Ecological and evolutionary consequences of size-selective harvesting: how much do we know?

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Abstract

Size-selective harvesting, where the large individuals of a particular species are preferentially taken, is common in both marine and terrestrial habitats. Preferential removal of larger individuals of a species has been shown to have a negative effect on its demography, life history and ecology, and empirical studies are increasingly documenting such impacts. But determining whether the observed changes represent evolutionary response or phenotypic plasticity remains a challenge. In addition, the problem is not recognized in most management plans for fish and marine invertebrates that still mandate a minimum size restriction. We use examples from both aquatic and terrestrial habitats to illustrate some of the biological consequences of size-selective harvesting and discuss possible future directions of research as well as changes in management policy needed to mitigate its negative biological impacts.

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Introduction

Body size is generally considered to be one of the most important traits of an organism because it correlates with many aspects of its biology, from life history to ecology (Peters 1983; Calder 1984). Size-selective harvesting, where large individuals of a particular species are preferentially taken, is a common practice in both terrestrial and marine habitats. Such harvesting practices are not only prevalent among people taking animals for food and other needs, but are also mandated by the management plans for many fish, invertebrate and game species. In fact, evidence for size-selective harvesting goes back to some of the earliest archaeological records of human settlement, dating back to at least the Middle Stone Age (Jerardino *et al.* 1992; Siegfried 1994; Mannino & Thomas 2002; Klein *et al.* 2004). It is not surprising that large individuals make up the bulk of the specimens in those archaeological deposits since they are the easiest to find and give the highest yield of protein per unit effort (Raab 1992). However, as subsistence and artisanal harvesting have given way to

commercial exploitation and industrial fishing, an increasing number of species worldwide have been subjected to size-selective harvesting. There is growing evidence that decades of size-selective harvesting has led to the reduction in body sizes of many species and that such artificial selection against large body size affects not only the targeted species but also the surrounding community (see below). However, the effects of size-selective harvesting are multifaceted and often species and system specific. Thus, even though size-selective harvesting is increasingly being recognized as a cause for concern (Birkeland & Dayton 2005), so far the ecological and evolutionary consequences of this practice have been explored only for a limited number of species.

In this paper, we first provide an overview of the scope and nature of size-selective harvesting. In particular, we estimate the number and types of species that are known to have been affected by size-selective harvesting practices and look at how that information has changed over the last few decades. We then briefly review the effects of size-selective harvesting on life history, demography and ecology of the exploited species, and discuss the evolutionary consequences of such impacts. A potential complication here comes from the fact that in the case of some species, both terrestrial and aquatic, harvesting preferentially

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targets large individuals of a specific sex. For example, trophy hunters usually take the largest (and oldest) males in a population and/or those with the most impressive (i.e. largest) horns, antlers or tusks (Milner-Gulland & Mace 1991; Ginsberg & Milner-Gulland 1994; Coltman *et al*. 2003; Milner *et al*. 2007). Because such harvesting preferentially targets large individuals, albeit of a specific sex, we include it under our general definition of size-selective harvesting. However, it is important to keep in mind that from an evolutionary standpoint, this practice is different from the more common one of harvesting large individuals without regard to their sex, since the traits under direct selection are different (size in one case, size of a particular sex in the other). Thus, where appropriate, we have treated these two types of size-selective harvesting separately. We end the paper with a brief discussion about fruitful directions for future research and also changes in management policy necessary to mitigate the negative biological impacts of size-selective harvesting.

Literature search

Although size-selective harvesting takes place both on land and in the ocean, at present it is unclear what proportion of the biota are affected by this practice. In order to get a better estimate of the scope and nature of the problem, we undertook an extensive search of the literature extending back to 1975 to identify species that are known to have been affected by size-selective harvesting. Our search criteria excluded studies that are solely based on theoretical models or simulations and focused only on animals. There are many examples of size-selective harvesting of tree species (e.g. Ledig 1992; Hall *et al*. 2003), but for practical reasons, we limited our analyses to animal species.

We used two different search strategies to estimate the number of species being affected by size-selective harvesting. Our first approach is conservative in that we only included species if the author(s) explicitly stated that exploited populations (species) are size-selectively harvested or if they used some variation of the following phrases: the large individuals are preferentially harvested; the large size classes experience higher harvest mortality; changes in life history are a response in part due to the size-selective nature of the harvest regime; the larger sex of a sequentially hermaphroditic or sexually dimorphic species is preferentially harvested.

Our second approach is more comprehensive in that we also included species for which there is only indirect evidence for size-selective harvesting, such as a reduction in mean or maximum body size through time or between exploited and protected areas. Under heavy harvesting pressure, even when it is not necessarily size selective, a truncation of the largest (oldest) size classes of a population

is expected (Trippel 1995; Law 2000; Heino & Godo 2002), because of which, it can be difficult to distinguish the effects of overharvesting per se from size-selective harvesting just by comparing size-frequency distributions. In practice, we found this issue to be relevant primarily for marine fish, where many species and populations are under intense harvesting pressure. Despite this complication, we include the results of this more comprehensive search not only because it includes species potentially missed by the previous search but also because, strictly speaking, almost all fisheries are inherently size selective by nature (Policansky 1993; Law 2000; Heino & Godo 2002; see below).

