The threat of fishing to highly fecund fishes

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The last decade has witnessed a growing awareness that fishes can not only be severely overfished but could also be threatened with extinction through over-exploitation. Among commercially important species, those particularly at risk are large and slow to mature, iteroparous and may have sporadic recruitment. The threat of extirpation or extinction may be greater if species are particularly valuable, have a limited geographical range, are part of mixed-species fisheries, or are distributed solely within areas of intense fishing activity. Significantly, there is little empirical or theoretical basis for hypothesizing that highly fecund species are any less at risk than those of low fecundity, as is often assumed. Indeed, the use of fecundity in estimating reproductive output in long-lived, highly fecund, pelagic egg-producing species, may be deeply flawed. A general resistance to accepting that fecund marine fishes could become endangered through exploitation stems from poor understanding of population dynamics, especially in the early post-settlement phase, coupled with assumptions of fishery models that ignore critical components of life history theory. Moreover, faith in the ability to manage exploited species effectively leads to the perception that severe declines are management, rather than conservation, issues. The growing list of threatened marine species and a realization of the many factors that place them at risk indicate the need to be precautionary about the possibility of extinction, and about the criteria used to assess such risk, with important implications for research, monitoring and management.

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Key words: fishery; extinction; overexploitation; conservation; endangerment; management; life history strategy.

INTRODUCTION

In the early 1990s, Sadovy (1993) recorded the disappearance of spawning aggregations and declines of the Nassau grouper, *Epinephelus striatus* (Bloch), and questioned whether this species could become endangered, or was simply 'unlucky' in being so vulnerable to fishing. This fecund fish is the largest of a multi-species, multi-gear, reef fishery, easy to catch as a juvenile and during its brief annual spawning aggregations. At the time, severe declines had already been documented for several elasmobranchs and teleosts but, in general, the idea that highly fecund, commercially important, fishes could become endangered was rarely considered seriously (Hendrickson, 1979; Huntsman, 1994). Declines were generally perceived to relate to overfishing, resolvable by fishery management, rather than to merit conservation attention. In 1996, however, the Nassau grouper was listed as endangered on the IUCN (the World Conservation Union) Red List and is currently a candidate under the United States Endangered Species Act (ESA). Aggregations continue to decline.

The situation with freshwater fish faunas by the early 1990s was very different from that in the marine environment, for documentation from around the world

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clearly indicated that many freshwater fishes were already threatened. Conservatively, it was estimated, in 1992, that 20% of all freshwater fishes, 1800 species, were already extinct or in serious decline. Five reasons for declines and extirpations were identified: competition for fresh water, habitat alteration, pollution, introduction of exotic species and over-exploitation. The fifth, overexploitation, was considered the least important single threat to freshwater fishes, although most declines appear to result from multiple cumulative long-term effects of several factors (Moyle & Leidy, 1992; Bruton, 1995).

In the marine environment, exploitation has emerged as the major overall threat to commercially important fishes and the conservation status of marine, exploited, fishes is attracting closer scrutiny (Culotta, 1994; Roberts & Hawkins, 1999). The reasons are several and involve both a scant understanding of extinction risk in the marine environment and misconceptions about the resilience of marine fish populations to heavy exploitation. The various global listings of endangered and threatened species reflect this history. The Convention on International Trade in Endangered Species (CITES) includes few, mainly freshwater and specialized, relict fishes, which are limited in distribution. The sole marine examples are the totoaba *Totoaba macdonaldi* (Gilbert) and the coelacanth *Latimeria chalumnae* Smith. In 1996, the IUCN convened its first workshop to look specifically at marine fishes and almost 150 species were listed (Baillie & Groombridge, 1996; Mace & Hudson, 1999). More recently, the American Fisheries Society recognized 82 species and subspecies of marine fishes vulnerable to extirpation (Musick *et al.*, 2000) while a recent summary of species included in the threatened fishes of the world series of the journal *Environmental Biology of Fishes*, included just six marine species out of 97 listed, about a third of which were threatened by over-exploitation (Cambray, 2000).

