

Life histories of fishes and population responses to exploitation

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Most of the world's fisheries are either fully exploited or overexploited (Botsford *et al.*, 1997). While there is scope for further exploitation of some fish stocks, the global picture is not encouraging, with declining catches despite increasing fishing effort. We are running out of new stocks to exploit, as we fish in deeper waters (Merrett & Haedrich, 1997) and work our way down the food chain (Pauly *et al.*, 1998).

Are declines in exploited fish populations really conservation problems? Clearly, this depends on what we mean by 'conservation problem' (Mace & Reynolds, Chapter 1). If we are concerned about the continuing availability of a resource upon which people depend for their livelihoods and social traditions, the word 'problem' is obviously a considerable understatement. If we are concerned about possible effects on other parts of the ecosystem due to declines in specific species, this too may be an important problem, though generalisations are difficult (Kaiser & Jennings, Chapter 16; Hall, 1999; Gislason & Sinclair, 2000; Jennings *et al.*, 2001). If we are concerned with the possibility of extinction of fished species, the evidence is much less clear. In fact, there are still no documented cases of any marine fish species having yet become extinct due to exploitation (Roberts & Hawkins, 1999). However, local extirpations have definitely occurred (Brander, 1981; Casey & Myers, 1998; Dulvy *et al.*, 2000; Powles *et al.*, 2000; Stevens *et al.*, 2000), and some fish populations have declined by 99% in 20–30 years (Reynolds & Jennings, 2000).

We think it is useful to ask about fish conservation in relation to life histories for two reasons. First, on theoretical grounds exploited fish populations provide a good model system for establishing links between population dynamics under harvesting regimes and life histories. Fishes show a huge diversity of life histories, including fecundities that vary by five orders of magnitude, and fisheries create large-scale experiments that yield data on population dynamics over many generations. Secondly, and particularly relevant to the theme of this book, it is important to derive generalisations

from species that we know a great deal about so that we can improve the conservation of species of which we know little. This is particularly true of tropical reef fisheries, where it will never be practical to collect the large amount of information that feeds the insatiable appetites of sophisticated models used in many temperate fisheries (Johannes, 1998). Yet some key tropical species such as groupers (Epinephelinae) are particularly susceptible to severe population declines and even extirpation under fishing pressure (Sadovy, 1994). Furthermore, even in temperate areas where research is well funded, the mandate of most scientists is geared strongly toward attaining sustainable exploitation of a small number of economically important species. This means that other species, which may be killed as a by-catch, can decline precipitously without anyone noticing. Thus the extirpation of the 'common' skate *Dipturus batis* from the Irish Sea and the decline of its western Atlantic counterpart, the barndoor skate *D. laevis* were not reported until at least 20 years after they occurred (Brander, 1981; Casey & Myers, 1998). We therefore need simple 'rules of thumb' for predicting population declines of poorly studied species, and life history characteristics such as body size, age at maturity, fecundity, and natural mortality rate seem fruitful avenues for exploration.

The aim of this chapter is to establish links between life histories, mortality rates and population trends. First, we provide a brief review of the theoretical links between life histories and population dynamics. Then we test predictions from this theory, based on comparative analyses of various species. Finally, we use the combination of theory and empirical observations to consider simple rules of thumb that might aid in making *a priori* predictions of responses to exploitation, and in prioritising species for conservation assessment.

THEORY

Links between life histories and sustainability

A number of theoretical analyses have indicated how life histories should determine responses to fishing (Adams, 1980; Stokes *et al.*, 1993; Kirkwood *et al.*, 1994; Pope *et al.*, 2000). These confirm the expectation that higher fishing mortality should be sustainable by species with faster life histories, i.e. earlier age at maturity and faster body growth. For example, Adams (1980) used classical yield-per-recruit analyses to show that species with faster life histories should both sustain higher mortality rates and produce higher yields per recruit. Kirkwood *et al.* (1994) used an age-structured population dynamics model that suggested that the potential

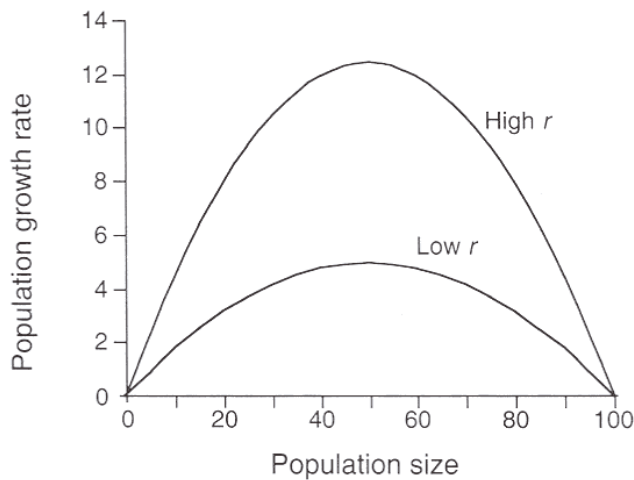


Figure 7.1. Population growth rate (individuals per unit time) as a function of population size for high ($r = 0.5$) and low ($r = 0.2$) intrinsic rates of natural increase. Species with higher intrinsic rates of increase provide greater yields to exploitation.

yield measured as a proportion of unexploited biomass should be proportional to natural mortality rates. For a range of potentially realistic levels of density dependence, they suggested that the percentage yield may be between about 10% and 15% of the natural mortality rate multiplied by the virgin biomass. This is a nice theoretical synthesis, but it is difficult to put these ideas into practice due to difficulties in measuring the key parameters in the sorts of data-poor situations where this sort of rule of thumb could be most useful.

