

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

Chapter 19.

Life histories, population dynamics and extinction risks in chondrichthyans

Nicholas K. Dulvy¹ & Robyn E. Forrest²

¹ Department of Biological Sciences
Simon Fraser University
Burnaby, V5A 1S6
Canada

² Fisheries Centre
AERL, 2202 Main Mall,
University of British Columbia,
Vancouver, BC, V6T 1Z4,

DRAFT

Contents

19.1 Introduction

- 19.1.1 Life histories and population dynamics
- 19.1.2 Life history strategies
- 19.1.3 Life histories and the intrinsic rate of population increase r
- 19.1.4 Density-dependent mortality and productivity of shark populations
- 19.1.5 Comparative demographic studies of chondrichthyan populations
- 19.1.6 Age-structured models incorporating density-dependence in juvenile survival
- 19.1.7 Management implications of life histories and demography

19.2 Decline, extirpation and extinction of sharks and rays

- 19.3.1 Documented population declines of sharks and rays in the Mediterranean Sea
- 19.3.2 Steep declines of Australian deepwater sharks
- 19.3.3 Extirpation of the British Columbia basking shark
- 19.3.4 Local extinctions of North Atlantic skates
- 19.3.5 Regional extinction of the angel shark
- 19.3.6 Regional extinctions of guitarfishes and sawfishes

19.3 Global threat status – a brief summary of IUCN Red List process

- 19.3.2 The global status of chondrichthyans
- 19.3.3 Regional variation in chondrichthyan threat status
- 19.3.4 The distribution of threat is evolutionarily and ecologically non-random

19.4 Future threats to sharks and rays due to climate change

- 19.4.1 Climate change, fishing and extinction risk in the Australian grey reef shark
- 19.4.2 Vulnerability of Australian sharks and rays to climate change

19.5 Prioritization for action: which sharks and rays require most urgent attention?

19.6 Research required to manage and conserve chondrichthyans

Abstract

Over the last century fishing activities have spanned the ocean ranges and trawled deep into former refuges of chondrichthyans. More recently, rapid anthropogenic climate change poses a global emerging threat. Here, we show that many chondrichthyans are intrinsically sensitive to elevated mortality due to their slow life histories, which results in low population growth rates which limit the yield of chondrichthyan fisheries and the potential for recovery of collapsed and depleted populations. The high intrinsic sensitivity to elevated mortality combined with high exposure to fishing mortality particularly in shelf seas and in the pelagic zone of the oceanic high seas results in the raised vulnerability and elevated extinction risk observed today. We review modeling approaches for understanding links between life history and risks of overexploitation. We summarize evidence for extirpation, local and regional extinction and the likelihood of impending global extinction of chondrichthyans, based on the IUCN Red List assessments for three regions – NE Atlantic, Mediterranean Sea and Australia and Oceania. Finally, we consider the relative vulnerability of chondrichthyans to climate change, which suggests that freshwater, estuarine and reef sharks have low to moderate vulnerability to climate change, mainly due to their high exposure to the physical impact of climate change and their high sensitivity to change, this is offset to some degree by their high adaptive capacity and habitat flexibility. A large proportion of chondrichthyans are threatened and there is relatively little scientific, management and conservation capacity, prioritization is essential to focus this limited effort.

19.1 Introduction

The greatest potential threat to chondrichthyan (sharks, rays and chimaeras) populations and species is fishing mortality. This can come from directed fisheries targeting sharks (Bonfil 1994, Walker 1998, Punt et al. 2005); mortality imposed as bycatch in more valuable crustacean fisheries (Stobutzki *et al.* 2001), demersal fish trawling (Graham et al. 2001, Ellis et al. 2005), pelagic trawling (Zeeberg *et al.* 2006), pelagic line fishing (Gilman et al. 2008), recreational fisheries (Anderson 2002) or through finning of sharks captured as bycatch in pelagic fisheries (Clarke *et al.* 2006).

The response of a chondrichthyan population or species to elevated mortality, and its risk of achieving threatened status or a raised risk of extinction, depends largely on the intrinsic life history of the population. Life histories of chondrichthyans vary widely, particularly their reproductive traits - indeed they could arguably be among the most diverse of all vertebrates. Chondrichthyans exhibit considerable interspecific life history variation: gestation period (2 - 42 mo), egg hatching period (1 - 27 mo), ovum diameter (0.5 - 600 μ m), reproductive mode (egg-laying, live-bearing), maternal investment (yolk-only versus uterine milk, uterine cannibalism, placentation), fecundity (1 - 400 offspring), offspring size (20 - 1800 cm long), age at maturity (1.5 - 30+ y) and longevity (5 - 50+ y) (Compagno 1990, Dulvy & Reynolds 1997, Cortés 2000, Goodwin et al. 2002, Goodwin et al. 2005). However compared to teleosts, chondrichthyans in general tend to be longer-lived, have slower growth, later maturity and lower fecundity - characteristics that tend to predispose species to being more vulnerable to overfishing (Hoenig & Gruber 1990, Pratt & Casey 1990, Smith et al. 1998, Cortés 2002).

Life history information can provide considerable insight into the response of shark populations to exploitation. For example, different life history strategies give rise to very different responses to fishing in two similarly-sized sharks in the family Triakidae (*Mustelus antarcticus* and *Galeorhinus galeus*), targeted in the same Australian fishery. One species (*M. antarcticus*) matures relatively early, living to about 16 years, and consequentially has a fairly high rate of population growth. The fishery for this species has been assessed as sustainable. In contrast, *G. galeus* matures later, grows slowly, lives for around 60 years and has a much lower rate of population growth. This species had been consistently overexploited, despite being subject to similar fishing pressure (Stevens 1999). Other studies have shown that large-bodied species tend to decline more steeply than their smaller-bodied relatives (e.g., Dulvy et al. 2000; Dulvy and Reynolds 2002).

There have been a large number of studies in recent years, linking life history to risk of overexploitation and extinction in chondrichthyans (Hoenig & Gruber 1990, Kirkwood et al. 1994, Cortes 1998, Smith et al. 1998, Heppell et al. 1999, Musick 1999, Cortés 2002, Gedamke et al. 2007, Au et al. 2008, Forrest & Walters in review). One of the main reasons for the strong interest in using life history approaches to inform management of chondrichthyans is the extreme lack of data worldwide for conventional stock and risk assessments (Bonfil 1994, Walker 1998, FAO 2000, Stevens et al. 2000). Reliable time series of catch, catch per unit effort or other indices of abundance are usually unavailable because sharks are caught as bycatch or are otherwise of low management priority (Bonfil 1994). Life history data describing growth, fecundity, age at maturity and maximum age are, however, routinely collected in many parts of the world.

Here, we review advances in understanding links between these life history data and chondrichthyan population dynamics and discuss implications for management. We then summarize evidence for extirpation, local and regional extinction and the likelihood of impending global extinction of chondrichthyan populations, based on the IUCN Red List assessments. Finally, we consider the relative vulnerability of chondrichthyans to climate change.