Of these listings, the debate has been particularly intense over the possible threat of extinction to commercially important marine species that have high fecundity and a dispersive egg-larval phase. Fuelling this debate is a paucity of records of marine extinctions and the differing perspectives of ichthyologists and conservationists on the one hand, and fishery scientists and managers on the other, regarding extinction risks to such species and their potential for recovery (Beverton, 1992; Carlton *et al.*, 1999; Mace & Hudson, 1999; Hutchings, 2001). Clearly something is wrong: a significant proportion of documented world fisheries are over-exploited, recoveries are often slower than predicted by fishery theory, profound ecosystem changes have been noted and declines in a number of species have been precipitous (Safina, 1995; Pauly *et al.*, 1998; Hutchings, 2000*a*). But do such changes herald extinctions? Examples of population extirpations might suggest so and are increasing as more is learnt about marine species. However, among marine pelagic spawners, few species extinctions have been recorded, and none of them fishes (Carlton *et al.*, 1999; Roberts & Hawkins, 1999). Whether the absence of extinction records is a true indication of low extinction risk reflects a general lack of information on marine organisms, or indicates attitudes regarding the potential for endangerment in non-mammals, is not yet clear. Certainly, the gradual shift in management objectives from maximizing yield (and avoiding growth overfishing) to ensuring sufficient spawning biomass (to avoid recruitment overfishing) reflects a poor record of management success and a growing recognition of shortcomings in management

thresholds. Recruitment overfishing is but one step down the slippery slope to possible extirpation and should be seriously noted by managers and conservationists alike (Musick, 1999). On the other hand, biomass declines of well over 50%, which might concern conservationists and which fall within certain IUCN thresholds for assigning threat (within a specified time frame), are often a goal of fishery managers who seek to maximize surplus yield in a way that is theoretically sustainable. In marine fishes, it is difficult to estimate population size and rates of population increase and recovery, or to find a reliable proxy for abundance such that changes in abundance can be determined. This makes assessments of risk particularly onerous and conservation status determined solely by declines in landings could either overestimate or underestimate risk (MacKenzie, 1995; Matsuda *et al.*, 1997).

Out of this debate has emerged a need to examine the paradigms that inform the perspectives of commercially exploited and fecund fishes, especially the circumstances around known declines and extirpations. The aim of this paper is to examine assumptions about resilience in highly fecund (those producing $\geqslant 10^4$ eggs per year), marine pelagic egg producers. Patterns of vulnerability and the more pressing shortcomings of data are identified. The present review does not focus on extreme cases of vulnerability, such as exceptionally rare or highly restricted species, for which there is relatively little disagreement (Hawkins *et al.*, 2000). Instead, it is directed at commercially important, fecund species, around which the debate centres.

SYNTHESIS

A characteristic widely assumed to confer resilience on many exploited species that produce pelagic eggs is their high fecundity, the production of tens of thousands to millions of eggs by individual females each year. The implication is that the production of large numbers of pelagic eggs allows depleted populations a better potential for recovery, through sheer numbers, compensatory responses and the dispersive capability of pelagic eggs and larvae, once the threat is released, relative to less fecund species. Evidence for each possibility will be examined.

FECUNDITY, LIFE HISTORY AND RESPONSE TO FISHING

There are fundamental weaknesses to the argument equating high fecundity with resilience that stifle the debate on extinction threats to marine pelagic spawners (Hutchings, 2000b, 2001). The first, and most obvious, is that not all eggs are created equal. It makes little sense, for example, to compare, egg by egg, the tens of well-nourished and protected packages produced by an oviparous skate, to the million tiny, fragile eggs produced by a similarly sized fish and conclude that the fish must therefore be more resilient. The eggs in these examples are not equivalent units, for their respective probabilities of survival to a reproducing adult can differ by orders of magnitude. Such differences in egg size and zygote survivorship have arisen through phylogenetic and environmental constraints and represent very different life history strategies and trade-offs between, even within, different taxonomic groups (Partridge & Harvey, 1988; Stearns, 1992). Among pelagic spawners, broadcast spawning

(bet-hedging) of large numbers of eggs might have evolved to maximize egg number in response to large-scale spatial and temporal patchiness in food supply or suitable habitat wherein only a few young will ultimately survive (Phillipi & Seger, 1989). Where such patchiness does not exist, the best strategy might be, instead, to produce few and large offspring, each with a good chance of survival. The important point is that these adaptations to different constraints and environments are equivalent in achieving replacement at equilibrium (Hutchings, 2001). Thus it is not surprising that, although pelagic spawners vary by up to six orders of magnitude in fecundity, their maximum reproductive rates do not vary by more than a single order (Myers *et al.*, 1999; Hutchings, 2001).

Rather than broad taxonomic comparisons (i.e. between turtles and tuna, or sharks and salmon), possible relationships between fecundity and resilience should be examined among related species. Phylogeny can be controlled for by taking the comparative approach (Harvey & Pagel, 1991). If fecundity and resilience are directly linked it might reasonably be predicted that the more fecund among related species, similar in other aspects of life history and exploited in similar ways, are less likely to be extirpated by fishing. For example, some sharks and rays (elasmobranchs) have declined in abundance following fishing, especially when directly targeted, relative to groundfish stocks (Brander, 1981; Dulvy *et al.*, 2000; Rogers & Ellis, 2000; Stevens *et al.*, 2000). However, among elasmobranchs, two skates, the barndoor skate *Raja laevis* (Mitchill) and the common skate *Raja batis* (L.) represent the most extreme examples of depletion, yet skates are among the more fecund all elasmobranchs. Clearly, factors other than fecundity are involved. These could be related to life history or to fishing pressure and fishing selectivity.