The simplest way to incorporate life histories into predictions about sustainable exploitation is to consider the direct links between life history parameters and population dynamics. The intrinsic rate of population increase, denoted r , is a fundamental parameter in models that predict rates of population change per unit time. This is the rate of growth of a population at low densities (once it has reached a stable age distribution). Some authors also refer to this as r_{\max} , to distinguish it from an observed rate of population increase at higher densities. If the population follows a logistic growth pattern, the rate of change in number of individuals per unit time, dN/dt , will depend on r and the carrying capacity, K (Ludwig, Chapter 2).

$$dN/dt = rN(1 - N/K). \quad (7.1)$$

This provides the familiar parabolic relationship between population growth rate and population size shown in Figure 7.1. Two curves are shown, one for a species with a high intrinsic rate of population increase ($r = 0.5$), and the other for a lower one ($r = 0.2$). The maximum sustainable

yield that can be taken occurs at intermediate population sizes. The species with the higher intrinsic rate of increase can provide a higher yield. Many species show strong density-dependent responses to the additional mortality imposed by fishing and can sustain fishing mortalities two to three times the natural mortality without declining to extinction (Shepherd & Cushing, 1990).

Obviously, the next step towards our goal of linking population productivity to life histories would be to measure r for different species. If only life were so simple! The problem is that empirical measurements of rates of increase rarely give useful values of r because they depend critically on density dependence, and density dependence is notoriously difficult to quantify in field studies of any species (Sutherland & Gill, Chapter 12). One might be tempted to measure surrogates for r by looking at fecundity and mortality rates in the laboratory under uncrowded conditions. But this value will be hopelessly artificial, depending on food, temperature, safety from predators and diseases. While we are on a pessimistic note, we should also mention that the so-called carrying capacity, K , is also a difficult parameter to measure with any confidence, especially in marine environments where fish population sizes often fluctuate wildly from year to year, according to biotic and abiotic conditions that affect recruitment.

Correlations among life history traits

If we cannot measure r directly, the next best thing might be to measure life history traits that are correlated with it. Classically, people have described r -selected species as those that live in environments that select for rapid production of many small offspring, and K -selected species as those living in stable environments that select for delayed reproduction of fewer, larger offspring. Today, these terms have gone out of fashion because additional forms of selection such as bet-hedging against unfavourable or variable conditions can produce similar or mixed suites of life history traits (Roff, 1992; Stearns, 1992). For example, a female Atlantic cod *Gadus morhua* may not reach maturity until it is seven years old, yet it may produce millions of tiny eggs. We see little point in trying to call this an r - or K -selected animal.

At first sight, the demise of the r – K continuum does not seem to bode well for our search for correlations among life history traits that can lead to predictions of sustainable levels of exploitation. However, it is still possible to find surrogate measures for those aspects of life histories that determine responses to exploitation because of fundamental trade-offs between life history parameters (Beverton & Holt, 1959; Beverton, 1963, 1987, 1992; Pauly, 1980; Charnov, 1993; Jensen, 1996; Stamps *et al.*, 1998). Some of

Table 7.1. Parameters used to describe fish life histories

Parameter	Meaning
T_{mat}	Age at maturity ^a
L_{mat}	Length at maturity ^a
T_{max}	Maximum recorded age ^b
k	Rate of growth from von Bertalanffy growth equation
L_{∞}	Theoretical maximum size from von Bertalanffy growth equation
M	Instantaneous rate of natural mortality

^aFor fish populations, T_{mat} and L_{mat} are usually taken as the age and length at which 50% of individuals in the population attain maturity. This is determined from a logistic curve fitted to the relationship between proportion of individuals that are mature and their age or size.

^bMaximum recorded age in an unexploited or very lightly exploited population. Today, this usually has to be determined from historical data.

the main parameters used to describe fish life histories are given in Table 7.1. They include the rate of body growth, k towards a theoretical asymptotic size L_{∞} :

$$L_t = L_{\infty} (1 - e^{k(t-t_0)}) \quad (7.2)$$

Where L_t is the length at age t , and t_0 is the time at which length is zero on the modelled growth trajectory (Beverton & Holt, 1957). The equation provides a very good fit to size-at-age data for many species of fishes with indeterminate growth.

Beverton & Holt (1959) and Beverton (1963) were the first to study the interrelationships between life history parameters in fishes. They showed that: (1) body growth, k , is correlated with M , the rate of natural mortality (or $1/T_{\text{max}}$ as an index of M) (Figure 7.2); (2) body growth is inversely correlated with asymptotic size, L_{∞} ; and (3) the length at maturity, L_{mat} , occurs at a similar proportion of asymptotic length. Such relationships have since been demonstrated for many other groups of vertebrates (Charnov, 1993), and have been particularly useful to fishery scientists because they allow parameters such as M to be estimated from the more easily measured von Bertalanffy growth parameters (Pauly, 1980). The ratios between parameters are dimensionless numbers and are relatively constant within taxonomic groups: the life history invariants. The existence of invariants suggests that the evolution of life histories is governed by some very general trade-offs (Charnov, 1993; see also Kokko *et al.*, Chapter 14). For example, delayed reproduction might increase lifetime reproductive success through increases in age-specific fecundity, despite higher probabilities of mortality before the age of maturity (Roff, 1991, 1992). Maturation