19.1.1 Life histories and population dynamics

Predictive population models can be used to help gain a more formal understanding of how life history characteristics contribute to risks of overfishing and extinction. One of the simplest models linking life histories to population dynamics is the logistic model of population growth. In this model, the change in population size (dN) over a period of time (dt) is modelled as a function of the intrinsic rate of population increase (r) and the carrying capacity of the population (K), determined by size, productivity or quality of ecological habitat (Jennings et al. 2008). The change in numbers of a population over time (t) is described by

$$dN_t/dt = rN_t (1 - N_t/K)$$

Under the assumptions of this model, species or populations with higher values of r recover more rapidly from small population sizes and reach carrying capacity more quickly than those with lower rates of population increase. There are two parts to the equation which capture the two key determinants of a species productivity and resilience to fishing: the intrinsic rate of population increase r and the strength of density-dependence in population growth rate, represented here by $1 - N_t/K$.

For fished populations, the model is modified by subtraction of annual yield or catch C_t , (Schaefer 1954).

$$dN_t/dt = rN_t (1 - N_t/K) - C_t$$

For any given species, there is a theoretical constant long-term harvest rate (U_{MSY}) that would achieve long-term maximum sustainable yield (MSY). Here the long-term sustainable catch rate U_{MSY} is expressed as the proportion of the population killed each year. Under the assumptions of this model, U_{MSY} is equal to half the intrinsic population growth rate ($r/2$). Annually, killing a proportion of the population greater than the intrinsic rate of population increase r would lead to eventual extinction of the population. The parameter r is therefore representative of the intrinsic productivity of a population and also a direct determinant of its resilience to fishing. The intrinsic rate of population increase is determined by life history traits and the constraints and trade-offs imposed by the acquisition and metabolism of energy. While the logistic model has now largely been replaced by the use of fully age-structured models that account for age schedules of survival and maturity, it provides a valid and useful means of illustrating linkages between life history, productivity and impacts of fishing on different types of species (Figure 19.1).

In the following sections, we first we review the links between life histories and r . Second we explore the role of density-dependence in population dynamics in relation to chondrichthyans. Third we explore life history strategies, and finally the comparative demography of chondrichthyans and recent modeling approaches for determining linkages between sustainable exploitation rates and life history.

19.1.2 Life history strategies

The logistic growth equation underlies the concept of an r - K life history continuum (Pianka 1970). Under this scheme, species living in highly variable, unpredictable environment and suffering repeated catastrophic mortality events (hence unlikely to reach carrying capacity) were termed r -selected species. These r -selected species tended to be characterised by frequent colonisation/recolonisation, with broad niches, small body size, early reproduction, high fecundity and short lifespans, high production to biomass (P/B) ratios and a high degree of density-independent mortality. At the other end of continuum K -selected species were more typically found in more stable, predictable habitats and exhibited narrower niches, larger body sizes, low fecundity, long life spans and a predominance of intrinsic density-dependent mortality. While this conceptual framework energised ecology in the 1960s and 1970s it is now viewed as incomplete, particularly since it overlooks high fecundity bet-hedging strategies exhibited by many broadcast spawning fishes and plants (Reznick et al. 2002). In recent years, the idea has been extended by various authors, in recognition of the limitations of the one-dimensional r - K continuum. Following Grime's (1974) classification of plant life histories, a triangular life history continuum consisting of three strategies (opportunistic; periodic and equilibrium) has been described based largely on teleost fishes (Winemiller & Rose 1992, Winemiller 2005). In this realm, opportunistic strategists are categorised by short generation time; small body-size; and high lifetime reproductive output with low batch fecundity and low parental investment per offspring. Periodic strategists are characterised by long generation time; large body size; and moderate reproductive output with large batch size and low investment per offspring. Finally, equilibrium strategists are characterised by long generation time and low reproductive output with low batch fecundity and high parental investment per offspring. Equilibrium strategists conform most closely to the idea of K -selected species and would typically include most chondrichthyans. They are expected to exhibit relatively low interannual variability in recruitment and, rather, to respond in consistent density-dependent manners to changes in habitat quality or resource availability (Winemiller 2005, Goodwin et al. 2006). In general, longer-lived species tend to have evolved mechanisms, such as large body size and fast growth through smaller size classes, to reduce adult mortality and have age at maturity and reproductive rates that reflect life history strategies either dependent upon strong iteroparity (repeated breeding events), as in many teleosts (Roff 1984, Heppell et al. 1999) or high juvenile survival rates, as in many chondrichthyans (Branstetter 1990, Hoenig & Gruber 1990, Gruber et al. 2001).

19.1.3 Life histories and the intrinsic rate of population increase r

Life history traits are static measures of fishes’ life history which can provide considerable insight into the response of populations and species to exploitation. The key life history traits include the von Bertalanffy growth completion rate (K), age at maturity (a_a), lifespan (a_{max}) and natural mortality rate (M) or survival rate (e^{-M}). These traits form the backbone of the demography and dynamics of populations, and also contribute to risk of population decline or eventual extinction. It turns out that surprisingly few metrics describe and limit the range of possible population dynamics for chondrichthyans. This can be understood in terms of the trade-offs among life-history traits, or, put another way, is because there is no “free lunch”, i.e., there is no such thing as a fast-growing, highly-fecund animal that matures late and lives for a long time (Law 1979). Such a ‘Darwinian Demon’ cannot exist anywhere in our universe because the laws of thermodynamics constrain metabolic processes. Organisms survive and reproduce by acquiring energy through foraging and feeding and by transforming it by somatic (body) growth, metabolism, excretion and reproduction. Because energy cannot be created or destroyed, the transformation of energy imposes fundamental constraints or trade-offs on the possible combination of life histories. These could almost be considered as the rules of life:

The faster you grow the quicker you die,	$M = K \bullet 1.65 \text{ to } 2,$
the faster you grow the smaller your maximum size,	$L_\infty = K^{-0.33}$
the quicker you die the shorter your lifespan,	$M \approx 1/a_{max} \text{ or } a_{max}^{-1}$
the shorter your lifespan the earlier you must breed,	$L_a = L_\infty \bullet 0.66 \text{ to } 0.73$
and	$M = 1.65 / a_a$

where L_∞ is the asymptotic maximum length and L_a is length at maturity. It follows that the shorter your active reproductive life the more offspring you must produce each year, and *vice versa*. It also follows that greater reproductive investment this year may limit future investments (Beverton & Holt 1957, Charnov 1993, Jensen 1996).