It is important to note that the aim of our literature search was to identify a representative set of papers that would permit an unbiased evaluation of the taxonomic scope and the nature and consequences of size-selective harvesting, rather than an exhaustive list of all publications on size-selective harvesting. We restricted our search to the peer-reviewed journal articles and ignored sources such as technical reports.

In order to compare the patterns across different groups we classified each species into one of three general categories: terrestrial vertebrates, fish (freshwater and marine) and marine invertebrates. For our analyses of temporal trends we only used the earliest publication date that reported size-selective harvest for each species. For example, five separate papers in our data set report size-selective harvesting of the limpet *Lottia gigantea* but only the earliest of these, Pombo & Escofet (1996), is used for this analysis.

How pervasive is size-selective harvesting?

The conservative literature search identified a total of 108 species of fish, invertebrates and terrestrial vertebrates that are known to have been subjected to size-selective harvesting pressure. Of these, 87 are aquatic (marine and freshwater) and 21 are terrestrial. The aquatic taxa include 48 species of fish (freshwater and marine) and 39 species of invertebrates (only marine). Ungulates make up the majority of terrestrial examples (15 species), the rest are carnivores/omnivores (4 species), elephants and kangaroos. The only difference between the conservative and the more comprehensive estimate is that the latter increases the number of size-selectively harvested fish species to 76, raising the total number of species to 136.

Commercial and artisanal harvesting involves many more species of fish and shellfish than terrestrial vertebrates, which is reflected in the very strong bias towards aquatic species seen in our data. Thus, in terms of species numbers, size-selective harvesting is primarily a concern for aquatic species, especially those living in the ocean, and to a lesser extent for some large terrestrial vertebrates.

In the latter case, harvesting is usually both sex and size selective. While the bias towards aquatic species is likely to be real, our search also revealed that the scientific literature on size-selective harvesting is still relatively limited, and does not capture the true scope of the problem. The selective loss of larger individuals is an inevitable consequence of most commercial and recreational fisheries (Sluka & Sullivan 1998; Beard & Kampa 1999; Law 2000; Law 2001; Longhurst 2006), which suggests that the number of fish species estimated to be affected by size-selective harvesting even by our comprehensive search is too low. In addition, illegal poaching of terrestrial vertebrates also tends to be size selective (Milner-Gulland & Mace 1991; Milner-Gulland *et al*. 2003), but again our knowledge of the biological consequences of such harvesting is presently limited to only a handful of species. However, the number of exploited species for which we have some information in the peer-reviewed literature has been increasing over the last couple of decades (Fig. 1). The increase is evident for all the groups in our database, but is particularly strong for fish and invertebrates (Fig. 1). Furthermore, the trend is qualitatively the same whether we use the conservative or the comprehensive search (Fig. 1a).

The mechanisms used by commercial, recreational and artisanal fisheries and hunters to preferentially remove large individuals are almost as diverse as the number of species affected by such harvesting practices. For example, commercial fisheries tend to select larger fish through the use of different kinds of fishing gear such as trawls and gillnets (based on mesh size), longlines and trap nets (Bohnsack *et al*. 1989; Policansky 1993; Dahm 2000; Law 2000), while some recreational fisheries, such as spear fishing for groupers in the Florida Keys, involves searching for individuals over certain size thresholds (Sluka & Sullivan 1998). Actively searching for and selecting large individuals is also common when people harvest marine invertebrates such as abalone and limpets (Branch & Moreno 1994; Lindberg *et al*. 1998; Murray *et al*. 1999; Moreno 2001), or hunt large terrestrial vertebrates (Ginsberg & Milner-Gulland 1994). Interestingly enough, one of the largest sport hunting activities in the USA tends to preferentially remove the smaller rather than the larger individuals in a population. Duck hunters generally shoot individuals of lower overall condition (i.e. lower body mass) because they are more abundant at feeding decoys (Weatherhead & Ankney 1984). This is exactly the opposite of the trend seen for most other species where the largest and presumably most fit individuals are preferentially hunted. In fact, there are many documented examples of increased hunting mortality of lower condition ducks (Greenwood *et al*. 1986; Hepp *et al*. 1986; Reinecke & Shaiffer 1988; Dufour *et al*. 1993; Heitmeyer *et al*. 1993).
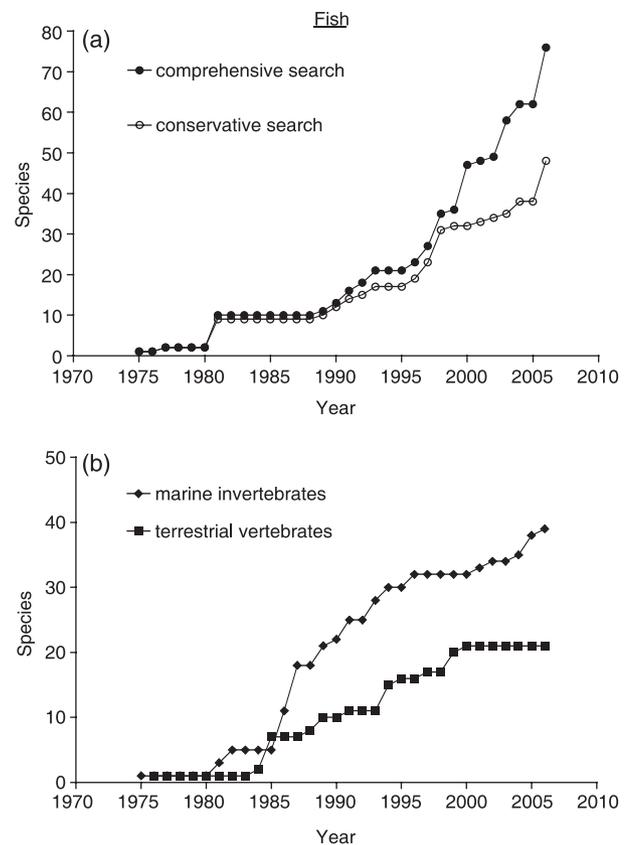