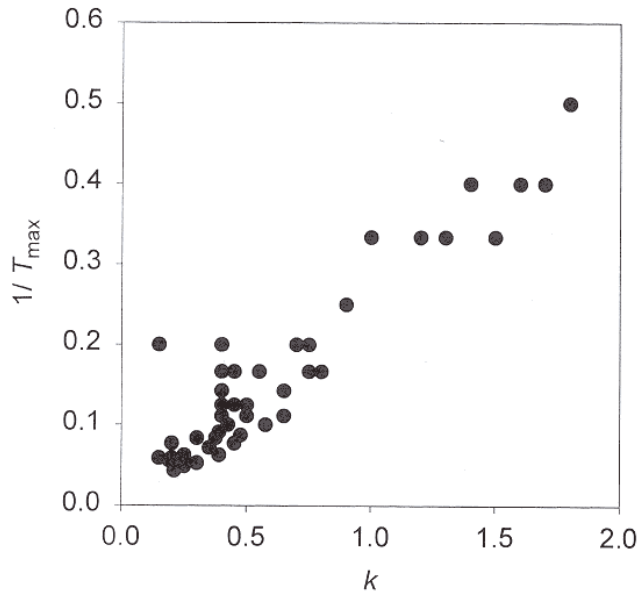


Figure 7.2. Cross-species relationship between $1/T_{\max}$ (T_{\max} = lifespan) and body growth rate, k , for clupeid and engraulid fishes. (Data from Beverton, 1963.)

has costs because energy has to be partitioned from growth to gonadal development. This implies that an early maturing female will be smaller at a given age. Smaller females produce fewer eggs and may compete less effectively for resources.

The net effect of these trade-offs is that fishes show life history strategies ranging from fast growth, high natural mortality, early maturity and small asymptotic size to slow growth, low natural mortality, late maturity and large asymptotic size. Reproductive output is closely linked to these characteristics (Beverton, 1987; Gunderson & Dygert, 1988; Jennings & Beverton, 1991; Gunderson, 1997). Gunderson & Dygert (1988), for example, showed that fish with higher gonad mass to body mass ratios had higher natural mortality, and Jennings & Beverton (1991) showed that herring populations with greater asymptotic size and higher age at maturity had lower annual reproductive output.

Thus, within and among species, generation time and reproductive output, which are key determinants of r , are themselves correlated with many easily measured life history parameters such as age and size at maturity, body growth rates, and body sizes. Body size data are available more often than the others. Asymptotic size, L_{∞} , is usefully approximated by the largest fish seen in a population, ideally an unexploited population. However, even if populations are already being fished intensively at the time of the assessment, we may still be able to use maximum size for predicting vulnerability in data-poor situations.

COMPARATIVE STUDIES

Phylogenies matter

We need to discuss phylogenetically based comparative methods because these are important for understanding the results of several recent studies. First, consider the traditional cross-species approach whereby one might regress changes in population sizes of various fish stocks against the life history variable of interest, such as age at maturity. One could then ask, for example, whether stocks with late maturity undergo a steeper decline in populations for a given level of fishing mortality. This approach is illustrated for four stocks in Figure 7.3. The table at the top of this figure shows data for two species from the Northeast Atlantic (Jennings *et al.*, 1998). When abundance data for the period 1975–94, controlled for differences in fishing mortality, are plotted against mean age at maturity for each stock, the trend supports the hypothesis that stocks with later maturity have declined more steeply. However, the two top data points are both for stocks of

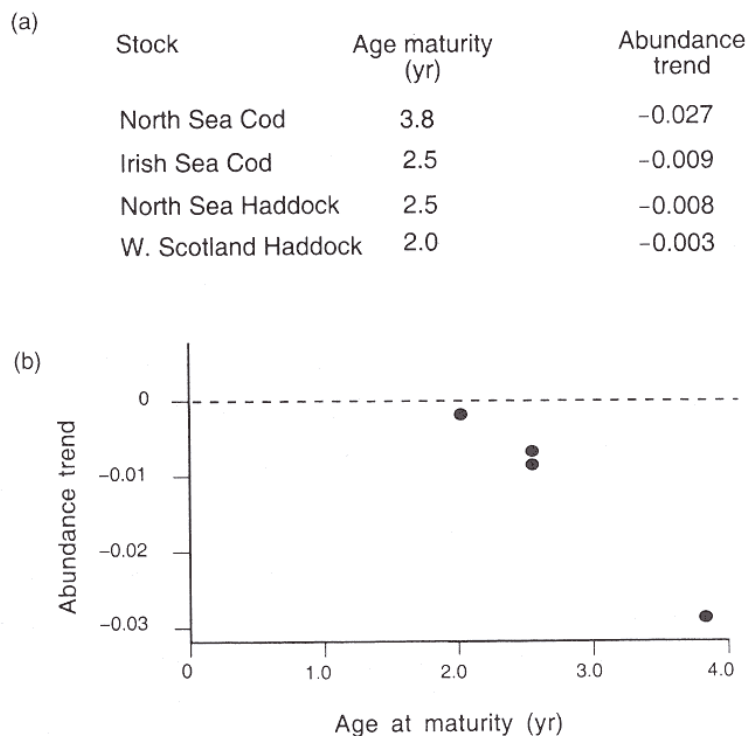


Figure 7.3. Traditional cross-taxonomic comparisons of relationships between age at maturity and abundance trend of four stocks of Northeast Atlantic fishes, measured as the slope of the relationship between \ln -transformed abundance and time (1975–94). (a) Data in tabular form. (b) Data plotted.