The rules of life were originally discovered by Ray Beverton and Sidney Holt (1957, 1959) who noticed that ratios of these life history traits greatly simplified the mathematics of fisheries catch models (Jennings & Dulvy 2008). These ratios appear to be robust across a wide range of taxa and are now known as life history dimensionless ratios or life history invariants, which form the foundations of life history theory (Beverton 1987, Beverton 1992, Charnov 1993). Despite their widespread acceptance and use, there have been relatively few estimates of life history invariant ratios for elasmobranchs. Fortunately, this gap has recently been addressed by Frisk et al. (2001). Their results suggest that invariant ratios for elasmobranchs (especially large pelagic species) may differ considerably from teleosts and reptiles. The rules of chondrichthyan life so far are:

The length at maturity is typically 70% of maximum size	$L_a \sim 0.70 \bullet L_{max},$
age at maturity occurs at around 38% of maximum age	$a_a \sim 0.38 \bullet a_{max},$
natural mortality rate is 42% of the growth rate	$M \sim K \bullet 0.42.$

Ultimately trade-offs among life history traits tend to result in large-bodied species having lower intrinsic rates of population increase. The intrinsic rate of population increase is difficult to measure. However, a simple approximation can be used to show the relationship between rate of population increase and body size. In this approach, potential population increase r' is calculated as $r' = \ln(\text{fecundity}) / t_{mat}$ (Jennings et al. 1998, Frisk et al. 2001). The potential rate of population increase of 18 shark and skate species has been shown to be negatively related to maximum size (L_{max}) with slope -0.52 ± 0.16 (see Figure 19.2 and Frisk et al. 2001). This slope was slightly higher than expected from metabolic theory of ecology which predicts the intrinsic rate of population increase should scale with body mass B as $r \sim B^{-1/4}$ (Savage *et al.* 2004). This discrepancy was probably because of the use of an indirect measure of r and because temperature was not controlled for (Brown *et al.* 2004). An analysis of the intrinsic rate of population increase derived from 63 European marine teleost stock-recruit relationships showed that $r \sim B^{-0.308}$. This was not significantly different from the -0.25 scaling predicted from metabolic theory (Denney et al. 2002, Maxwell & Jennings 2005). Hoenig and Gruber (1990) present results from several empirical studies showing a strong negative relationship between r and body size and between r and generation time. Studies such as these illustrate the role of constraints and trade-offs in producing predictable negative relationships between intrinsic rate of population increase and body size (see also Jensen 1996). Further analytical and empirical evidence suggesting that smaller elasmobranch species may have greater resilience to fishing and/or rebound faster from depleted states than larger species has been presented (van der Elst 1979, Dulvy et al. 2000, Myers et al. 2007, Au et al. 2008). There are, of course, exceptions to this general rule, notably Australian school shark (*G. galeus*) and several species of dogshark in the order Squaliformes (Smith et al. 1998, Cortés 2002, Braccini et al. 2006b, Forrest & Walters in review). Other factors contributing to overexploitation and extinction risk in these species include spatial effects resulting from species distribution and vulnerability to fishing gear (Stevens 1999) and extremely low fecundity in some smaller species such as dogsharks (Daley et al. 2002, Forrest & Walters in review). However, an understanding of fecundity alone is not necessarily sufficient to understand how populations will respond to elevated mortality or the rate at which they will recover from depletion. If survival rate of eggs or young sharks is dependent on the size of the adult population, density-dependent mortality can be an important, and often overlooked, consideration.

19.1.4 Density-dependent mortality and productivity of shark populations

Most animal populations exhibit some form of compensatory density-dependent population regulation resulting from improvement in rates of growth, fecundity or survival of young as the population size is reduced (Myers 2001, Rose et al. 2001, Brook

& Bradshaw 2006, Goodwin et al. 2006)¹. Compensatory density-dependent population regulation forms the ecological basis for sustainable fishing. Without such negative feedback control, any fishing regime removing a constant proportion of the population would eventually lead to extinction of the population (Hilborn & Walters 1992). In low fecundity elasmobranchs, density-dependent increases in fecundity might seem to be the most important mechanism conferring resilience to increased fishing mortality (Holden 1973, Holden 1977). However, simulation approaches have shown that density-dependent improvement in fecundity is unlikely to be sufficient to offset increased mortality due to fishing in many shark populations (Wood et al. 1979, Brander 1981, Bonfil 1996). In sharks, as in most exploited fish populations, measurable compensatory effects are most likely to be realized as improvement in the survival rate of juveniles at lower densities (Wood et al. 1979, Brander 1981, Hoenig & Gruber 1990, Gruber et al. 2001, Gedamke et al. 2007).

Mechanisms for improved juvenile survival at lower population sizes include decreased territorial behaviour, reduced competition for resources and decreased vulnerability to predation or cannibalism at lower densities (Branstetter 1990, Walters & Korman 1999, Gruber et al. 2001, Rose et al. 2001, Heupel & Simpfendorfer 2002). Newborn sharks are well-formed and have little difficulty in finding and catching food (Branstetter 1990). Predation (by other sharks) is therefore likely to be the most important source of mortality in young sharks, although such effects may be reduced in species that employ nursery grounds for their young (Gruber et al. 2001, Heupel & Simpfendorfer 2002). Branstetter (1990) reviewed the reproductive and early life history strategies of 26 Carcharhinoid and Lamnoid sharks and concluded that shark species have evolved a number of alternative strategies to achieve sufficient survival of cohorts for maintenance of the population. The main conclusions of his review were:

- The attainment of a length of approximately 100 cm is likely to be a critical factor in survival of juvenile sharks as they are then large enough to deter predators and actively avoid predation by fast swimming;
- A common strategy to achieve this is large size at birth followed by rapid growth in early life (14 of the 26 species considered);
- Alternatively, if nursery grounds are protected from predators, growth may be slower;
- Small species with maximum size close to 100 cm that may be vulnerable to predators throughout their life can offset this higher rate of mortality with greater fecundity; and
- Because of limited uterine space and the advanced state of development of shark eggs or pups, there is a negative relationship between number and size of young.

¹ Here, we will only discuss compensatory processes, where population growth rates decrease with increasing population size. Depensatory processes, where population growth rates decrease with decreasing population size appear to be less common in nature (but see Liermann and Hilborn 1997) or only occur at extremely low population sizes. Mechanisms for depensation include the “Allee effect”, where low density of adults results in inability to find mates; and predatory effects, where predation rates increase as juvenile numbers decrease. This last effect is exacerbated if predators have benefited from a reduction in the number of their own predators due to fishing (Rudstam et al. 1994; Walters and Kitchell 2001). Depensatory effects such as these can lead to population biomass becoming trapped at low levels and, in the worst cases, lead to local extinction.

The magnitude of compensatory improvement in juvenile survival is variable among populations and, because it is one of the main determinants of the resilience of fish populations to fishing, is of principal concern in management of fisheries. Density-dependence in juvenile survival is usually represented using standard stock-recruit functions that plot the average number of surviving recruits against average spawning stock biomass or eggs produced (Ricker 1954, Beverton & Holt 1957). These average relationships are typically asymptotic, representing the near-ubiquitous observation in exploited fish populations that average number of surviving recruits is stable over a wide range of population sizes (Myers 2002). Asymptotic stock-recruit relationships arise directly from the assumption of linear increase in natural mortality with population density (Beverton & Holt 1957). A fundamental assumption of stock-recruit relationships in assessment models is that density-dependent effects occur before individuals are first vulnerable to fisheries, although this assumption may not always be true (Heupel & Simpfendorfer 2002, Gedamke et al. 2007, Gazey et al. 2008).