Fig. 1 (a) A plot of the cumulative number of fish species (marine and freshwater) reported to be affected by size-selective harvesting since 1975. The data points marked by closed circles represent the temporal accumulation of size-selectively harvested species using our comprehensive approach and those marked by open circles represent the results of our conservative approach (see text for details). Each species was added to the plot based on the earliest record (publication date) in our database of it being subjected to size-selective harvesting. (b) A plot of the cumulative number of marine invertebrate and terrestrial vertebrate species reported to be affected by size-selective harvesting since 1975. See text for details of the search protocols.

Consequences of size-selective harvesting

Size-selective harvesting can affect many aspects of the biology of an organism, from life history, demography, genetics and behaviour to the local abundance and biomass of populations. One of the biggest challenges to understanding the biological effects of size-selective harvesting is that many of the details tend to be taxon-specific. In some cases, it can also be difficult to distinguish between the effects of heavy but not necessarily selective exploitation and size-selective harvesting. As mentioned above, truncation of the large size classes and consequent changes in life history and demography are expected under both of these situations (Conover 2000; Heino & Godo 2002). For species

where we have information about harvesting practices, it is relatively straightforward to determine whether a population has been subjected to size-selective exploitation. For example, the largest individuals of many intertidal invertebrate species are selectively harvested for food since they provide the most meat for the effort (Siegfried 1994). Similarly, trophy hunters almost always target large males (Ginsberg & Milner-Gulland 1994; Coltman *et al.* 2003; Milner *et al.* 2007). But in the case of commercially harvested marine fish, it can sometimes be difficult to determine how much of the observed changes in life history and demography are due to intense exploitation vs. increased fishing mortality of the largest size classes (i.e. size-selective harvesting). Most fisheries only catch individuals above a minimum size that is mandated by fisheries managers or determined by the gear (e.g. mesh size). Furthermore, historical data show that almost all fisheries start out by preferentially harvesting the large individuals (Jennings & Kaiser 1998; Jackson *et al.* 2001). Thus, in a strict sense, most commercial marine fisheries harvest individuals in a size-selective manner (also see Policansky 1993; Heino & Godo 2002). However, many marine species are currently under intense harvesting pressure and the minimum size mandated by management plans may be quite small relative to the maximum sizes that have been historically attained by individuals in exploited populations (see Jackson *et al.* 2001). In these species, most size classes rather than just the largest ones experience elevated mortality due to fishing, which can lead to changes in life history and demography. Clearly, defining what constitutes size-selective harvesting is somewhat arbitrary and it is important to recognize that most harvesting strategies can lead to increased adult mortality rates and a reduction in the number of large individuals present in a population. In the discussion below, where appropriate, we have attempted to separate the effects of size-selective harvesting per se from those due to intense exploitation (or overharvesting) but in some cases, it may be difficult to disentangle the two.

Changes in body size and mortality rate

The primary effect of size-selective harvesting and exploitation in general is an overall reduction in body size and an increased mortality rate of the harvested species. Body size declines attributed either partly or primarily to size-selective harvesting have now been documented in many species of marine and freshwater fish (e.g. Ricker 1981; Beard & Kampa 1999; Zwanenburg 2000; Harvey *et al.* 2006), marine invertebrates (e.g. Branch 1975; Siegfried 1994; Moreno 2001; Branch & Odendaal 2003; Roy *et al.* 2003) and some terrestrial vertebrates (e.g. Coltman *et al.* 2003). When size-selective harvesting targets a particular sex, reductions in body size are evident only for that sex. For example, hunting of bighorn trophy rams

leads to a significant reduction in body size of males in the population (Coltman *et al.* 2003). In most cases, relatively little information exists about how long size-selective harvesting has been taking place or the rate of decline over time. Quantifying the rate of decline requires historical information about body sizes (Jackson *et al.* 2001) and although such information is potentially available for many species of marine invertebrates, so far only a few studies provide such analyses (e.g. Roy *et al.* 2003). In contrast, many studies of exploited fish species provide information on how sizes have declined over time (e.g. Handford *et al.* 1977; Ricker 1981; Zwanenburg 2000; Jackson *et al.* 2001; Harvey *et al.* 2006; Hsieh *et al.* 2006).