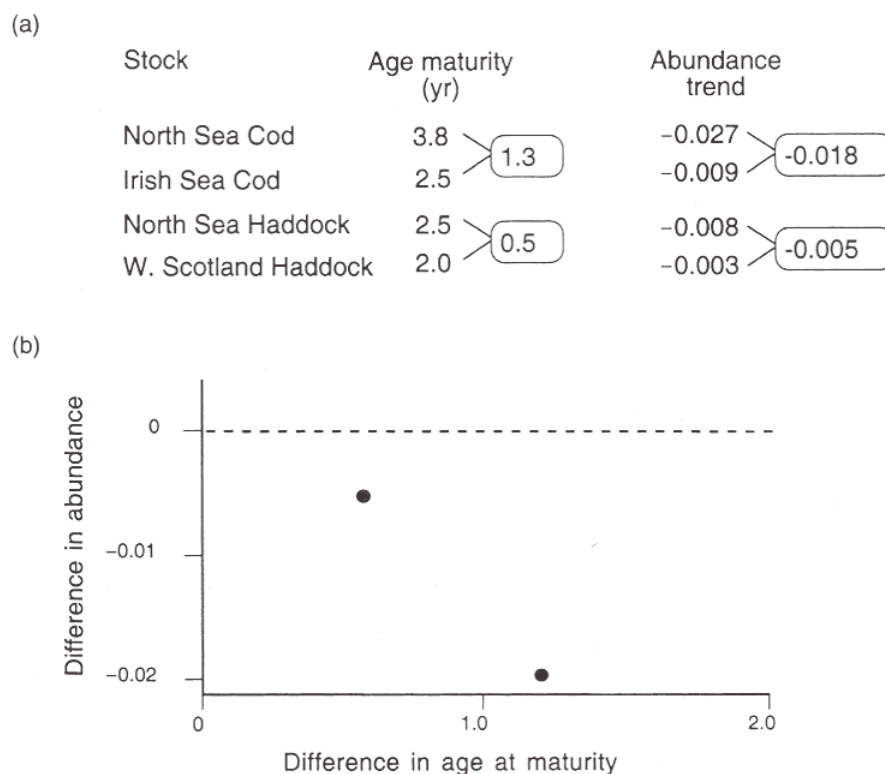


Figure 7.4. Derivation of phylogenetically based comparison of the same relationships as in Figure 7.3. Note that differences among pairs of stocks are (a) calculated and (b) plotted.

haddock *Melanogrammus aeglefinus* and the two bottom ones are for Atlantic cod. Therefore, we do not really have a sample of four independent data points that support the hypothesis: since the two stocks of haddock are obviously closely related to each other, as are the two cod stocks, one might argue that we have only two independent data points (Harvey & Pagel 1991; Harvey, 1996). The stocks will not have evolved their life history traits independently; they will have inherited many aspects of life histories, ecology and behaviour from common ancestors. Therefore, if we treat the stocks as statistically independent of one another we run a strong risk of pseudo-replication.

There are several ways to test for and avoid the problem of taxonomic non-independence in comparative studies, all of which incorporate the phylogenetic relationships of the taxa explicitly into the analyses (Harvey & Pagel, 1991; Pagel, 1999). In Figure 7.4 we present one of the simplest methods, which has been applied to several recent studies of life histories of exploited fishes. A phylogeny has been added beside the data to show the

relationships between the pairs of stocks. Any differences between the two cod stocks must have evolved after the ancestor of this species split from the ancestor of the haddock. This means that *differences* between cod stocks in age at maturity will be independent of *differences* in age of maturity of haddock. Thus, subject to assumptions about the particular model of evolution underlying the divergence of the taxa, we can use 'paired independent contrasts' (Felsenstein, 1985) to calculate differences between close relatives in the variables of interest. This is shown in the circled numbers in Figure 7.4a. These differences, or 'contrasts', are now plotted against one another as in Figure 7.4b. One can also make an additional comparison between the species, based on the mean values for each stock within species (Harvey & Pagel, 1991). The data show that the pair of stocks with the greater difference in maturity also has the greater difference in abundance trend, as predicted by the hypothesis. Note that for presentational purposes the *x*-axis has been set to positive, i.e. by subtracting the smaller value of age at maturity from the larger one in each pair of taxa. Such data may be analysed statistically either by a binomial test or by a regression forced through the origin (Harvey & Pagel, 1991). Newer methods for testing for and correcting phylogenetic non-independence are given by Pagel (1999).