What life history factors other than fecundity could account for extirpations of several skate species and what might be the role of selective fishing (Casey & Myers, 1998)? Walker & Hislop (1998) showed differences among skate species in a south-west North Sea fishery in apparent response to fishing. Several species declined (*R. batis* and thornback ray, *Raja clavata* L.), while others had increased since 1930, such as the starry ray *Raja radiata* (Donovan). These skates show a wide range in ages and lengths at maturity and maximum size, but most length and age classes of all species were taken in the trawl fishery where all species have commercial value except for *R. radiata*, an incidental bycatch. Shifts in skate species composition over time show that those of lowest length-age at maturity and highest rate of population increase have come to dominate catches, while larger species, with late ages of maturity, are those that have severely diminished. Although it is difficult to assess the precise role played by fisheries in altering the abundance of skates and rays in the North Sea without knowing about oceanographic conditions and changing fishing practices, there does appear to be a general trend of lower resilience to fishing in the larger species, which are slow to become sexually mature. Brander (1981) concluded that the response to exploitation of *R. batis* is more importantly determined by net survival to maturity than by fecundity *per se*, while Stevens *et al.* (2000) found that age at maturity was the strongest correlate of shark rebound potential, and Dulvy *et al.* (2000) concluded that replacement rate in skates is inversely related to body size.

Among pelagic spawning fishes, comparative studies, where the confounding effects of both fishing selectivity and phylogeny have been accounted for,

indicate that, as for some elasmobranchs, large size and low potential rates of population increase, but not fecundity, affect resilience to intense exploitation. Jennings *et al.* (1998), for example, looked at life-history correlates of 18 intensively exploited temperate groundfish stocks over the same time period (mackerel *Scomber scombrus* L., sole *Solea solea* (L.), plaice *Pleuronectes platessa* L., herring *Clupea harengus* L., cod *Gadus morhua* L., haddock *Melanogrammus aeglepinus* (L.), saithe *Pollachius virens* (L.)). Pair-wise comparisons among related species showed that those maturing later, attaining a larger maximum size, and with low potential rates of population increase, had greater relative abundance declines. The analysis also showed that neither fecundity or low growth rate were significant determinants of responses to heavy exploitation. A comparative analysis with similar outcomes was conducted on three tropical reef fish families in a multi-species Fijian fishery that took a wide range of life history stages (Jennings & Lock, 1996). Among heavily exploited snappers (Lutjanidae) and groupers (Serranidae), those species that declined most in abundance, compared to their nearest relatives, attained a greater maximum size, suggesting that size, or some correlate thereof, may facilitate the prediction of vulnerability to fishing (Jennings *et al.*, 1999a). Among the lightly targeted parrotfishes (Scaridae) on the other hand, no such relationship was detected. Whether this is because different life history correlates are involved (or none), or because the effects only become apparent at low population levels, and under intense exploitation, is not known. In both studies, greater declines of larger species were not evident when traditional cross-species analyses were performed. Comparative analyses among related species, therefore, where fishing selectivity is eliminated as a confounding factor, represent a powerful analytical tool for assessing vulnerability of fish populations to exploitation and help to eliminate correlated characteristics among taxa being compared. Understanding what makes one species more vulnerable than another, among related species, greatly enhances predictive capability in identifying species at risk (Jennings *et al.*, 1999a, b).

Rockfishes (Scorpaenidae) typically produce one to several batches of thousands to several million live young per year but, although highly fecund, other life history attributes render them susceptible to overfishing (Parker *et al.*, 2000). They are long-lived (some >100 years) and may take many years to mature. They are also heavily exploited and often marketed well before attaining sexual maturity. Two medium-sized species, the copper rockfish *Sebastes auriculatus* Girard and the quillback rockfish *Sebastes maliger* (Jordan & Gilbert), are being reviewed under the ESA, and the boccacio, *Sebastes paucispinis* Ayres, one of the larger rockfishes (attaining 0·91 m total length, L_T, and 30 years), is listed as critically endangered on the IUCN Red List, having been reduced by over 90% with little recovery in decades (Parker *et al.*, 2000). It is not clear why recovery is so slow but larger rockfishes appear to be particularly susceptible to fishing.

