properties at the food web scale. If niche width and competition intensity are small then distinct trophic levels evolve. When niche width or competition intensity are large then clear trophic levels do not emerge, consistent with patterns seen in many aquatic food webs.

One feature of many marine species is their large scope for individual growth. Thus, individuals of most species begin life as larvae feeding at the base of food chains, but can end life as large terminal predators. Size-based predation and the large scope for growth in aquatic animals are significant because, at least over the course of a species' life cycle, body size will be a better indicator of trophic level than species identity (see Woodward & Warren, this volume). This observation provides a compelling reason to adopt size rather than species-based analysis of aquatic food webs; treating small individuals of a large species as functionally equivalent to large individuals of small species (Kerr & Dickie, 2001). While such size-based analyses are necessarily simplifications, they provide an excellent means of understanding the development of size structure and assessing the effects of mortality (Jennings, 2005; Persson & De Roos, this volume).

Attempts to model the processes that lead to the emergence of size spectra have included simple models based on fundamental ecological principles (Kerr & Dickie, 2001; Brown & Gillooly, 2003) and detailed process-based models of predator-prey interactions (Shin & Cury, 2004). Almost all models are underpinned by the recognition that the scaling of metabolism with body size determines the energy requirements of animals in different size classes.

The time-averaged slopes of abundance-body mass relationships in size-based food webs are principally determined by the availability of energy to animals in
each size class (Kerr & Dickie, 2001). Availability of energy at size, and hence the scaling of abundance and body mass, can be predicted by extending the theory of energetic equivalence that applies to communities that share energy. For these communities, such as phytoplankton using sunlight, numerical abundance (N) typically scales with body mass (M) as $M^{-0.75}$. Since the scaling of individual metabolic rate and body size can be approximated as $M^{1.75}$ (Eq. (14.1)), the rate of energy use is expected to be independent of body size (Damuth, 1981), a prediction that has since been referred to as energetic equivalence (Nee et al., 1991). In the case of phytoplankton communities, for example, the sunlight energy used by plankton cells in a size class is the same as in any other size class (Li & Charnov, 2001).

Food chains are not characterized by the sharing of energy, but by larger predators eating smaller prey. Thus the availability of energy falls with size and trophic level (Ware, 2000). The rate at which available energy falls will depend on the efficiency of energy transfer and the number of predator-prey interactions that transfer energy from small to large body-size classes. The latter depends on the ratio of the mean predator size to mean prey size (PPMR), which in most aquatic ecosystems ranges from 100 to 1000:1 by mass (Cushing, 1975). Cyr (2000) and Brown and Gillooly (2003) proposed that knowledge of PPMR and transfer efficiency (TE) could be used to predict the changes in energy available to animals of different body sizes in a complete size spectrum and hence the slope. Their analysis helped to explain the remarkable consistency in the observed slopes of size spectra (Boudreau & Dickie, 1992). This is because PPMR and TE place significant constraints on the slope of abundance-body mass relationships and because PPMR and TE are remarkably consistent in different ecosystems (Jennings, 2005). Brown and Gillooly's (2003) analysis, as further developed in Brown et al. (2004), was based on a series of trophic levels, each of which extended over a range of body sizes. In most aquatic communities trophic level actually rises continuously with body size (Jennings et al., 2002). Jennings and Mackinson (2003) formalized the approach of Brown and Gillooly (2003) for application to such a community, and showed that the method provided good predictions of the slope of the size spectrum.

These methods for predicting the slope of size spectra are helpful in understanding the size structure of communities and for providing a baseline for assessing the relative effects of exploitation. However, they do not allow prediction of the consequences of various levels of exploitation. To achieve this, models that account for the growth and mortality of individuals are required. This is the interface between understanding the dynamics of populations and understanding how population dynamics contribute to community structuring.

**Describing and predicting responses to mortality**

It can be difficult to link changes in fishing mortality to changes in the slopes of size spectra empirically, because mortality data for communities are hard to
obtain. However, available evidence suggests that the slopes respond principally
to fishing rather than to other drivers such as temperature. Blanchard et al.
(2005), for example, considered the effects of fishing and climate variation on
size-based metrics, including slope of the size spectrum, in the Celtic Sea. Their
analysis suggested that size-based metrics responded clearly to the effects of
fishing in variable environments, reflecting the ubiquity of size-based processes
in defining community structure and responses to mortality. This is consistent
with theory. While temperature will have a marked effect on rates of biomass
turnover and energy flux in the spectrum (Eqs. 14.1 & 14.2), TE and PPMR are
largely temperature independent.

Much work on size spectra has focused on fishing effects on fish communities,
but benthic invertebrate communities are also directly impacted by bottom fish-
ging gears such as trawls and show strong size-based responses to fishing.
Comparisons among areas subject to different levels of trawling disturbance
have shown that the frequency of bottom trawling disturbance in the central
North Sea had a greater effect on the size structure of the fauna in a soft-sediment
benthic community than other environmental variables such as sediment
particle size and depth (Duplisea et al., 2002). Size spectra became steeper and their
heights decreased with increased trawling disturbance. As a result, the total
production of infaunal invertebrates fell with increasing trawling disturbance
while relative production of the infaunal community rose significantly. The
increases in relative production were largely attributable to the dominance of
smaller animals in the trawled community and did not compensate for the loss of
biomass and production of larger animals (Jennings et al., 2001b).