Tests for life history correlations with population changes

The first phylogenetically explicit test for relationships between life histories and population responses to fisheries involved a study of nine pairs of stocks or related species in the Northeast Atlantic (Jennings *et al.*, 1998). This study controlled for differences in fishing mortality. Differences among taxa in maximum length, age at maturity, and a crude surrogate for *r*, all proved to be related to changes in population size. Examples for age at maturity and maximum length are shown in the top panels of Figure 7.5. The key for interpreting such figures is that in all but two comparisons in each analysis, the stock or species with the latest age at maturity had declined more than its sister taxon. Interestingly, a traditional cross-taxonomic comparison that ignored phylogenetic relationships showed no patterns whatsoever, despite a doubling of apparent sample size (Figure 7.5, bottom panels). This shows a benefit of using phylogenetically based calculations; comparisons of differences between related taxa help to control for spurious differences among unrelated species in other variables that may obscure patterns. This increase in resolution is similar to the advantages of a paired design in experiments compared with an unpaired design.

As noted above, body size of fishes and other animals tends to be

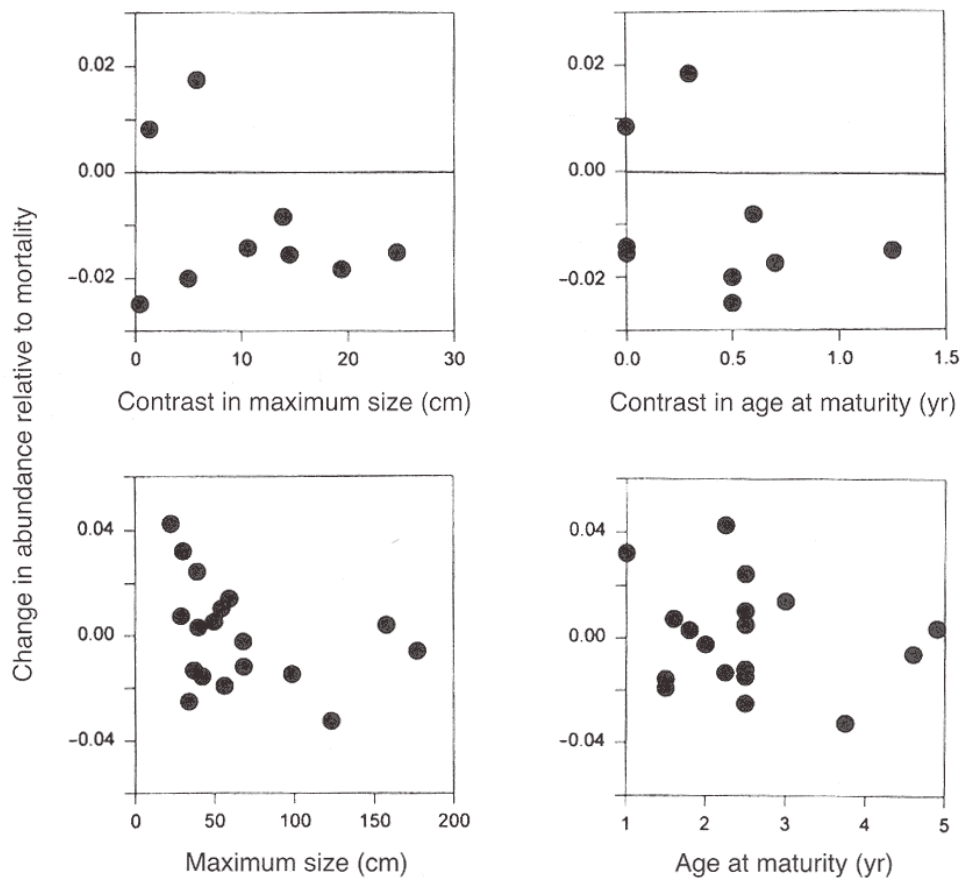


Figure 7.5. Relationships between trends in population size and life history characteristics of nine pairs of stocks or closely related species of Northeast Atlantic fishes. Top panels are phylogenetically based differences among pairs of stocks, and bottom panels are traditional cross-taxonomic comparisons. Abundance trends are the slopes of the relationships for each stock between \ln -transformed abundance and time (mostly 1975–1994). (From Jennings *et al.*, 1998.)

strongly correlated with many other components of life histories, including growth rates, age at maturity, and fecundity (Roff, 1992). Thus it is not surprising that similar results were found in the Northeast Atlantic study for three of the four variables considered. It remains to be seen whether some are more relevant than others. However, from a pragmatic point of view, these correlations involving body size are helpful because size is often the only life history variable known for many fish species.

A similar approach has recently been used for reef fishes in Fiji (Jennings *et al.*, 1999a). This fishery exemplifies the kind of data-poor situation typical of tropical fisheries. Underwater visual censuses of fish

species yielded data on abundance and a literature search was used to determine maximum body size of each of the 33 species of parrotfish (Scaridae), grouper (Epinephelinae) and snapper (Lutjanidae) species recorded. Fishing effort was estimated in 10 fishing grounds by dividing the length of productive reef fronts by the number of villagers, on the basis that all villagers have fishing rights. All of these estimates are imprecise, reflecting the realities of working with reef fisheries. The results showed that 11 of 17 parrotfishes, 5 of 6 groupers and 9 of 10 snappers decreased in abundance with increasing fishing intensity. Due to limited phylogenetic information only nine comparisons could be made between closely related species. These supported the hypothesis that larger species declined significantly more than smaller ones. As with the study of fishes in the Northeast Atlantic (Figure 7.5), a traditional cross-species analysis that ignored phylogenetic relationships missed this trend.