The groupers (Serranidae) include some of the most fecund of all reef fishes, females releasing thousands or millions of eggs each spawning season. Like the rockfishes and other long-lived species, groupers are heavily exploited but most can withstand only light levels of fishing pressure (Huntsman *et al.* 1994; Coleman *et al.*, 1996, 1999; Crouse, 1999). During the last decade, there has been growing concern over the conservation status of several groupers and two

are currently candidates for the ESA, the jewfish *Epinephelus itajara* (Lichtenstein) and *E. striatus*, which had dropped to just 1% SPR [the ratio of the fished spawning stock biomass per recruit (SSBR) to the unfished SSBR and used to evaluate the condition of the spawning stock and to establish criteria for managing spawning potential (Goodyear, 1989; Sadovy & Eklund, 1999)]. The largest grouper and biggest of all reef fishes, the giant (or Goliath) grouper, *Epinephelus lanceolatus* (Bloch), is listed as vulnerable on the 2000 IUCN Red List which included 13 groupers in threatened categories. As for rockfishes, snappers and sharks, larger species have low natural mortality and large size at maturity, and appear to be more vulnerable than smaller species. Many groupers also exhibit complexities of reproductive biology that make them particularly susceptible, such as hermaphroditism or aggregation-spawning (Sadovy, 1993; Vincent & Sadovy, 1998; Crouse, 1999; Huntsman *et al.*, 1999).

That large size, or some life history correlate thereof, and low potential rates of population increase, rather than fecundity, may determine vulnerability is consistent with examples of extreme declines in other large, highly fecund marine or estuarine teleosts. Sciaenid (croakers) females can produce millions of eggs a year. The two largest species attain 2 m L_T and count among the most threatened of all marine fishes. *Totoaba macdonaldi*, from the Sea of Cortez, declined so drastically that it was included on CITES Appendix 1 in 1976 and numbers have still not recovered (Barrera Guevara, 1990; Cisneros-Mata *et al.*, 1995). The giant yellow croaker *Bahaba taipingensis* (Herre), found only along the coast of southern China, is not only commercially extinct in Hong Kong (Pitcher *et al.*, 1998) but has all but disappeared throughout its range and is considered a state protected species in China (Y. Sadovy & W-L. Cheung, unpubl. data). While human activities in and around the estuarine habitats on which these species partially depend surely contribute to their threat, as it does for several other croakers (Musick *et al.*, 2000), it is fishing pressure that is almost certainly the major cause for their decline. The highly valued *Thunnus maccoyii* (Castelnau), listed on the IUCN Red List as critically endangered, is at record low levels with declines in adult biomass of >90%; this species attains 40 years and almost 2·5 m (Hayes, 1997). One of the largest of all reef fishes (Labridae), the humphead wrasse *Cheilinus undulatus* Rüppell, is severely depleted throughout much of its range (Sadovy & Vincent, 2002; Donaldson & Sadovy, 2002). None of these large species has evidently been protected by their high fecundity and they represent some of the most extreme examples of commercially significant marine pelagic spawners at risk, largely or entirely from overexploitation.

In summary, once fishing selectivity and phylogenetic relatedness are controlled for, comparative analyses indicate that large size, long life, late maturation and low rates of natural increase render some elasmobranchs and many marine teleosts particularly vulnerable to fishing, some to the point of endangerment. The finding that fecundity per se is not directly linked to vulnerability is consistent with life history theory. Many long-lived marine teleosts share a suite of life-history characteristics of delayed sexual maturity, long reproductive lifespan, sporadic recruitment and iteroparity. These are adaptive responses and predictable 'trade-offs' to low probabilities of successful reproduction, due to high egg mortalities of millions of small pelagic eggs, in any given year (Roff,

1981; Leaman, 1991; Stearns, 1992; Ferreira & Russ, 1995; Crouse, 1999). Reproductive potential in long-lived species may be further compromised when population age structure becomes truncated through fishing by loss of larger, older fish, and when many juveniles are taken, commonly the case in long-lived species and multi-species fisheries (Beverton, 1986; Leaman, 1987). Short-lived fishes, by contrast, combine early sexual maturation and high rates of intrinsic population growth and are theoretically more resilient to fishing (Roff, 1983; Stearns, 1992; Hutchings, 2000a).