A decline in body size because of exploitation is also associated with changes in the mortality schedule of affected populations. There are two sources of mortality that natural populations have evolved with, intrinsic and extrinsic (Stearns 1992). Intrinsic sources of mortality are those that contribute to patterns of senescence and ageing, whereas extrinsic sources of mortality are associated with factors such as predation. Human harvesting acts to increase the extrinsic sources of mortality in affected populations to such an extent that for many species, it is the most common cause of adult mortality (Heino & Godo 2002; Festa-Bianchet 2003). Size-selective harvesting by humans is therefore a source of extrinsic mortality where the larger size classes experience higher harvest mortality than the smaller size classes. Although any increase in total mortality rate is expected to have an influence on life-history traits (Stearns 1992; Conover 2000), the response is likely to be more extreme when harvest mortality is size (age) specific (Stokes *et al.* 1993; Ginsberg & Milner-Gulland 1994; Conover 2000; Law 2000; Moreno 2001; Heino & Godo 2002; Milner *et al.* 2007). Thus, the net result of harvest-induced elevated mortality is an overall decline in the number of individuals surviving to older ages and larger sizes, which can lead to a multitude of cascading effects (see below).

Growth and survival of offspring

The quality of offspring is perhaps the most nonintuitive trait to be affected by size-selective harvesting, yet there is increasing evidence for such an effect in both marine and terrestrial species. The size and quality of larvae of some exploited marine fish has been shown to be positively correlated with maternal length and age (Berkeley *et al.* 2004). For example, older mothers of *Sebastes melanops* (black rockfish) provide larger oil globules for their larvae than younger and smaller females, which can enhance the growth rate and survival of the larvae (Berkeley *et al.* 2004). Similarly, older (larger) females can produce higher quality eggs, leading to enhanced survival of their larvae (Trippel 1995; Kjesbu *et al.* 1996; Vallin & Nissling 2000). Given these and other maternal effects, removal of the oldest and largest

females has the potential to affect the size, growth and survival of larvae of a number of fish species (Vallin & Nissling 2000; Berkeley *et al*. 2004; Birkeland & Dayton 2005; Longhurst 2006). However, whether such maternal effects on larval quality are present in most fish species or whether they are clade specific remains unknown. Similarly, while maternal size has been shown to influence larval survival in some marine invertebrates such as bryozoans (Marshall & Keough 2004), it is unclear how common these characteristics are in invertebrate species that are exploited for human consumption.

Among terrestrial animals, some sex-selectively (and hence size-selectively) hunted ungulate populations show a reduction in offspring weight. For moose (*Alces alces*) and reindeer (*Rangifer tarandus*), reduced offspring weight may occur when females are forced to mate with young males after hunting reduces the number of older males (Saether *et al*. 2003; Holand *et al*. 2006; Milner *et al*. 2007). This reduction is not a direct result of lower male physiological health but an indirect result of delayed parturition dates for offspring sired by younger males (Milner *et al*. 2007). Female behavioural avoidance of less mature young males early in the season drives lower calf weight at birth later in the breeding season (Holand *et al*. 2006), which is a direct result of there being fewer large (older) males in the population because of sex-selective harvesting pressure. In the case of both grizzly bears (*Ursus arctos*) and African lions (*Panthera leo*), large and socially dominant males are also selectively hunted as trophies. This can result in an unfortunate side-effect of reduced survival among juveniles triggered by an increase in infanticidal behaviour by less dominant males (Swenson *et al*. 1997; Whitman *et al*. 2004; Loveridge *et al*. 2007). Once the dominant male has been removed from the population, the younger and peripheral males seek to increase their fitness by killing the offspring of the hunted dominant male and thus, reducing the interbirth period required to sire the next litter of cubs (Milner *et al*. 2007).

Reproductive investment

For long-lived species with low natural adult mortality rates, size-selective harvesting may cause shifts in life-history traits that are linked to adult survival, such as reproductive investment. The expected contribution to population growth of an individual (reproductive value) changes with age such that juveniles have low reproductive value (RV), mature adults have high RV, and in long-lived organisms, RV declines slowly with age (Kokko *et al*. 2001). It is therefore not surprising that size-selective harvesting of mature adults with the highest RV can lead to a decline in population growth rate. The most likely consequence of high adult mortality through harvest pressure is an increase in reproductive investment of young adults (Festa-Bianchet 2003). For hunted ungulate

populations, subadult males are more likely to reproduce at a younger than normal age because of the reduced number of competitive older males during the rutting season (Milner *et al*. 2007). The effects of size-selective harvesting on the reproductive investment of invertebrate species are very poorly studied. But indirect evidence suggests that at least for some sex- and size-selective crab fisheries, where large males are preferentially taken, the surviving younger and smaller males attempt to reproduce more frequently than they normally would in the presence of larger and older males (Carver *et al*. 2005).