Differences between the slopes of size spectra in exploited communities and
those that are predicted for unexploited communities can be used to assess the
effects of fishing on abundance in different ecosystems. In addition, given well-
established scaling relationships between body size and biological properties,
the size spectrum can be parameterized to estimate the effects of fishing on
production (P) or turnover time. To assess the overall effects of fishing on the
North Sea fish community, Jennings and Blanchard (2004) attempted to com-
pare a theoretical abundance-body mass relationship for the unexploited
North Sea with an abundance-body mass relationship estimated from contem-
porary data (Fig. 14.2). The slope of the unexploited size spectrum was predicted
from PPMR and TE (using the methods introduced above under Size-based
structuring of marine communities) since there was little evidence that either
parameter was affected by exploitation to the same extent as biomass (B).
By comparing the unexploited theoretical and observed size spectra they
predicted that the scaling of B with M had changed from $M^{0.10}$ (unexploited)
to $M^{1.0}$ (exploited). This suggested that the current biomass of large fishes
weighing 4–16 kg and 16–66 kg was 97.4% and 99.2%, respectively, lower
than would be expected in the absence of fisheries exploitation. The mean
turnover time of the exploited community (1/P:B) was almost twice as fast as that of the unexploited community, falling from 3.5 to 1.9 years.

Comparisons such as these are useful for comparing the magnitude of fishing effects in different ecosystems and for assessing the relative impacts of fishing on a range of community and ecosystem properties. However, such static descriptions cannot be used to guide management and to modify fishing to achieve desirable community structures, such as those that provide good yields of target species while ensuring that large and vulnerable species do not go extinct.
Models of the effects of varying fishing mortality on the slope of size spectra have focused on the various processes that lead to changes in slope, specifically: (1) the differential reduction in the abundance of larger species that are more vulnerable to a given rate of mortality, (2) within-population changes in mean body size and life history due to the direct effects of fishing on the population, (3) genetic changes in life history and (4) predator–prey relationships in the community that result in proliferation of small species and individuals that are better able to tolerate a given rate of fishing mortality and benefit from depletion of their predators. Responses (1) and (2) are governed by the links between body size, life histories and response to mortality that we considered above. Existing theoretical models that describe the structure of size spectra and their response to fishing have principally focused on (1), (2) and (4) (e.g. Boudreau et al., 1991; Dickie, Kerr & Boudreau, 1987b; Kerr, 1974; Thiebaux & Dickie, 1993). Response (3) is arguably as important as the others in the medium- to long-term and there is a developing body of theory and empirical observation at the population level that would allow genetic effects to be addressed (Law, 2000; Law & Stokes, 2000; Heino & Godo, 2002). Some recently published modelling results suggest that the effects may not be intuitive due to the interplay between the selection caused by fishing and changes in predation pressure on different size classes (Thygesen et al., 2005; Persson & De Roos, this volume).

In models of fishing effects on community size structure, the capacity to partition the direct and indirect effects of fishing and to understand how they interact is critical in providing insight into the effects of fishing. Gislason and Rice (1998) used a combination of existing length-based fishery models and multispecies models to predict the slopes and intercepts of size spectra for a community consisting of 11 fish species that account for much of the fisheries production in the North Sea. Fishing mortality increased the slope of the size spectrum. Building on this approach, Pope et al. (2006) generalized the model for a community of species defined by their maximum body sizes (asymptotic length $L_{\infty}$ as defined in the von Bertalanffy growth model, in 10 cm length classes from 10 cm to 130 cm). We discuss this model in a little detail, as it gives important insights into the links between size-based population and community responses to fishing and could provide a basis for predicting and managing the impacts of fishing on size-based communities.

For each species ($S$), the number $(N)$ surviving from one length class $(L_1)$ to the next, where successive length classes are denoted 1 and 2 was given as:

$$N_{2S} = N_{1S} \left[ \frac{L_{\infty}(S) - L_2}{L_{\infty}(S) - L_1} \right]^{z_{L1}L_1} \left[ \frac{L_{\infty}(S) - L_2}{L_{\infty}(S) - L_1} \right]^{z_{L1}L_1}$$

(14.5)

based on the fisheries assessment method of length cohort analysis (Jones, 1974), where $z(L_1, S)$ is the total mortality rate ($y^{-1}$) at length $L_1$ for the species and $k$ is the Brody growth parameter from the von Bertalanffy growth model.
that reflects the rate of growth towards asymptotic length \( L_{\infty} \). One limitation of the application of this approach was that the assumption of a fixed relationship between \( L_{\infty} \) and growth rate, means that the modelled rates of growth persist regardless of the level of available resources. The average number of fish per year \( \bar{N}_{l,1.5} \) in the \( L1 \) length group by species is given by:

\[
\bar{N}_{l,1.5} = (N_{l,1.5} - N_{l,2.5}) / Z(l,1.5) \tag{14.6}
\]