FECUNDITY AND MEASURING RATES OF POPULATION INCREASE

Although fecundity is clearly not an indicator of resilience to fishing, it is widely used to estimate the rate of natural increase of populations, with the aim of comparing vulnerability, or recovery potential, across populations or species. There are several problems with its use, in this context. Because r, the intrinsic rate of natural increase (i.e. per capita instantaneous rate of increase of a population with a stable age distribution) is hard to estimate, and because absolute population sizes are so difficult to determine for fishes, proxies are typically used. One of several such proxies is r_{est} which approximates to ln $R_o T^{-1}$ (where T is generation time, the average age of mothers giving birth, and R_o is the net, per generation, reproductive rate, or the number of daughters expected per female per lifetime) (Stearns, 1992). The fundamental problem with this approach is that age distribution and age-specific survival rates are assumed to be stable. Since this is rarely the case for longer lived species, an alternative indicator of potential for rate of population increase has been proposed, ' reproductive value ' ($RV_t = \Sigma_{t=i}^{t_{max}} S_i E_i$, where S_i is survival rate until spawning season of age i and E_i is the fecundity of female in age class i, and t_{max} is maximum age) which weights the contribution of individuals of different ages to population growth rate (Fisher, 1930; Goodman, 1982; Stearns, 1992; Katsukawa, 1997). RV incorporates probabilities of survival and expected number of offspring by age class and is equivalent to spawning per recruit of a recently recruited individual used in SSBR analyses in fish stock assessments (Goodyear, 1989).

The use of fecundity in such estimates of rate of population increase is a fundamental problem. The parameters R_o or E_i, intended as measures of reproductive output, are typically represented either by annual fecundity or by adult female biomass. Using egg production (egg counts), or adult female biomass, to estimate reproductive output for long-lived pelagic egg producers is problematic for four reasons: spawner-recruit relationships, estimation of annual fecundity, determination of adult female biomass, and complexity of behaviour or life history trade-offs. For spawner-recruit relationships, given high mortality in the planktonic/larval phase, the number of pelagic eggs produced is unlikely to reflect the number of individuals surviving to recruit (settlement). Spawner-recruit relationships tend to be more obscure in high fecundity than low fecundity species which means that spawner (or egg) biomass, or SPR, do not reflect reproductive potential, or adult numbers subsequent juvenile recruitment (Murphy, 1968; Robertson et al., 1993; Shepherd & Brown, 1993; McShane, 1995; Boehlert, 1996; Roberts, 1996). Among related species, stocks with higher fecundity have higher recruitment variation (Rickman et al., 2000). Estimates of

annual fecundity are extremely difficult in long-lived pelagic spawners because (1) spawning frequency per female in multiple spawners is difficult to estimate; (2) annual fecundity is particularly difficult to estimate in repeat batch spawners that might spawn frequently over long reproductive seasons; (3) not all mature females reproduce every year e.g. yellowfin bream *Acanthopagrus australis* (Günther), gag grouper *Mycteroperca microlepis* (Goode & Bean), and orange roughy *Hoplostethus atlanticus* Collett (Pollock, 1984; Koslow *et al.*, 1995; Koenig *et al.*, 1996) and (4) high variation and sporadic recruitment events in space and time, for many longer lived or more fecund pelagic spawners, make annual estimates difficult (Murphy, 1968; Leaman & Beamish, 1984; Grimes & Turner, 1999; Rickman *et al.*, 2000). Adult female biomass may not be a reliable proxy for fecundity in red snapper *Lutjanus campechanus* (Poey); one large female of 12·5 kg is equivalent in fecundity to 212 smaller females averaging 1·1 kg each, yet 12·5 kg of females each 1·1 kg each (*c.* 11 fish) would be substantially less fecund that one female of the same mass because of the form of the fecundity-body mass curve (Plan Development Team, 1990) (see also annual fecundity estimates, above). Complex behaviours or life history trade-offs can affect the number of eggs produced even within species, or among closely related species (see also depensatory effects below). For example, the inverse relationship between egg size and number of eggs, and the positive relationship between egg survivorship and egg size can confound the use of egg number alone to meaningfully compare reproductive output among species (Smith & Fretwell, 1974; Elgar, 1990).

There is a need to discard the widespread notion that fecundity and resilience in marine pelagic spawning species are intimately linked and to examine carefully the use of fecundity in estimating rates of population increase. The foregoing strongly suggests that more appropriate estimates of the potential for population increase, and hence recovery, need to be developed for long-lived fecund fishes. Estimates could focus on the post-planktonic phase when post-settlement mortality by age can be factored into calculations of life history tables. From a conservation perspective, life-history correlates could be used to identify particularly vulnerable species, as discussed above. Improved and consistent, fishery-independent, monitoring of exploited populations would enable more reliable estimates of changes in abundance to be made over time.

Significantly, fecundity is an inappropriate criterion for identifying extinction risk. Even with the caveat that it has low priority relative to rate of population increase (which also involves the use of fecundity) (Musick *et al.*, 2000), its very inclusion signals an apparent relevance which is not supportable (Hutchings, 2001). Moreover, the use of r_{est} may not reflect the intrinsic rate of natural increase if fishing-induced phylogenetic or phenotypic changes have already occurred and the problem with the use of RV is that age-specific fecundities and survival are known for relatively few species (Musick, 1999; Hutchings, 2001).