Growth and age (size) at maturity

Nearly all of the studies looking at the effects of size-selective harvesting on growth and age (size) at maturity have focused on fish (e.g. Handford *et al*. 1977; Spangler *et al*. 1977; Ricker 1981; Stokes *et al*. 1993; Law 2000; Heino & Godo 2002; Engelhard & Heino 2004; Baskett *et al*. 2005). Although a reduction in the age at maturity of harvested fish stocks is well documented, particularly for species with relatively late maturation times (Haug & Tjemsland 1986; Bowering & Brodie 1991; Rijnsdorp 1993; Trippel 1995; Rochet 1998; Law 2000; Grift *et al*. 2003), the underlying processes are not always clear (for an excellent review on this subject see Heino & Godo 2002). For example, fishing may indirectly select for either an increase or decrease in individual growth rates depending on any number of factors, including the size-selective nature of the harvest regime (Heino & Godo 2002). The size selectivity of the fishing gear and/or minimum size restrictions may preferentially remove faster growing individuals that 'recruit' to the fishery at a younger age, leaving individuals with a genetic tendency to grow more slowly. While some laboratory experiments have provided support for this hypothesis (Conover & Munch 2002), the extent to which selection for slow growth affects maturation times remains poorly known for a number of reasons. First, fishing, whether size selective or not, will reduce the stock abundance and decrease the total number of intraspecific competitors for food resources (Policansky 1993). This improvement in food access may result in accelerated juvenile growth and an overall younger age at maturation (Policansky 1993; Trippel 1995; Law 2000; Heino & Godo 2002; Engelhard & Heino 2004), potentially dampening any effects of selection for slower growth. Furthermore, harvesting-induced elevated mortality by itself (whether selective or not) is expected to lead to a very small number of individuals surviving to old ages and large sizes, leaving relatively young individuals to dominate the population. Individuals with a tendency to mature at an early age will contribute more of their genes to the next generation than individuals with a tendency to mature at older ages simply because of their probability of successfully reproducing before being harvested (Law

2000; Heino & Godo 2002; Engelhard & Heino 2004). This concern that harvesting might cause genetic changes in growth or maturation times for exploited fish stocks was first put forth by Miller (1957) and later by Spangler *et al.* (1977), Handford *et al.* (1977) and Borisov (1978), but was not intensively examined until the early 1990s (Rijnsdorp 1993; Stokes *et al.* 1993). More recent studies have implicated genetic change as being partly responsible for observed changes in maturation times of some heavily exploited fish stocks (Grift *et al.* 2003; Barot *et al.* 2004; Olsen *et al.* 2004). But for most species, it remains unclear to what extent the observed changes in maturation time are due to phenotypic plasticity or evolutionary change (Grift *et al.* 2003). In addition, physical factors such as increased surface water temperatures caused by global warming can also contribute to accelerated juvenile growth rates and associated changes in life history (Thresher *et al.* 2007). Finally, because growth typically slows after maturation, a younger maturation time should result in a smaller size at age in the future (Heino & Godo 2002). Thus, regardless of the specific cause, a reduction in the age at sexual maturity of exploited fish stocks is likely to be followed by an overall reduction in yield (Law 2000; Conover & Munch 2002; Heino & Godo 2002; Ernande *et al.* 2004).

Whether these effects seen in fish also apply to other marine organisms remain unclear at present. As mentioned above, comparable studies of marine invertebrates are scarce, but studies of exploited marine limpets in South Africa and Costa Rica show surprisingly little impact of harvesting on growth rates and age at maturity (Ortega 1987; Branch & Odendaal 2003).

Fecundity and biomass

In fish and invertebrates, fecundity not only increases with size (Kido & Murray 2003; Birkeland & Dayton 2005) but in many species, relative fecundity (i.e. fecundity per gram of body weight) can be higher in older and larger individuals (Longhurst 2006). For example, reproductive output of a size-selectively harvested intertidal marine limpet *Cymbula oculus*, inside a marine protected area (MPA) was found to be 80-fold higher than that of exploited populations (Branch & Odendaal 2003). For this species, the biomass of protected populations was also substantially higher (30–90%) than exploited ones (Branch & Odendaal 2003), and similar differences exist in other species such as *Lottia gigantea*, an intertidal limpet from California that is also size-selectively harvested (P.B. Fenberg and K. Roy, unpublished). It is important to note that a reduction in biomass by itself does not necessarily indicate that harvesting is size selective; increased mortality due to harvesting in general is expected to reduce the standing biomass of exploited populations and it is now well documented that the current biomass of many exploited

fish stocks represent a fraction of their historical levels (e.g. Jackson *et al.* 2001; Myers & Worm 2003). What separates the effects of size-selective harvesting from overexploitation is the observation that the former has the potential to change the fundamental scaling relationship between size and biomass predicted by macro ecological theory (Jennings & Blanchard 2004). When removal is size selective, the slope of the size–biomass relationship tends to change abruptly between size classes that are protected from fishing and those that are not, with the former slope being consistent with that predicted from energy-equivalence theory (Jennings & Blanchard 2004).