Two processes could account for the patterns documented in Fiji: differences in mortality (large species are more valuable), or differences in ability of populations to respond to mortality. Without data on species-specific mortality rates, we cannot distinguish between these alternatives. However, given that mortality data are almost never available for tropical reef fishes (Johannes, 1998), from a practical standpoint it is still helpful that predictions could be made about species-specific responses to fishing pressure based solely on body size.

Studies of the responses of tropical reef fishes to marine reserve protection also highlight the significance of life history in governing vulnerability. Russ & Alcala (1998) examined patterns of decline and recovery in families of fish as marine reserve protection first collapsed and was later reinstated. Large predatory species such as snappers, emperors (Lethrinidae), sea basses (Serranidae) and jacks (Carangidae) were fished intensively and had low rates of natural mortality and growth that should make them vulnerable to fishing (Bannerot *et al.*, 1987; Sadovy, 1996). These species declined in abundance rapidly as fishing pressure increased, and recovered slowly when fishing ceased.

A recent meta-analysis of studies of the effectiveness of marine reserves for protecting fish populations has confirmed the expectation that the largest-bodied species of fishes would benefit most from protection (Mosquera *et al.*, 2000). This result was not due simply to larger-bodied species being most heavily targeted by fishers, since the result held when the analyses were restricted to species that were not targeted directly but which were probably killed as by-catch.

Can we extrapolate from these studies to predict larger-scale community shifts over long time periods? This was attempted for the northern North Sea, based on a dataset extending from 1925 to 1996 (Jennings *et al.*, 1999b). Data were available for 23 species of fish, representing over 99% of all individuals caught during bottom-trawling surveys. All fish were pooled together, to examine gross trends in the community. The study showed that the mean growth rates of the community rose over this period. Furthermore, the mean age at maturity decreased from about 2.6 years at the start of the time series to about 2.3 years at the end. This was accompanied by a drop in mean maximum body length of about 10 cm, and mean length at maturity of about 5 cm. Phylogenetically based comparisons supported the hypothesis that these trends were due to differences among taxa in declines in abundance in relation to life histories. For example, in eight of nine pairs of taxa, the species that declined in abundance the most also had the largest body size. Interestingly, these trends were not revealed by traditional cross-taxonomic comparisons that ignored relatedness among taxa. There were no obvious environmental trends over this time period that could explain the combined species abundance trends (e.g. salinity, temperature, pollutants). Thus intensive commercial fishing over a 70-year period has shifted the average value of life history characteristics in the community.

Sharks and skates: particular causes for concern?

Sharks and skates (Elasmobranchii) have been well served by their 'slow' life histories for nearly all of the 400 million years since this superorder first arose. But of course evolution has no foresight, and ages of maturity of 10 years or more, combined with low fecundities and long gestation periods for live-bearers, have left elasmobranchs ill equipped to deal with modern fishing pressures. The cause of skates (Rajidae) has not been helped by a flat, square body shape which must be the worst possible design when encountering a fishing net! Indeed, the fact that some species are 10 cm or more from wingtip to wingtip when they emerge from their egg cases means that they may face fishing mortality from the moment they hatch.

Table 7.2 shows a sample of life history characteristics of selected skates and rays encountered by fisheries in the Northeast Atlantic. Note that even the smallest species, the starry ray, does not reach maturity until age five years, while common skates and thornback rays may take 10 or more years. These data, when cast in an age-specific context, can be used to calculate the maximum total mortality (fishing plus natural mortality) that the

Table 7.2. Life history characteristics of selected species of skates and rays (Rajidae) that are caught by commercial trawlers in the North Sea. Estimates are for females (Walker & Hislop, 1998; Walker, 1998, p. 121)

Species	Length maximum (cm)	Length mature (cm)	Age mature (yr)	Fecundity (eggs)	Growth rate (<i>k</i>)	Estimated mortality	Theoretical replacement mortality (<i>r</i> = 0)
Common skate	237	180	11	40	0.06	0.70	0.38
<i>Dipturus batis</i>							
Thornback ray	85	72	10	140	0.14	0.60	0.52
<i>Raja clavata</i>							
Spotted ray	75	58	8	60	0.21	0.72	0.54
<i>R. montagui</i>							
Cuckoo ray	70	59	8	90	0.23	0.65	0.58
<i>Leucoraja naevus</i>							
Starry ray	60	40	5	38	0.22	0.70	0.73
<i>Raja radiata</i>							

r, rate of population increase.

population could withstand, provided that each female replaces herself in the population (see e.g. Brander, 1981; Walker & Hislop, 1998). An age-structured Leslie matrix is used to estimate r , the intrinsic rate of population increase (see e.g. Kokko *et al.*, Chapter 14). This is based on the Euler–Lotka equation:

$$1 = \sum_a^d e^{-rx} l_x m_x. \quad (7.3)$$

Here a is the age at maturity, d is the maximum age attained, and l_x and m_x are, respectively, survival and number of offspring produced at each age, x . One can then calculate the replacement mortality, i.e. the total mortality where $r = 0$. This hypothetical mortality rate for a stable population is given in column 8 of Table 7.2, and can be compared with estimates of actual mortality in column 7. This comparison suggests that only the smallest species of ray is being killed sustainably. This result is particularly sensitive to age at maturity, rather than fecundity (Brander, 1981).