DISPERSAL CAPABILITY AND GEOGRAPHIC RANGE IN RELATION TO POTENTIAL FOR RECOVERY AND PERSISTENCE UNDER FISHING

If high fecundity per se does not confer resilience to fishing and a high potential for population recovery, why does the perception persist that it does? Perhaps some pelagic spawners are indeed more resilient than less fecund species

because of egg and larval dispersal, recolonization, or compensatory (density-dependent) responses at reduced population levels.

Evidence for dispersal-recolonization

A planktonic egg-larval phase would appear to confer considerable potential for recolonization of reduced or extirpated populations from propagules originating elsewhere. However, while many marine species have wide geographic distributions, not all have long-range larvae and, even among those that do, the potential for dispersal may never be realized. Significant recent advances in molecular and other techniques have made it possible to examine questions of species status in the sea and population structure. Such studies have revealed regional genetic differentiation previously not apparent, as well as evidence for self-recruitment which suggests limits to the potentially wide dispersal of pelagic eggs and larvae in fishes (Planes, 1993; Culotta, 1994; Planes et al., 1998; Jones et al., 1999; Swearer et al., 1999). Some species with pelagic larvae have extremely restricted ranges, despite a planktonic egg and or larval phase (Hawkins et al., 2000). Moreover, recovery of heavily fished populations through dispersal from elsewhere can only occur if there remains an ' elsewhere '. Despite a pelagic phase, some species have geographic ranges entirely within heavily fished areas and there may remain little in the way of refugia as a source of recruits. For example, the China Seas are among the most heavily fished in the world and several species with limited ranges in the region have declined heavily, with little apparent opportunity for recovery despite their high fecundity. Examples include the Hong Kong grouper *Epinephelus akaara* (Temminck & Schlegel), and the giant yellow croaker (Sadovy & Cornish, 2000; Y. Sadovy & W-L. Cheung, unpubl. data).

Evidence for density-dependent or compensatory responses

Fishery theory suggests that over time, and within a range of exploitation intensities, a stock will adjust to increased rates of mortality brought about by fishing through compensatory adjustments in growth and recruitment (such as changes in size and age of sexual maturation, fecundity, and survivorship) (Ricker, 1975; Hilborn & Walters, 1992; Rochet, 1998). What is the evidence for compensatory, density-dependent responses at low population levels for fecund pelagic spawners and are the changes sufficient to allow recovery?

Compensatory or density-dependent responses to fishing are highly variable, may be genetically constrained, may be inadequate, or may not occur at all (Law, 2000). In plaice, sole and cod from the North Sea there was little evidence of variability in reproductive parameters related to changes in population density (Rijnsdorp et al., 1991). Results from this study showed differing trade-offs among maturity and growth, density and egg production, pointing to complex interactions between growth, reproduction and maturation. Trade-offs were often not strongly density-dependent and may be constrained by genetic factors. In general, onset of maturity may depend more on age, in short-lived species that mature early, and on size in longer-lived, late-maturing species, with developmental or genetic constraints more evident in longer lived species (Roff, 1982, 1983; Archibald et al., 1983; Leaman, 1991; Jennings & Lock, 1996).

Even if compensation does occur, and there are many examples of increased growth at reduced density or abundance, it may be insufficient for recovery from heavy fishing. For example, when size, rather than age, is an important determinant of sexual maturation, a compensatory response of increased growth rate to attain size of sexual maturation more quickly can mean lower fecundity at sexual maturation (Adams, 1980; Roff, 1983). Moreover, a relatively small increase in fecundity may have an insignificant effect on recruitment and population recovery (Leaman & Beamish, 1984; Sale, 2000). A minor increase in fecundity (by attaining sexual maturation faster) may compensate little for major declines in lifetime reproductive output resulting from the loss of larger, more fecund, individuals through truncation of average lifespan through fishing (Leaman, 1991). In heavily exploited rockfish, such as *S. alutus*, for example, there is limited compensatory phenotypic plasticity, and little apparent buffering against the effects of reduced lifespan, while in the grouper, *M. microlepis*, heavy fishing produced no substantial change in size of female sexual maturation over more than 10 years (McGovern *et al*., 1998). In the orange roughy, *Hoplostethus atlanticus*, mean fecundity increased by only 20% during a 5 year period during which time stock size declined two-fold, although there was also an increase in the number of spawners during this same period (Koslow *et al*., 1995).