Changes in sex ratio

For some species size-selective harvesting can directly or indirectly lead to the preferential harvesting of one sex and thus has the potential to alter the breeding sex ratio. In the aquatic environment this is most commonly seen in sequentially hermaphroditic fish and invertebrates, where all individuals start out as one sex and then change to the other as they grow older and larger. Size-selective harvesting of these species thus preferentially removes the larger sex and can limit the reproductive potential of the population if it alters the sex ratios (Birkeland & Dayton 2005). As with age at maturity, life-history theory predicts that individuals should change sex at a younger age in response to high adult mortality and show changes in growth rate if sex change is under exogenous control (Warner 1975; Charnov 1979; Charnov 1981). If adult mortality rates are unnaturally high because of size-selective harvesting it is predicted that the age (size) at sex change will be reduced in order to compensate for the impacts on breeding sex ratio (Charnov 1981; Armsworth 2001; Platten *et al.* 2002). Such trends are evident in some size-selectively harvested fish (Cowen 1990; Buxton 1993; Platten *et al.* 2002; Hawkins & Roberts 2004) and invertebrate species, particularly shrimp (Charnov 1981; Hannah & Jones 1991). On the other hand, this compensatory response may not occur if harvesting pressure is intense enough to not allow adequate time for sex change (Coleman *et al.* 1996; Hawkins & Roberts 2004). Additionally, if size at sex change is fixed, as it appears to be for some species (Branch & Odendaal 2003; Munday *et al.* 2006), then early age (size) at sex change is not likely under harvesting pressure. In these cases, the loss of larger individuals leads to drastic changes in the population sex ratio (Branch & Odendaal 2003).

Even for non-hermaphroditic aquatic species, size-selective harvesting can disproportionately affect one sex. Many crab and lobster fisheries preferentially harvest (directly or indirectly) the larger males in the population, resulting in female-biased sex ratios (Paul & Adams 1984; Wenner 1989; Smith & Jamieson 1991; Castilla *et al.* 1994; Sato *et al.* 2005; Sato & Goshima 2006). A skewed sex ratio can limit

the reproductive potential of fished populations via sperm limitation or delayed mating (Sato & Goshima 2006). However, field observations are usually difficult and only indirect evidence exists for the effect of male-focused crustacean fisheries on reproductive success (Smith & Jamieson 1991; Carver *et al.* 2005; Sato *et al.* 2005).

In some freshwater eels, sex is environmentally determined with males differentiating at a younger age and smaller size than females, and extreme male biases found in harvested eel populations have been partly attributed to the size-selective nature of the fishery (McCleave & Jellyman 2004; Beentjes *et al.* 2006). Population sex ratios can be more directly impacted when harvesting is both size and sex selective. For terrestrial species, a female-biased sex ratio is perhaps the most common direct effect of sex-selective hunting (Ginsberg & Milner-Gulland 1994; Milner *et al.* 2007). However, at least for polygynous species, a skewed sex ratio is commonly assumed to have little negative effect on population growth since one male can potentially inseminate many females (Caughley 1977; Ginsberg & Milner-Gulland 1994). In fact, recruitment rates for some ungulate populations are resilient to unnaturally skewed sex ratios (Milner *et al.* 2007) and somewhat ironically, male-selective hunting may have actually contributed to an increase in population growth rate and the eventual overabundance of deer populations across much of Europe and North America (along with other factors such as reduced natural predation and increased food availability; Cote *et al.* 2004). But of course, there is a limit to the bias in sex ratio on the long-term viability of a population. Population crashes attributed to reduced fecundity of sex-selectively hunted ungulate populations have been documented for species such as the saiga antelope (*Saiga tatarica tatarica*) (Milner-Gulland *et al.* 2003; Milner *et al.* 2007).