The slope of a straight line fitted through a stock-recruit relationship at any given stock size represents the average rate of juvenile survival at that stock size. It follows, therefore, that if the number of recruits is stable over a wide range of stock sizes, the rate of juvenile survival (surviving recruits per egg) must increase as stock size is reduced (see Fig 19.3). The maximum rate of juvenile survival therefore occurs at very low stock sizes where density-dependence is minimal. The slope of the stock-recruit function near the origin (i.e., maximum juvenile survival rate, α), is proportional to the maximum intrinsic rate of population increase (Myers et al. 1997, Myers et al. 1999). The strength of density-dependence can be measured as the compensation ratio - defined as the ratio of α to the unfished juvenile survival rate (Goodyear 1993). This unitless ratio represents the maximum possible improvement in juvenile survival as population size is reduced (Myers et al. 1999). It is important to note here that the equilibrium unfished juvenile survival rate (shown as line (ii) in Fig. 19.3) can be calculated from life history data alone, as it occurs in the absence of fishing. It is given by the summation across ages a
$$\sum_{a=1}^{amax} e^{-M(a-1)} f_a$$
 where f_a is fecundity at age, the term $e^{-M(a-1)}$ represents survivorship at age, and all density-dependent processes are assumed to occur during the first year of life. All other parameters equal, the unfished juvenile survival rate is inversely proportional to fecundity - the biological interpretation being that, for an unfished population to maintain itself at equilibrium, production of fewer eggs must be accompanied by greater survival rates of those eggs. Accurate estimation of α and CR requires long time series of catch and abundance data which reflect the rate of change of population growth over a wide range of population densities (Hilborn & Walters 1992). The key challenge is that there are few such datasets available for chondrichthyans. We are aware of only four estimated stock-recruit relationships – all populations of spurdog or piked dogfish (*Squalus acanthias*) (da Silva 1993, Myers et al. 1995). However, life history strategies exhibited by many chondrichthyan populations may provide constraints to the magnitude of the compensatory response that make the unavailability of time series data less of an issue than for many teleost populations.

As far as we are aware, there have been only three studies that have attempted to directly measure the survival rate of juvenile elasmobranchs (Manire & Gruber 1990, Gruber et al. 2001, Heupel & Simpfendorfer 2002). Gruber et al. (2001) estimated the

survival rate of a population of age 0 lemon sharks (*Negaprion brevirostris*) in a lagoonal nursery area to be between 38% and 65% over a four year study. A fifth year of data, consistent with the original observations, has since been added (Gedamke et al. 2007). Preliminary results suggested that the survival rate of age 0 sharks was almost linearly related to the density of juveniles, with the highest survival rate (65%) occurring at the lowest density, although only five years of data were available. Although densities in the lagoon were unlikely to have resulted from changes in adult population size over such a short period of time, results were nonetheless consistent with the assumption of a linear relationship between mortality and density that underpins conventional stock-recruitment theory (Beverton & Holt 1957, Walters & Korman 1999, Walters & Martell 2004). The equilibrium unfished juvenile survival rate for lemon sharks has been estimated from a demographic model to be 39% (Hoenig & Gruber 1990). In this example, it is easy to see that there is only limited room for improvement in the juvenile survival rate as density of juveniles is reduced from its maximum (only a 2.5-fold improvement on a 40% unfished survival rate would result in a maximum of 100% survival).

Equilibrium unfished juvenile survival rates were calculated, accounting for uncertainty in life history parameters, for 12 species of dogshark caught in trawl fisheries on the continental slope of southeastern Australia (Forrest & Walters in review). Many of these species have been depleted by fishing (Graham et al. 2001), and are believed to have very low fecundity and late maturity (Daley et al. 2002), resulting in mean estimates of unfished juvenile survival rates ranging from between around 0.05 to 0.2 for the different species (Forrest & Walters in review). The maximum possible compensation ratio for these species (i.e., that which results in all individuals surviving at low population densities) would therefore range between around 5 and 20.

It is easy to see that a life history strategy dependent on high rates of survival of few large young places a fundamental constraint on the possible magnitude of the compensatory response, thereby reducing the amount of uncertainty in stock assessment that is due to uncertainty in recruitment. This is in contrast with teleosts, where the magnitude of compensatory response may be very large in some populations; although increases greater than 100-fold, compared to the unfished state, are rare even in teleosts (Myers et al. 1999, Goodwin et al. 2006). The low fecundities and high juvenile survival rates exhibited by many shark species has led a number of authors to suggest that density-dependence in recruitment can be ignored in sharks, especially with regard to giving management advice such as sustainable harvest rates (Branstetter 1990). However, while the magnitude of any compensatory response to change in population size is undoubtedly extremely low for many chondrichthyan species, especially those that produce few live young, it may still play a key role in determining the response of a population to fishing and its rate of recovery from depletion, even if the magnitude is low (Hoenig & Gruber 1990, Cortés 2007, Gedamke et al. 2007). It is also important to remember that many smaller or more fecund shark species may have unfished juvenile survival rates more comparable with large teleosts (Au et al. 2008) and, therefore, greater potential scope for compensatory effects that it would be unwise to ignore.

19.1.5 Comparative demographic studies of chondrichthyan populations

The previous section alluded to age-structured demographic approaches that can be used in conjunction with life history invariants to derive insights into the population dynamics of exploited chondrichthyan populations. Comparative demographic approaches aim to indicate relative responses of populations to perturbations, such as fishing, by providing methods to estimate r (Simpfendorfer 2005a). These types of studies have proved particularly important for gauging the impacts of fishing and climate change on data-limited chondrichthyan populations and have now been applied in a large number of studies (Hoenig & Gruber 1990, Au & Smith 1997, Cortes 1998, Smith et al. 1998, Heppell et al. 1999, McAllister et al. 2001, Cortés 2002, Mollet & Cailliet 2002, Frisk et al. 2005, Gedamke et al. 2007, Au et al. 2008, Cortés 2008). Essentially, demographic models are age-structured models that enable estimation of the rate of population increase r under a fixed set of parameters, assuming no density-dependence (but see Au & Smith 1997, Smith et al. 1998, Gedamke et al. 2007, Au et al. 2008). Demographic models that have been applied to chondrichthyans have been reviewed by Simpfendorfer (2005a) and Gedamke et al. (2007) and readers are referred to these papers and the references above for a full description of the approach. Briefly, there are two general approaches for estimating r from demographic models: (i) life tables; and (ii) matrix models. Both approaches provide similar results if used in comparable ways and, therefore, the choice of which method to use is a matter of preference, although matrix models are more common in the literature (Simpfendorfer 2005a). One advantage of matrix models is they allow calculation of the elasticity (i.e. proportional sensitivity) of estimates of population growth rate to changes in individual parameters (Heppell et al. 1999, Simpfendorfer 2005a). They can therefore be used to identify which part of the life cycle has the greatest contribution to population growth rate and, therefore, where best to direct data-collection and management efforts (Heppell et al. 1999, Cortés 2002, Frisk et al. 2005, Braccini et al. 2006b). From these studies, the population growth rate appears to be relatively insensitive to fecundity (in agreement with Wood et al. 1979, Brander 1981, Bonfil 1996). Instead, the most sensitive part of the life history tends to be the survival of juveniles to maturity, particularly for longer-lived sharks (Cortés 2002, Frisk et al. 2005).