While there is a wide literature, both theoretical and empirical, in support of compensatory, density-dependent responses, among industrial fisheries, few examples refer to long-lived species at very low population levels, and others are contradictory. There is evidence for density-dependent responses at very low stock levels in fisheries of small pelagics (Beverton, 1990). An analysis of 90 stocks of gadids, flatfishes, sparids and scombrids showed that recovery, after cessation of fishing and 15 years after reductions of 45–99% in reproductive biomass' was slower than predicted by theory: shorter-lived clupeiforms, on the other hand, fared much better than longer-lived species, indicating better compensatory responses, although the confounding effects of fishing selectivity could not be ruled out (Hutchings, 2001). The resilience of clupeiforms indicated by these two, and other, studies, suggests that these fish may not, in fact, serve as appropriate models against which to judge the resilience of longer-lived fished species in general. Perhaps clupeiforms are even exceptional in their resilience, or, perhaps the nature of their fisheries means that fishing can be better controlled than in more mixed-species situations. On the other hand, Mace & Sissenwine (1993) analysed 91 sets of spawner-recruit data and found that, after depletions, larger species, with low natural mortality, could recover from lower percentage biomass relative to virgin biomass better than smaller species.

According to fishery theory, compensation can also aid population recovery by increasing reproductive output, or egg survivorship, at low population levels on the assumption that populations are limited by factors such as food, disease shelter and predation pressure. There is little evidence that survivorship of small pelagic eggs is higher at low population densities. Moreover, Myers *et al*. (1999) looked at maximum reproductive rates of temperate species at low population sizes by examining 500 *S-R* relationships and showed that the maximum reproductive rate not only was relatively constant within species but also that the rate is rarely >7 and is more usually *c*. 3. This is significant in as much as such rates approximate those of terrestrial vertebrates, notwithstanding the almost

six-fold difference in fecundity among the fishes (Hutchings, 2001). These authors found scant evidence for increased survival at low spawner biomass and concluded that their 'unexpected' finding of a maximum reproductive rate suggested an inability to sustain intense fisheries (Myers & Barrowman, 1996). In general, there is clearly a need for more work to evaluate compensatory responses in pelagic egg producers at low population levels, particularly where populations may be recruitment-limited, as in some reef fishes, or where there is large annual variation in recruitment (Leaman, 1991; Hilborn & Walters, 1992; Roberts, 1996).

Evidence for depensation

Depensation is the response whereby an increase in recruits produced per spawner with an increase in spawning stock occurs indirectly through one of two processes: predation or the 'Allee' effect (Ricker, 1975; Hilborn & Walters, 1992; Walters & Kitchell, 2001). Predation can act through a process where, as egg production increases, the predation risk per egg decreases if predation is constant. Most discussion on depensation in fisheries literature focuses on this form of depensation, while in the conservation literature it is on the Allee effect (Stephens & Sutherland, 1999). The Allee effect is the inability to find a mate, or brings about reduced fertilization success, at low numbers and has been reported in fishes and other vertebrates (Hilborn & Walters 1992; Wielebnowski, 1998; Courchamp *et al.*, 1999; Møller & Legendre, 2001). Since this review is particularly concerned with populations at very low levels, and the risk of extinction, the possibility of Allee-type depensation must be considered. Depensation may be difficult to detect, particularly because data from depleted populations are uncommon, but several studies do suggest depensatory responses among commercial species. While evidence for depensation in three out of 129 stocks examined in four taxa (salmonids, gadiforms, clupeiforms and pleuronectiforms) led to the initial conclusion that the effects of overfishing were generally reversible, even at low population levels (Myers *et al.*, 1995), re-analyses of the same dataset revealed that depensation could not be ruled out in many cases. Moreover, the finding that recovery of north-east Atlantic cod has still not occurred after 7 years of closure indicates problems with the general assumption of compensation, which should have led to an estimated tripling of stocks by now, and suggests some level of depensation (Liermann & Hilborn, 1997; Myers *et al.*, 1997*a*, *b*; Shelton & Healey, 1999).

It is often implied that the Allee effect is insignificant in marine fishes, but the idea that, if a population drops below some critical density the intrinsic rate of population increase may not be realized because breeding activity may cease, cannot be readily dismissed and a number of possible Allee effects have been noted. In salmon at low stock densities, reduced reproduction can be caused by difficulties in finding mates in a sparse and scattered population (Neave, 1954). Heavy fishing pressure can disrupt spawning in Atlantic cod leading to lowered reproductive output (Hutchings *et al.*, 1999). Many larger reef fish species aggregate to spawn and some of these aggregations have been heavily fished (Sadovy, 1996). The reduction in number caused by aggregation fishing or by exploitation of aggregating species may have produced direct or indirect impacts on aggregating and reproductive behaviours. Examples include extended

spawning seasons in heavily fished stocks, reduced courtship behaviour when numbers are low and high male aggression when sex ratios become male-biased (Colin, 1992; McGovern *et al*., 1998; Johannes *et al*., 1999). The significance of such apparent behavioural changes in terms of reproductive output is not known but it is quite possible that aggregation formation may require critical densities for successful reproduction, while aggregating behaviour presumably reflects some biological imperative for sociality during the reproductive season (the location of spawning sites may also be critical in some way). Indeed, if there is a fitness advantage to high-density aggregations (mate choice, fertilization success, predator protection) then reproductive success could be compromised if numbers are low. Moreover, fish migratory behaviour to spawning sites may be critical for social transmission among age groups leading investigators to suggest that altered migration patterns of collapsed cod and herring stocks may have changed forever (Helfman & Schultz, 1984; Dodson, 1988; Frank & Brickman, 2000).