There are important caveats for these calculations. First, we have already seen that it is very difficult to make accurate measurements of r . Indeed, density dependence is rather lost in these calculations: the true sustainability of these populations depends on how the life history parameters that determine rates of population increase change with population size. Secondly, it was assumed that mortality is constant with age for individuals that were more than one year old. While predation risk will probably decrease with age, fishing mortality could either increase if older animals become more vulnerable because of their size, or it might decrease if older animals can actively avoid fishing gear. Nevertheless, the calculations provide a rough indication of the rank order of vulnerability of the various skates according to their life histories.

The links between life histories and vulnerability described for skates also apply to other elasmobranchs (Smith *et al.* 1998; Stevens *et al.* 2000; Frisk *et al.* 2001). For example, for Pacific sharks maximum age and to a lesser extent body size appear to be reasonable predictors of their rebound potential, r_{2M} , an estimate of the rate of potential population growth at a standard theoretical density (Smith *et al.* 1998). This was indicated by cross-species comparisons, and we have also verified these relationships by analysing the data with paired independent contrasts, based on the phylogeny by Dulvy and Reynolds (1997). As we indicated earlier, one needs to be cautious about inferences from surrogate measures of r because relationships with true r are not known. However, these studies

provide compelling evidence that larger elasmobranchs are more vulnerable because they have reduced rates of population increase.

Studies of rays in the seas west of Britain have confirmed the predictions of life history theory regarding vulnerability, and highlighted potentially serious conservation concerns. The first warning came in 1981 when Keith Brander published a paper in the journal *Nature* warning that the 'common skate' had become extirpated from the Irish Sea during the 1960s. An age at maturity of approximately 11 years, combined with low fecundity, were blamed for the inability of this population to withstand mortality due to trawlers.

Recent analyses confirm that this species has still not recovered, with only six individuals having been caught during research surveys from 1988 to 1997 (Dulvy *et al.*, 2000). Unless trawling activity for targeted species such as cod and flatfish declines, there is no reason to expect recovery by common skates. Furthermore, two more species have disappeared from the Irish and Celtic Seas west of Britain – white skates *Rostroraja alba* and long-nose skates *Dipturus oxyrinchus*. These species are reported as having been targeted by long-line fisheries during the late 1880s. Among five additional ray species for which there were sufficient data, the three largest species (blonde, thornback and painted rays *Raja microocellata*) have declined whereas the two smallest species (spotted and cuckoo rays) have increased in number. This increase may be due to competitive release as the larger species have declined. Thus the three largest species have been extirpated, the intermediate-sized species are declining, and the smallest species are increasing. Similar findings of size-related changes in populations of skates and rays have also been reported from the North Sea (Walker & Heessen, 1996).

From a conservation viewpoint these trends are particularly worrying because nearly all European countries have been pooling their fishery statistics among species. Therefore, while fisheries landings for all species of skates and rays combined look reasonably stable, this hides changes in species composition (Dulvy *et al.*, 2000). The extirpations and declines of European rays exemplify the differing goals of fisheries managers and conservationists (Mace & Reynolds, Chapter 1). Rays have not been of sufficient economic value in relation to other species to have been deemed worthy of any specific management to date. However, they are taken into account in new regulations implemented on the 1 January 1998 setting mesh size regulations for fixed nets, and scientists within the International Council for the Exploration of the Sea are aiming to improve data collection and develop assessment methods.

Nearly 20 years after the saga of the common skate was published, Casey & Myers (1998) discovered a similar extreme decline in another species on the other side of the Atlantic. The similarities are eerie. The barndoor skate also was extirpated over a large part of its range (formerly from the waters of the Maritime provinces in Canada to southern New England) during the 1960s, and again the collapse occurred without anyone noticing until decades later. As with the common skate, this species is vulnerable as a by-catch of other fishing operations. Finally, the barndoor skate is in the same genus as the common skate, and is also quite large. It undoubtedly shares the common skate's 'slow' life history, though little is known about its biology. Publication of Casey & Myer's paper led to a flurry of publicity that culminated in the barndoor skate being formally considered for listing under the United States Endangered Species Act. Further research by the National Marine Fisheries Service indicated that the skate's numbers have been on a slight upswing in recent years, and the decision was made not to include it in the Act.

INCORPORATING LIFE HISTORIES INTO CONSERVATION ASSESSMENTS

Towards rules of thumb

It is ironic that many of the species that cause the greatest conservation concern are those that we know least about. Species with slow life histories that are taken as by-catches are particularly vulnerable, as shown in the case of skates and rays. Yet, their low economic value renders them invisible to most fishery assessment biologists. Many fishes caught by developing nations are also beyond the reach of modern assessment techniques. Simple rules of thumb are needed for such species (Johannes, 1998).

We have reviewed a number of studies in both temperate and tropical regions which indicate that traits such as body size may provide some information about the likelihood of decline under fishing pressure. In the few studies that have compared body size with other traits including fecundity, body growth rate and age at maturity, body size has worked as well as or better than anything else. Can body size really be used for proactive conservation assessment? A recent attempt was made for the world's skates and rays (Dulvy & Reynolds, 2002). A database was assembled containing body sizes, latitudinal ranges and depth distributions for 230 species. All species were scrutinised to see whether there was evidence that larger species had undergone greater population declines than smaller ones. The body size of the barndoor skate was used as a specific benchmark, to see whether spe-

cies larger than this were more apt to be of conservation concern. The analysis identified ten species larger than the barndoor skate and, among these, there was evidence to confirm that three have indeed undergone significant population declines. Three species inhabited deep, abyssal plains currently out of the range of fishing gears. No information could be found about the status of the remaining four species, and it was suggested that these should be prioritised for conservation assessment.