There are five advantages of demographic approaches: (i) they incorporate the best biological information available; (ii) they can be used to develop biological characteristics compared to those obtained from alternative stock assessment approaches (e.g., aggregated surplus production models); (iii) they allow examination of constraints imposed by life history traits; (iv) they can be used to evaluate the effects of harvesting; and (v) they allow for species-specific assessment and management (Cortes 1998). Life table approaches, particularly those that incorporate life history information, tend to produce more conservative and realistic estimates of r than aggregated surplus production models (Cortes 1998). However, the two approaches can be combined in a Bayesian framework, where a surplus production estimate is improved by incorporating prior probabilities of r derived from a demographic model (McAllister *et al.* 2001). These authors found estimates of r for the sandbar shark (*Carcharhinus plumbeus*) were an order of magnitude lower than those obtained without demographic information using this approach.

Despite the advantages of demographic approaches, a shortcoming of most demographic models is they do not account for density-dependence in juvenile survival

of juveniles (Heppell et al. 1999, Gedamke et al. 2007). This is especially a problem with the many demographic models that do not include a fishing component to the mortality, as the resulting estimate of r from these models represents the unfished population growth rate and fails to account for the likelihood of increased population growth rates under increased mortality rates associated with fishing (Cortes 1998, Gedamke et al. 2007). These approaches are therefore unable to identify sustainable fishing mortality rates, which are necessary for successful management of sharks in targeted fisheries or in multispecies fisheries where they are an unavoidable bycatch. This assessment problem may be worse for smaller, more fecund species than for low-fecundity, live bearing species, where the compensation ratio is highly constrained and there is, therefore, less uncertainty in the magnitude of density-dependent effects on population growth rates (see above).

One approach to address density-dependence in juvenile survival in demographic models is to include an estimate of fishing mortality at maximum sustainable yield MSY (assuming $F = M$) and incorporate it into the model (Au & Smith 1997, Smith et al. 1998, Au et al. 2008). The intrinsic ‘rebound potential’ r_{2M} is then estimated as the rate at which the population rebounds from the ‘MSY’ state after the fishing mortality is removed. The approach is based on the assumptions of the surplus production model, where $F = M$, although in recent updates this has been revised to a level considered more appropriate for sharks, $F = 0.5M$ (Au et al. 2008, Cortés 2008, Smith et al. 2008). While the intrinsic rebound method is unable to produce an estimate of the maximum rate of intrinsic increase (and therefore the maximum sustainable fishing mortality that the population can withstand), the method still provides a logical framework for directly comparing relative productivities of different populations with different life histories, accounting for density-dependence (Gedamke et al. 2007). In one of the first major applications of the approach to chondrichthyans, Smith et al. (1998) calculated r_{2M} for 26 species of shark. The study suggested that the most important parameter determining ‘rebound’ potential for sharks is age at maturity, i.e., those with the lowest expected resilience to fishing were those that matured late.

19.1.6 Age-structured models incorporating density-dependence in juvenile survival

A recently-developed approach has avoided the assumption of density independence in age-0 juvenile survival by using fully age-structured models that incorporate a Beverton-Holt (1957) stock-recruit function, therefore assuming that all density-dependent mortality occurs in the first year of life (Forrest & Walters in review). The approach was based on work by Forrest et al. (2008), who presented an analytical relationship between maximum juvenile survival rate α and U_{MSY} and showed that the relationship between the compensation ratio and U_{MSY} is strongly influenced by life history (notably natural mortality, growth rate and maximum age) and selectivity parameters (age at first capture). Therefore, the degree to which density-dependence determines sustainable harvest rate is unique to an individual population under a given selectivity regime. Under some parameter-combinations, and assuming Beverton-Holt recruitment, Forrest and Walters (in review) showed that U_{MSY} approaches an asymptotic maximum value as the compensation ratio (CR) increases, with the maximum possible value of U_{MSY}

constrained by the particular combination of life history (and selectivity) parameters of the population. For species with very slow life histories and low fecundity, the upper limit to U_{MSY} could be shown to be very small indeed. This is illustrated in Fig 19.4, which shows the relationship between the CR and U_{MSY} for Harrison's dogshark (*Centrophorus harrissoni*) under three different ages at 50% first capture. Fig 19.4 illustrates that the maximum possible value of occurs at around 0.04 when age at 50% first capture is 1 and increases to 0.09 if first capture is delayed until sharks are 15 years old (note that this incorporates an assumption, based on known length at maturity, that these sharks mature around 18 years old). Application of this model to 12 species of Australian dogshark suggested that U_{MSY} for deepwater dogfishes is very low (5-10%), especially when individuals are caught at very young ages (Forrest & Walters in review). These authors were also able to systematically show that later-maturing, slower-growing less-fecund species have a smaller range of possible values of U_{MSY} than shorter-lived, faster growing species (Figure 19.5). The main advantage of the approach is that it explicitly accounts for the degree to which density-dependence in juvenile survival determines sustainable harvest rates and shows that there are cases (e.g., in slow growing, live bearing species) where U_{MSY} is so highly constrained by factors such as low fecundity and slow growth, even under the highest possible recruitment compensation (100% survival of juveniles at low population density), that density-dependent effects would have a relatively minor effect on management decisions. Since the upper limit to U_{MSY} can be estimated using life history and selectivity data alone, this approach is appropriate for data-limited species. It must be noted, however, that the method estimates the upper limit of U_{MSY} , not U_{MSY} itself, as the true magnitude of compensation remains unknown. For more fecund, faster-growing species, the upper limit may be quite high, and uncertainty in the compensation ratio will become a more important concern, as it is in most teleost assessments. A key advantage of this method compared to demographic approaches is that it allows for explicit consideration of vulnerability to fishing gear and can therefore be used to search for selectivity schedules that would allow enough individuals to reproduce for fishing mortality to become insignificant (Myers & Mertz 1998). Another advantage is that it is flexible to a wide variety of assumptions about the adult mortality schedule - another limitation of demographic approaches (Walker 1998, Cortés 2007).