The \( \bar{N}_{l,1.5} \) may then be summed across species at each length group \( l \) from 10 to 130 cm to give the overall size spectrum \( \bar{N}_l \). Consistent with standard practice in multispecies fishery models, the components of \( Z \) considered were fishing mortality rate \( F \), non-predation natural mortality rate \( M1 \) and predation mortality rate \( M2 \). Thus:

\[
Z = F + M1 + M2 \tag{14.7}
\]

Predation mortality was set proportional to the sum of the power of biomass in larger size classes, modified by a size-preference function. Maturity was based on life-history invariants. Once mature, fishes produced recruits in proportion to their total abundance and length. A power term in the spawner-recruit relationship provided compensation, the density dependent reduction in recruitment at high spawner abundance that we discussed previously.

The slope of the size spectrum for fishes from 20–100 cm was broadly linear and became increasingly steep as a function of fishing mortality. Density dependent controls, due to predation mortality and the extent of compensation in the spawner-recruit relationship, were key mechanisms in maintaining the slope. When compensation exerted strong control, the model suggested that the role of fishing quickly dominated the effect of predation. The model also provided insights into the relative role of predation mortality and fishing in different size classes, building on the observations of Dickie (1976) who demonstrated that: (1) the ratio of biomass at successive trophic levels must be independent of sizes of individuals and, (2) the ratio of biomass at successive trophic levels is the ecological efficiency (ratio of food intake at two successive trophic levels) corrected by the ratio of predation rates. Thus Dickie (1976) showed that predation rate must be relatively higher at lower trophic levels, and that for a given amount of fisheries yield from a lower trophic level is a much smaller proportion of predation mortality rate than at a higher trophic level.

The Pope et al. (2006) model suggests that the reduction in the biomass of larger species and individuals in the community leads to the proliferation of smaller individuals. Using a method developed by Daan et al. (2005) to assess changes in the abundance of fishes in different size classes over time, there have now been three empirical demonstrations of increases in the steepness of size
spectra being partially driven by the proliferation of fish in smaller size classes: for the North Sea (Daan et al., 2005), Fijian reefs (Dulvy et al., 2004) and the Celtic Sea (Blanchard et al., 2005) (Fig. 14.3). The model of Pope et al. (2006) suggests that the relationship between the strength of compensation in the spawner-recruit relationship and body size play an important role in controlling the extent of prey release.

The Pope et al. (2006) size-based model is an important development because they have captured the dynamics of individual species within the size spectrum,
by associating species identity with a maximum length. This allows the model to be used to predict the proportion of species with different ultimate body sizes that "populate" any size class in the spectrum (Fig. 14.4). In the same way that Cohen, Jonsson and Carpenter (2003) and Cohen (this volume) uniquely linked species identity, body mass and abundance in a new approach to conventional food-web analysis, the Pope et al. (2006) approach attempts to bring species identity into size-based models and provides the basis for starting to investigate links between community processes and the diversity and persistence of populations.

Size-based models have also been used to predict fishing effects on benthic invertebrate communities. In benthic communities, the structure of the size spectrum is driven more by competition rather than predation, since the animals present in many size classes often share the same energy sources (Warwick, this volume). Duplisea et al. (2002) developed a competition-based model to assess the effects of size-selective mortality due to trawling disturbance on the size-structure of the benthic community. By applying size-related mortality, they showed that fishing increased the slope of benthic size spectra, consistent with empirical observation.

Conclusions
There are clear links between the metabolic processes that drive rates of living and dying, life histories, and the structure and function of populations and communities. Thus body size and body-size distributions, as easily measured attributes of individuals, populations and communities, can provide significant insight into responses to exploitation. It seems fitting that fisheries ecologists have made many contributions to the development and testing of theory that links body size, exploitation and conservation, since this reinvigorates a long but intermittent history of fisheries science contributing to wider ecological thinking (Frank & Leggett, 1994; Shuter & Abrams, 2005). Indeed,
some of the most influential scientists working on the development of fisheries assessment methods were responsible for theoretical developments that proved fundamental in understanding life histories (Beverton & Holt, 1957, 1959).

While fisheries scientists have consistently been aware of links between population biology and the ecosystem, the politics and practicalities of management have led to the development of management systems that were dominated by the assessment of single populations. This approach was accepted by most management agencies from the 1960s to the present, but two events in recent years have provided a strong driver for moving toward management systems that also focus on communities and ecosystems. First, there has been near universal commitment within international fora that fisheries must be managed in an ecosystem context to take account of conservation concerns (Sinclair & Valdimarsson, 2003). Second, there have been major advances in the development of food-web theory that may have management applications, and in the development of connected theory that helps to formalize many of the observed relationships between individual, population and community processes (Brown & Gillooly, 2003; Cohen et al., 2003; Brown et al., this volume; Cohen, this volume). The changing drivers for management, and these new developments in ecology, suggest that theoretical development should reinvigorate the development of new management and assessment methods.

Acknowledgements
We thank Nick Goodwin for providing the materials to prepare Fig. 14.1 and Julia Blanchard and Nick Dulvy for providing data to prepare Fig. 14.3.

References