Ecological effects

There is increasing recognition that exploitation has ecological consequences and can lead to large changes in community composition and the functioning of ecosystems. Much of this work has focused on the effects of overexploitation of fish species (Tegner & Dayton 1999), and it can be difficult to separate the ecological effects of overexploitation from that of size-selective harvesting. Moreover, the ecological consequences of harvesting depend, at least partly, on the functional role and competitive dominance of the target species (Kaiser & Jennings 2001). Thus, the effects are system specific and sometimes quite complex. In Chile, size-selective harvesting reduces the size and abundance of the large limpet *Fissurella picta*, resulting in an increased abundance of its macro-algal food source (Moreno *et al.* 1984; Godoy & Moreno 1989). In areas where *F. picta* is harvested (usually size-selectively), a co-occurring but nonharvested smaller limpet *Siphonaria lessoni* with a similar diet grows faster and reaches a bigger size in the absence of large individuals of the competitively dominant *F. picta* (Moreno *et al.* 1984; Godoy & Moreno 1989). Similarly, increases in the abundance of a sea urchin *Arbacia lixula*, has been attributed to size-selective harvesting of its competitor *Paracentrotus lividus* (Guidetti *et al.* 2004). In general, selective harvesting of some species can increase the growth rate, size and abundance of other nonharvested species because of release from competitive pressure (Godoy & Moreno 1989; Lindberg *et al.* 1998; Guidetti *et al.* 2004). Similar indirect effects should also be common where larger individuals of the target species are highly territorial. For example, a number of intertidal limpet species territorially defend their algal grazing area by 'bulldozing' any intruders such as barnacles, mussels and even other conspecifics (Stimson 1970; Branch *et al.* 1992; Shanks 2002). Selective loss of large individuals of these species can result in community level shifts in space occupancy (Griffiths & Branch 1997; Lindberg *et al.* 1998), which may be difficult to reverse even after harvesting is relaxed. As far as indirect effects are concerned, one of the most extreme examples come from the Canary Islands where size-selective harvesting of intertidal limpets may have partially contributed to the extinction of the oystercatcher *Haematopus meadewaldoi* (Hockey 1987; Branch & Moreno 1994).

Size-selective harvesting can also have an impact on behavioural ecology. One of the better examples of this comes from African elephants (*Loxodonta africana*) where hunters preferentially kill the largest and oldest elephants from a population for the international ivory trade (Milner-Gulland & Mace 1991). In non-hunted populations, male elephants typically enter a state of heightened sexual activity and aggressive behaviour known as musth between 25 and 30 years of age. At this age, they have become large and competitive enough to win encounters with other males (Poole 1987; Poole 1989; Slotow *et al.* 2000). However, hunted populations consist of inexperienced young males with smaller tusks. The lack of an older male hierarchy in these populations can cause the young males to enter musth at ages as young as 18 years old (Slotow *et al.* 2000). An unexpected side-effect of their inexperience and heightened aggression associated with entering musth at an early age is an increased incidence of young males attacking and killing individuals of rhinoceros (*Diceros bicornis* and *Ceratotherium simum,* Slotow *et al.* 2000; Slotow *et al.* 2001). This behaviour is uncommon in populations with normal age structures, and conservation managers have been able to solve the problem by introducing older males to some of the affected populations (Slotow *et al.* 2001).

Microevolution or phenotypic plasticity?

Size-selective harvesting clearly causes large and observable changes in life history and ecology of exploited species,

but whether these are evolutionary responses (i.e. have a genetic basis) or whether they represent phenotypic plasticity remain unclear (Law 2000). Laboratory experiments have shown that in some fish size-selective harvesting can select for genotypes with slower or faster growth rates depending on whether large or small individuals are selectively removed (Conover & Munch 2002). Thus, in principle, size-selective harvesting can lead to rapid evolutionary response and analyses of some wild populations have found evidence for such a response (Coltman *et al.* 2003; Grift *et al.* 2003; Olsen *et al.* 2004). Similarly, the failure of traits such as size at maturity to return to pre-exploitation levels when fishing is stopped is consistent with an evolutionary response (Conover & Munch 2002). On the other hand, the size of many species tends to increase once they are protected from exploitation (Halpern & Warner 2002; Branch & Odendaal 2003; Gell & Roberts 2003; Roy *et al.* 2003; Hawkins & Roberts 2004), suggesting that some of these changes reflect plasticity. In general, for the vast majority of exploited species, the information required to differentiate between evolutionary change and phenotypic plasticity is currently not available (Conover 2000). In fact, even though size-selective harvesting is widespread, we know little about the magnitude of selection differentials due to such exploitation (Stokes & Law 2000; Law 2001). Finally, for most exploited stocks, we have little quantitative data on how the exploitation pressure has varied over time. Some authors view changes in many marine fish stocks as a relatively recent phenomenon (i.e. latter half of the 20th century; Hutchings & Baum 2005), while others argue that such declines extend back a couple of centuries or longer (Jackson *et al.* 2001). Both views are probably correct given that humans have been exploiting some species of fish and invertebrates for thousands of years (Jerardino *et al.* 1992; Jackson *et al.* 2001; Klein *et al.* 2004) while other fisheries are much newer. From an evolutionary standpoint, the lack of such information makes it difficult to estimate how many generations have been subjected to selective harvesting. For taxa with a short or moderate lifespan, tens or maybe even hundreds of generations have already been subjected to size-selective harvesting, enough time for evolutionary responses (Conover & Munch 2002). On the other hand, many species of marine fish and invertebrates live for multiple decades and for these long-lived taxa, it may be too soon to see evolutionary changes even though they are likely in the long run (Conover 2000).