It is worth noting here that U_{MSY} is regaining popularity as a limit reference point for use in fisheries management, i.e., as a threshold to fishing mortality that should not be exceeded (Mace 2001, Punt & Smith 2001). It represents a biologically valid threshold to exploitation that will prevent both growth and recruitment overfishing if successfully implemented (Sissenwine & Shepherd 1987, Mace 1994, Cook et al. 1997, Punt 2000). Therefore, while achieving MSY is rarely a goal in management of shark populations, knowledge of U_{MSY} is still important for sustainable management, especially when capture of sharks is unavoidable in multispecies fisheries.

19.1.7 Management implications of life histories and demography

The above discussions have hopefully shown that one of the most important determinants of population regulation in chondrichthyans, and therefore of risk to overexploitation and extinction, is density-dependence in survival of very young individuals. The above

studies discussed mostly live bearing species, although the similar arguments could apply to egg-laying species, such as batoids (e.g. Frisk et al. 2005, Gedamke et al. 2007). Unfortunately, juvenile survival is very hard to measure and there have, to date, been only a handful of attempts to measure it empirically in elasmobranch populations (Manire & Gruber 1993, Gruber et al. 2001, Heupel & Simpfendorfer 2002). Over the last decade, a number innovative modelling approaches have been developed that have greatly improved understanding of the impacts of fishing on chondrichthyan populations. In particular, approaches based on readily-obtainable life history information help to overcome some of the problems of extreme data-limitation in most of the world’s fished chondrichthyan populations. A key management recommendation from these approaches is that management should focus on maintaining reserves of reproducing adults and protection of relatively abundant juveniles and young reproductive adults that have survived the first year of high mortality (Au et al. 2008). In coastal species, this may be achievable by creation of reserves where juveniles are known occur. In many cases, the greatest gains may be achieved by modifying fishing gear or fishing practices so that these portions of the population are not vulnerable to capture. Walker (1998) discussed effects of size-selectivity in gillnets for sharks but noted that there have been few selectivity studies of sharks in trawl nets. Bycatch reduction devices (BRDs), such as escape panels and grids, may be effective at reducing catches of sharks (Brewer et al. 1998). In a global study of pelagic longline fisheries, Gilman et al. (2008) found that longline fishers employed a range of methods to decrease shark catches, although these tended to only be employed when there were disincentives to catch sharks (e.g., legal shark retention limits and large fines). Sharks are often patchily distributed and one of the main methods employed by the fishers to reduce shark catch was avoid topographic features known to be favored by sharks. Vessel-to-vessel communication of shark ‘hotspots’ to avoid was also effective. Shark-repellent technologies, involving magnets or chemicals, are being developed to deter sharks from longline hooks but are currently still in testing phases (Gilman et al. 2008, Kaimmer & Stoner 2008).

A key lesson from recent modelling approaches is that while high adult and juvenile survival rates may suggest large reservoirs of biomass and, therefore, high potential returns for harvesting, the slow growth rates and long generation times exhibited by many of these species imply that even very strong compensatory responses in recruitment would be not be enough to offset high harvest rates (Heppell et al. 1999, Forrest & Walters in review). Therefore high harvests of low-productivity species achieved in the initial years of a fishery are analogous to the ‘mining’ of a non-renewable resource, i.e., large biomass reserves are fished down but are not replaced at a fast enough rates for the fishery to remain sustainable, resulting in a ‘boom and bust’ fishery. Such fisheries are exhibited by many sharks, such as the Californian soupfin shark and Norwegian spurdog fisheries and fisheries targeting deep sea teleosts (Ripley 1946, Holden 1979, Koslow & Tuck 2001). In fisheries where low-productivity species are bycatch (many of which catch chondrichthyans), it is an inevitability that low-productivity species simply cease to form a significant part of the catch or become extremely rare (e.g. Brander 1981, Dulvy et al. 2000, Graham et al. 2001). So the emerging life history and demographic theory is rapidly catching up with the increasing weight of empirical evidence to suggest that many chondrichthyan populations and species are declining and are threatened due to fisheries.

Next we highlight some case-studies of decline, extirpation, local and regional extinction and regional rates of threat in chondrichthyans.

19.2 Decline, extirpation and extinction of sharks and rays

19.3.1 Documented population declines of sharks and rays in the Mediterranean Sea

Over the past decade, there has been an increasing number of studies documenting declines of coastal and ocean sharks and rays. Increasing scientific awareness: (1) the relative intrinsic vulnerability of elasmobranchs; (2) the high degree of fishing mortality imposed on target and non-target species; and (3) the rapid development of novel methods for inferring population trends (such as sightings records and recreational catches) has led an increasing number of studies are appearing from more data poor regions, such as the Mediterranean Sea. For example, a combination of sightings records, commercial and recreational catch data were used to reconstruct nine time-series of abundance indices for parts of the Mediterranean Sea. Large pelagic sharks with adequate data, including hammerheads (*Sphyrna* spp.), blue shark (*Prionace glauca*), porbeagle shark (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*) and thresher shark (*Alopias vulpinus*) had declined between 96 to 99.99% relative to former abundance. These rates of decline would be consistent with an IUCN Red Listing of Critically Endangered (Ferretti *et al.* 2008). However, at the time of the last IUCN Red Listing exercise, (see section below on IUCN Red List assessment process), these data were not available and it was only then defensible to assign some of these species (smooth hammerhead *S. zygaena*, blue and thresher sharks) with a lesser threat status of Vulnerable. The porbeagle and shortfin mako were assigned Critically Endangered status listings, which were subsequently confirmed by these new trends in abundance indices (Cavanagh & Gibson 2007). The subsequent more detailed analyses confirm that the IUCN Red List categorization process is, if anything, conservative in the sense that commercially-exploited species are usually assigned a lower threat status than can be defended with more detailed retrospective analyses. IUCN Red list assessments do not raise false alarms – a comparison of IUCN threat status and fisheries management status (inside or outside safe biological limits) demonstrates that exploited Northeast Atlantic teleost fishes have always been designated as overexploited (outside safe biological limits) before a threatened status criterion is triggered (Dulvy *et al.* 2005)

19.3.2 Steep declines of Australian deepwater sharks

Around 12 species of dogshark (Order Squaliformes) are caught on the southeastern Australian continental shelf and slope. One species (*Centrophorus harrissoni*) has been listed as Critically Endangered on the IUCN Red List of Threatened Species (Pogonoski & Pollard 2003). Its congeners, *C. zeehaani*² and *C. moluccensis* are listed as Data

² This species was formerly thought to be the more widely-distributed *C. uyato* but has now been reclassified as a separate species endemic to Australia (White *et al.* 2008).

Deficient. All three species have recently been added to the Australian Federal Government’s Priority Assessment List, which could see them listed as threatened species in Australia (DEWHA 2008). Should they be listed, the government will be required to develop a comprehensive management plan to reduce further risks.