These results suggest that life history parameters might be used before formal population assessments have begun, to identify species that deserve a closer look. Thus, for the vast majority of the world's fish species whose population status is unknown, a manager might ask 'How big is it, and is it within reach of fisheries?' to help to decide whether to expend resources on population assessments of that species or a different one. Of course this is extremely crude, but for non-target species and many tropical reef species, it is often the best we can do, and, as the studies of skates and rays have shown, it might often work fairly well.

Classifying levels of threat

A more formal use of life histories in conservation assessment has been proposed to the American Fisheries Society (AFS) following their review of fish populations that are threatened or endangered (Coleman *et al.*, 1999; Musick *et al.*, 1999; Parker *et al.*, 2000). The idea is to incorporate life history information explicitly into the assignment of levels of threat faced by species (Musick, 1999). This is intended as an improvement over traditional categorisations of threat, as used in the *Red Lists* published by the World Conservation Union (IUCN). Under the IUCN rules, designations such as 'critically endangered', 'endangered', and 'vulnerable' are based solely on observed rates of population decline, small distributions, small population sizes, or quantitative predictions based on demographic parameters (IUCN, 1996). The suggestion to the AFS is to use a two-step process. First, one or more of the life history parameters listed in Table 7.1 (r , k , T_{mat} , T_{max} , or annual fecundity) would be used to assign species to a productivity index. If r is known, this is given precedence; otherwise the parameter corresponding to the lowest productivity category is used. For example, if r is estimated at > 0.5 or T_{mat} is < 1 year, the species is listed as having 'high' productivity. Conversely, 'very low' productivity would have $r < 0.05$ or $T_{\text{mat}} > 10$ years. These values are not meant as hard and fast criteria, but are intended as guidelines. The second step is to assign a threat category according to the combination of productivity as determined above, and observed population decline. For example, a 'high' productivity species

would need to decline by 99% over 10 years or three generations in order to be considered as 'vulnerable'. In contrast, under existing IUCN guidelines productivity is ignored and the decline threshold is fixed at only 20%. The corresponding thresholds for a listing of 'vulnerable' for species whose productivity indices are 'medium', 'low', and 'very low' are suggested as 95%, 85% and 70%, respectively.

We appreciate the basic logic of this proposal, since the evidence available to date does support the expectation that life histories should be important for determining the ability of fishes to withstand exploitation. However, we have three concerns. First, the decline thresholds required to trigger a listing of 'vulnerable' strike us as too high. Even species with the slowest life histories would be allowed to decline by up to 69% in 10 years or three generations (whichever is longer) before raising the minimum level of concern. Secondly, as we have noted, there are severe practical problems in trying to measure r . It was suggested that if one cannot measure this, then it would be ideal if the alternative life history parameters come from unexploited populations (Musick, 1999). This is surprising, since the intrinsic rate of increase, r , is normally taken to refer to populations at the other end of the spectrum, i.e. very low density. In any case, while we agree that r ought to be important (see e.g. Figure 7.1), we are sceptical about the chances of measuring it accurately, and we share the concern of Sutherland & Gill (Chapter 12) about interpreting it with respect to density dependence. Thirdly, even if we wish to settle for the other life history characteristics, information on these, too, is available for only a small subset of fishes. One might counter that this does not mean that we should ignore the information when it is available.

We do not expect this debate to be settled anytime soon, but ultimately we consider this to be an empirical issue with two components. First, are stocks with high potential rates of population increase inherently resilient, as has been traditionally believed? Secondly, can fisheries managers control population sizes? If you believe that the answers to both of these questions are 'yes', you would be well justified in being dismayed by the IUCN's listing of species such as Atlantic cod as vulnerable to extinction. A recent analysis sheds some light on this. Hutchings (2000) showed that most of the 90 stocks of fish that he examined had shown little, if any, recovery 15 years after they had been reduced by 45–99% in population biomass. This suggests that we should be cautious in the assumption that most stocks can bounce back readily from low numbers. This analysis does not consider changes in fishing mortality over the time periods. It is therefore not clear whether the results represent a failure of the resiliency assumption, or a

lack of effort to reduce fishing mortality. In other words, the explanation for the patterns may reside in either of the two questions we have posed above. Either way, it is an excellent first step towards an empirical resolution of how to reconcile differing views of conservationists and resource managers. Optimists argue that, although most populations have not been recovering, they still are not going extinct, and if there were clear signs that they were, managers would do something about it. Pessimists invoke the precautionary principle to argue that we should flag up declining species as vulnerable to extinction, and take them off the list after managers have proved that the populations have stabilised.

CONCLUSION

There is still much to be done to bring life history analyses more firmly into mainstream conservation assessments. Robust links to density dependence have been particularly elusive, and this is an area of theory development that would be well worth while. In addition, further comparative studies of population dynamics in relation to life histories should reveal the potential for the development of surrogates for more sophisticated modelling techniques. The relationship between life histories and population dynamics has featured prominently in debates concerning whether exploited fishes are threatened or safe. We feel that this is largely an empirical issue, which must be resolved before we can allow species to be declared safe on the basis of fast life histories. In the meantime, there is scope for using components of life histories to provide simple rules of thumb for prioritising conservation assessments of the many fish species about which little else is known.

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