Many long-lived fishes show complex social structures and mating systems. One distinctive example is hermaphroditism, found in many reef species and most frequently expressed as female to male sex change (protogyny). All detailed behavioural studies to date on the factors inducing sex change in fishes indicate that it is socially mediated, with females responding when males are lost through sex change (Warner, 1984; Shapiro, 1989). However, such sex switches are evidently subject to temporal and size constraints which may prevent a timely 1 : 1, female to male, replacement under heavy fishing (Vincent & Sadovy, 1998). In the heavily fished *Mycteroperca microlepis* (Goode & Bean), for example, adult sex ratios changed from 20 to 2% male, with the very real concern of severe curtailment of reproductive potential through insufficient males (sperm), despite sufficient female biomass (Koenig *et al*., 1996). In the angelfish *Centropyge potteri* (Jordan & Metz), density and minimum female size constrain sex change (Lutnesky, 1994, 1996) while in a protogynous sparid, the red porgy *Pagrus pagrus* (L.), the SPR fell below 1% and the population collapsed despite the continued presence of adult females (Huntsman *et al*., 1995, 1999). *Lopholatilus chamaeleonticeps* (Goode & Bean) is not hermaphroditic but has a complex mating system. Fishing may disrupt the breeding system, by removing behaviourally dominant males, resulting in reduced reproductive success (Grimes & Turner, 1999). In other species, spawning frequency, synchronization of spawning, gonad steroid levels and fertilization rates can vary significantly with group size or density with unknown effects at low or disturbed levels (Pankhurst & Barnett, 1993; Tyler, 1995; Warner *et al*., 1995). Where there may be constraints on socially mediated processes in reproductive activity, depensatory-type responses when population levels become significantly reduced, cannot be discounted. While cessation of fishing may allow such species to recover, lack of sufficient protection could severely compromise recovery from particularly low population levels, despite plenty of eggs.

DISCUSSION

The potential threat of exploitation to marine fishes as a conservation, rather than a management, issue has only recently received serious attention. The reasons for this are many and have to do not only the lack of documented

extinctions but also with widely held perspectives on the biology and response to fishing of targeted species, especially those that are highly fecund. Importantly, there is no theoretical or empirical support that high fecundity confers resilience relative to less fecund species.

Among widespread, commercially valuable, marine fishes, those most vulnerable are relatively large, long-lived and slow-growing, with late sexual maturation, and sometimes exhibiting complexities of social behaviour. They may be limited in geographic range (though not necessarily highly restricted), or distributed only within coastal areas where there is heavy exploitation and little scope for management. It is not uncommon that they carry a high market value, ensuring exploitation even at very low abundance and they may be just one component of a multi-species fishery. They may also be highly fecund.

The ability to recognize and effectively address declines in vulnerable species and, ultimately, to better understand the risk of extinction in commercially taken fishes depends not only on fishery science and management practice, but also on the quality of information available. For many fisheries, species-level information is scarce or lacking. For example, species-specific data are entirely absent for all but a few dominant trawled species, and for all reef-associated species, in much of the heavily fished northern sector of the South China Sea. In many regions of the world, species data are lumped and meaningless at species level. Even if collected, landings or catch per unit effort (CPUE) data may not be reliable indicators of population condition, if not taken from fishery-independent sources. There is also much to learn, in marine fishes, of minimum viable population sizes and depensatory and compensatory effects, genetic diversity, and meaningful ways of estimating intrinsic rates of population increase, and hence recovery potential from fishing. Such dearth of information makes it very difficult to recognize severe declines in vulnerable species and has led to alternative approaches to data acquisition and species assessments, with ' rules of thumb ' approaches for identifying vulnerable species (Johannes, 1998; Carlton et al., 1999; Dulvy et al., 2000; Morris et al., 2000; Reynolds et al., 2001).

The suggestion that fecund marine fishes should be exempt from quantitative criteria used to assign extinction risk, or that fecundity can be used as a means for assigning level of threat (Musick et al., 2000), is inconsistent with a precautionary approach to fishery management as well as to conservation of marine biodiversity. In seeking a way forward, it is critical for conservation biologists and fishery managers to collaborate, for despite differences in perspectives, extinction in the case of conservation biologists and sustainability for fishery managers, there is much common ground (Mace & Hudson, 1999).

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