These sharks can be considered particularly prone to risk of overfishing and extinction because of life history strategies that place them at the lower end of the shark productivity spectrum (Daley et al. 2002, Forrest & Walters in review). For example, *C. harrissoni* is thought to live for more than 40 years, does not reach maturity until close to its maximum length and has only 1-2 pups every two years (Daley et al. 2002). Growth parameters are not available, but other dogsharks have been reported to grow very slowly (Wilson & Seki 1994, Braccini et al. 2006a, Irvine et al. 2006). Like other dogsharks, is live bearing with yolk-only provisioning (ovoviviparous), giving birth to large (~40 cm) pups that are potentially immediately vulnerable to trawl nets or longline hooks (Daley et al. 2002).

During the 1970s, Australia’s fisheries were considered ‘underexploited’ and, with the impending 1979 declaration of the 200 nautical mile Australian Fishing Zone, (Rothwell & Haward 1996) the Australian government provided considerable funding for exploratory surveys of the waters of the southeast Australian slope to assess potential commercial opportunities (Tilzey & Rowling 2001). This led to a set of surveys by the Fisheries Research Vessel *Kapala*. The initial, exploratory upper-slope surveys were done in 1976-1977 and were not fully replicated until twenty years later in 1996-1997. This allowing for some striking comparisons of the abundance of many species (Andrew et al. 1997, Graham et al. 1997, Graham et al. 2001). In the twenty years between surveys, there had been significant declines in the abundance of many demersal sharks, skates and several teleost species. Notable declines were reported for deepwater dogsharks (*Centrophorus* spp., *Squalus* spp. and *Deania* spp.), as well as sawsharks (Pristiophoridae), angel sharks (Squatinae), school sharks (*Galeorhinus galeus*) and skates (Rajidae). Mean catch rates of *Centrophorus* spp. had declined by more than 99% in the period between the two surveys. The surveys were partially replicated in 1979, indicating that large declines in populations of some species may have occurred in the early years of the fishery, almost undoubtedly due to fishing (Andrew et al. 1997, Graham et al. 2001).

Commercial trawling on the slope began with two vessels in 1968, followed by rapid expansion of the fishery during the 1980s (Graham et al. 2001). Most vessels fishing in dogshark habitat (300-650 m) target valuable teleosts such as blue grenadier (*Macruronus novaezelandiae*), blue-eye (*Hyperoglyphe antarctica*) and pink ling (*Genypterus blacodes*). For these operators, dogsharks are bycatch, although they have some commercial value. Dogshark flesh is sold as ‘flake’, a generic term for shark fillets in Australia, popular in ‘fish and chips’ because they are boneless. Also, livers of *Centrophorus* spp. (and, to a lesser extent, *Deania* and *Centroscymnus* spp.) have a high content of squalene, an oil that is extracted, refined and exported for use in cosmetics, sometimes fetching very high prices per kilogram (Summers 1987, Deprez et al. 1990, Daley et al. 2002). However, despite the fact that dogsharks have been caught and marketed in southeastern Australia for more than three decades, there are a large gaps in the catch and effort data that limit their usefulness for assessment purposes (Daley et al. 2002, Walker & Gason 2007). These types of problems are common in fisheries around

the world, where there is a general lack of reliable data and low priority given to sharks (Bonfil 1994, FAO 2000). The lack of reliable data for dogsharks in Australia compromises the ability to perform risk assessment for them, despite current need for the three species of *Centrophorus* under consideration for threatened species listing (DEWHA 2008). Recent work has placed credible limits on productivity parameters for these species, showing that extremely low fecundity, slow growth and late maturity in these species imply very low sustainable harvest rates and possibly high extinction risk (Forrest & Walters in review). Demographic analyses of *Squalus* species have come to similar conclusions (Cortés 2002, Braccini et al. 2006a). In southeastern Australia, three spatial closures have been announced off the states of New South Wales, South Australia and Tasmania, aimed at protecting populations of *C. moluccensis*, *C. zeehaani* and *C. harrissoni* respectively. The success of spatial refugia as a harvest control measure depends upon spatial distribution and movement of the population, i.e., how much of the population is protected from fishing and how far outside the refuge individuals move on foraging or mating excursions (Gerber & Heppell 2004, Gerber et al. 2005). Very little is known about Australian deepwater dogsharks in these respects, although a recently-launched tagging programme, in collaboration with the fishing industry, may provide some answers (R. Daley, CSIRO, pers. comm.).

19.3.3 Extirpation of the British Columbia basking shark

Extirpation is a term usually reserved to describe extinction from part of a species former range or to convey some degree of uncertainty of the disappearance of the species. This usage, while widespread, is incorrect. Instead the use of the word extinction along with a sense of the spatial scale of the extinction, such as local extinction or regional extinction, might be preferred (Dulvy et al. 2003). Strictly-speaking extirpation is defined as the *intentional* eradication of a species. This usage is pejorative and directly implies the conscious proactive intention to eliminate a population or a species from part of its geographic range. There have been numerous population of sharks and rays have become locally extinct and have not recovered or returned to the area after several decades (Dulvy et al. 2009b). While these populations and species have disappeared, however, fishers and fisheries managers would claim it unfair to blame them by describing local and regional extinctions as extirpations, as it would imply that fishers and or fisheries management agencies have actively chosen to eradicate populations or species. Fishermen more often than not are motivated by the need for food and job security and have a high regard for the biodiversity and ecosystems that underpin their livelihoods. It seems unjust to suggest resource users willingly choose to extirpate populations and species, unless there is evidence of the intention of resource users to eradicate species. To illustrate our point we summarize the extirpation of the basking shark off the coast of British Columbia, Canada, which to our knowledge is the first extirpation, in the true sense of the word, of a marine species.

Sea monsters have been reported from the coast of British Columbia, Canada and the west coast of Vancouver Island for over a century. These sea monsters were probably basking sharks (*Cetorhinus maximus*). They were frequently entangled in set nets targeting the vast runs of Pacific salmon (*Onchorhynchus* spp.) as they returned to their spawning grounds in coastal rivers and lakes. The basking sharks were attracted, not by the Pacific salmon, but by the rich and locally-abundant phytoplankton blooms in coastal