Macroevolutionary consequences of size-selective harvesting

Size-selective harvesting is pervasive and there is no indication that the situation is going to change in the near future. Thus, it is reasonable to expect that such selection pressure would lead to reduction in body sizes of many species, especially given the high heritability of this trait and its close relation to fitness (Law 2001). As discussed above, such an evolutionary response has already been documented in some species. In other cases it is likely to be present but is yet to be detected. While virtually all of the discussion about evolutionary response to size-selective harvesting has focused on microevolution, size declines due to such exploitation also have macroevolutionary implications. In fact, body size is often thought to provide a direct link between microevolution and macroevolution (Jablonski 1996). The patterns and mechanisms of body size evolution at the species level have been studied in considerable detail and empirical data show that in many clades average body size tends to increase over time as the clade diversifies, a trend commonly known as Cope's Rule (Jablonski 1996; Alroy 1998; Hunt & Roy 2006). At present, there are two general explanations for this trend. Stanley (1973) suggested that most major clades tend to originate at small sizes, and as they diversify, they add both large and small species. However, because of a hard lower bound for body size, the ultimate result of such passive diffusion is an increase in both mean and variance in body size over time (Stanley 1973; Gould 1988; Jablonski 1996). Alternatively, Cope's Rule can result from directional selection towards larger body sizes (Brown & Maurer 1986; Jablonski 1996; Hunt & Roy 2006). In either case, the natural tendency of many clades is to add larger-bodied species over time. Human exploitation has the potential to disrupt this evolutionary trend by truncating the larger end of the size distributions as body sizes of many species get smaller because of size-selective harvesting, and many large-bodied species face extinction because of other anthropogenic impacts (Gaston & Blackburn 1995; McKinney 1997). Under such a scenario, new species in the future are likely to be small since they will be derived from small ancestors and body size is highly heritable even at the lineage level (Smith *et al.* 2004). In addition, size-selective harvesting and other human activities counteract the selective advantages of large body size and would thus reinforce the bias against large-bodied species.

Conclusions

Harvesting of natural resources by humans is selective by nature (Law 2001; Longhurst 2006) and archaeological data show that such exploitation has been going on since the dawn of civilization (Klein *et al.* 2004). Size-selective harvesting is just one example of such selective exploitation, but because body size correlates with so many different attributes of an organism, such exploitation has far-reaching ecological and evolutionary consequences. Arguably, the difference between the reductions in body size seen in archaeological kitchen middens (Jerardino *et al.* 1992) and those due to fishing over the last couple of centuries is essentially one of scale. Today, size-selective harvesting

affects many species and exploitation pressure is higher than ever before (Pauly *et al.* 1998; Baum *et al.* 2003; Myers & Worm 2003; Hutchings & Baum 2005). Yet we know very little about the evolutionary and ecological consequences of such exploitation. The majority of the information regarding changes in species life histories in response to size-selective harvesting have come from a handful of commercially important fish, largely from waters off developed countries (Hutchings & Baum 2005). The combination of taxonomic, geographical (little information exists for highly diverse tropical areas) and habitat-related bias (Hutchings & Baum 2005) makes it impossible to reach any general conclusions regarding the effects of size-selective harvesting. The situation is particularly bad for invertebrates where many species are harvested but not only do we lack information about their life history and ecology, but also reliable data on patterns of exploitation. Large databases of catch-rates and other information that permit stock assessments and analyses of population trajectories of many commercially important fishes (e.g. Baum *et al.* 2003; Myers & Worm 2003) are virtually unknown for most marine invertebrates.

Despite the paucity of specific information for many species, it is quite clear that size-selective harvesting is having a negative effect on the population biology of many species of vertebrates and invertebrates. Yet the problem is not recognized in most management plans for fish and marine invertebrates that still mandate a minimum size restriction (Conover & Munch 2002). In addition, illegal size-selective harvesting of intertidal invertebrates is a growing but under-appreciated problem in many parts of the world and even where regulations exist, they are rarely enforced (Branch & Odendaal 2003; Roy *et al.* 2003). Despite all this, the increases in size and biomass of exploited species within MPAs suggest that for many species, it may not be too late to reverse the negative ecological and evolutionary consequences of size-selective harvesting (Halpern & Warner 2002; Roy *et al.* 2003). However, achieving that would require us to stop preferentially removing the larger and older individuals in a population and design harvesting strategies that would preserve the size-frequency distributions that characterize the unexploited state of a species. Suggestions regarding such strategies are already available in the literature (e.g. Conover & Munch 2002; Jennings & Blanchard 2004; Birkeland & Dayton 2005; Hutchings & Baum 2005). More generally, mitigating the effects of size-selective harvesting would require us to shift from management strategies that are designed to maximize yield (Longhurst 2006) to those that can preserve the natural variations that characterize species and ecosystems.

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