bays and estuaries of salmon spawning streams. The entanglement of basking sharks resulted in damaged gear and lost fishing time. In 1949, basking sharks, like black bears, wolves, seals sea lions, merganser ducks and kingfishers, were officially classified as “destructive pests” by the federal Department of Fisheries and Oceans (DFO). This list reflected the perceived need for the control and eradication of this species. The local branch of DFO hunted and killed basking sharks by ramming them using a specially-modified patrol vessel called the *Comox Post*. The prow of these patrol boats were fitted with a forward-pointing large-curved blade and the intention was to ram and kill the shark. On 24th April 1956, the newly modified vessel put to sea it rammed and killed 34 basking sharks in Pachena Bay, Vancouver Island (Wallace & Gisborne 2006). According to DFO annual reports, the *Comox Post* killed 413 basking sharks in 14 years in the central West coast of Vancouver Island. Three other DFO vessels rammed any basking sharks encountered on their patrols, one vessel *Laurier* was estimated to have killed 200-300 individuals. DFO reports and newspapers covered only a small fraction of basking shark kills: entanglements with fishing gear are thought to have killed the greatest number of basking sharks (Wallace & Gisborne 2006). A single gillnetter caught seven basking sharks in the 1952 season alone. The true number killed by entanglement in fishing gears is unknown, but based on the extent of documented basking shark gillnet interactions it has been conservatively estimated that several hundred sharks were killed this way (Darling & Keogh 1994, Wallace & Gisborne 2006). Spearfishing for sport and harassment may have been responsible for the death of several hundred more individuals. Sharks were harassed by motor boaters who would use the basking sharks as ‘ski jumps’, whereas other were killed with harpoons, shooting and ramming. “For many coastal residents, harassing basking sharks was simply a way of life in the 1950s and 1960s” (Wallace & Gisborne 2006). Based on newspaper reports, anecdotes and the reports of DFO, “it is likely that several thousand sharks may have been killed in British Columbia between 1920-1970” (Wallace & Gisborne 2006). During the last decade only a handful of basking sharks have been sighted or caught. The British Columbia trawl fleet has had comprehensive observer coverage since 1996 and only four basking sharks have been captured, three off the Queen Charlotte Islands and one in Rennel Sound, in Northern BC. There have been no recent reports of capture in salmon gillnets, though fishing effort has decreased markedly in recent years. Now the likelihood of spotting a basking shark in the Eastern Pacific ocean and the Californian and British Columbian coastlines is vanishingly small. This species is currently being considered for legal protection under the Canadian Species at Risk Act.

19.3.4 Local extinctions of North Atlantic skates

The rapid decline in fisheries landings of the common skate (*Dipturus batis*) from the Irish Sea warned fisheries scientists to check on the status of the majority of fished species that were not typically subject to stock assessments or scientific scrutiny (Brander 1981). The common skate and other large species of skate were found to have disappeared and declined from both the Irish and North Sea. At least two of the largest species in the Irish Sea, the common skate, white skate (*D. alba*), and possibly the long-nosed skate (*D. oxyrinchus*) have disappeared virtually unnoticed (Brander 1981, Dulvy et al. 2000). Uncertainty remains over the long-nose skate as it is unclear whether this

species previously existed in the Irish Sea, though it is documented in the older taxonomies and species lists (Dulvy *et al.* 2000). An analysis of annual research survey data revealed that of the remaining five species, the two largest had declined and the two smallest had increased, with the intermediate-sized species remaining moderately stable over time (Dulvy *et al.* 2000). Fishermen tend to target larger individuals and species and this pattern remained even when the rate of fishing mortality was controlled for. A detailed demographic analysis of the North Sea skates (Rajidae) and demonstrated that demersal fishing mortality, typically of otter and beam trawlers, was 10 to 20% greater than the rate of replacement of the four largest species (Walker & Heessen 1996). The replacement rate of the starry ray (*Amblyraja radiata*), the smallest skate in the North Sea was greater than the (high) rate of fishing mortality and this species is now one of the most abundant large-bodied fishes in the North Sea (Walker & Heessen 1996, Ellis *et al.* 2005). This study provided a more detailed mechanistic link between the rates of fishing and the demographic capacity of each species to replace numbers killed by fishing. This study also showed how the replacement rates of these skates were sufficient to explain the current distribution and abundance of the skates remaining in the North Sea. The common skate is now only rarely caught on the northern fringes of the North Sea, the geographic distribution of the largest remaining skate (thornback ray) is now largely restricted to the Thames Estuary in the SW North Sea (Rogers & Ellis 2000, Ellis *et al.* 2005). The risk of extinction is the product or sum of the combination of *sensitivity* to a threat and degree of *exposure* to threat. Accordingly it is increasingly recognized that population trajectories, threat status and extinction risk result from the interaction of the intrinsic vulnerability of species and extrinsic fishing mortality. While an increasing number of studies have explored intrinsic vulnerability we are aware of only two that have explicitly considered both (Walker & Heessen 1996, Dulvy *et al.* 2000).

The disappearance of the largest skates and increases in the abundance and distribution of smaller skates has been repeated elsewhere – in the NW Atlantic shelf seas a large skate had also disappeared (Casey & Myers 1998). The barndoor skate (*Dipturus laevis*) – the second largest skate species after the common skate – was found to have been fished out across the shelf seas. This species remains on deep slope waters >450 meters deep, and appears to be recovering in the southern part of its range particularly in and around closed no-take areas on the Georges Bank and the Southern New England Shelf (Kulka 1999, Frisk *et al.* 2002, Kulka *et al.* 2002, Simon *et al.* 2002, Gedamke *et al.* 2008). More generally one wonders whether declines of large skates and increases in the smaller species are occurring in other temperate shelf seas fisheries.

19.3.5 Regional extinction of the angel shark

The angel shark (*Squatina squatina*) is a large benthic sit-and-wait predator and in the NE Atlantic shelf it was originally caught as bycatch in demersal trawl fisheries. This species was originally marketed and sold as ‘monkfish’ – so-called because the head of the angel shark resembled the cowl worn by monks. The decline and disappearance of this species throughout its range went undetected because as angel shark catches declined they were supplanted by catches of anglerfish (*Lophius piscatorius* and *L. budegassa*) which were marketed under the same ‘monkfish’ brand. While previously the subject of large fisheries by the 1980s they were virtually absent in the Irish Sea – they were sufficiently

rare and unusual that specimens were more often brought to public aquaria for display rather than sold on the market. One of us (NKD) saw a single captive specimen in an aquarium in St David’s, SW Wales in the mid-1990s. Aside from these anecdotal reports of previous abundance followed by current rarity, until recently there was little scientific evidence of the status of this species. A recent analysis of more than 29,000 research trawl surveys over the past three decades across most of the NE Atlantic range of this species (except the Mediterranean Sea) failed to uncover a single individual. This compilation spanned from the Bay of Biscay in the south to the Barents Sea in the North and from around 1980 to 2005 (ICES WGFE 2006). A voluntary tagging programme of monkfish (*Squatina squatina*) captured by recreational anglers was carried out in Tralee and Clew bays on the Atlantic coast of western Ireland (Fitzmaurice & Green 2009). A total of 1,107 individuals were marked between 1970 and 2001, with most captured in Tralee bay (939). To date 187 individuals (18.3%) have been recaptured, with most (179) recaptured around western Ireland with five recaptured in French waters, 2 captured in the Western English Channel and one captured off the North Coast of Spain. Almost half were recaptured by angling (47.6%), while 19.3% were caught by trawling, 21% by tangle and gill nets and five tags were washed ashore. There has been a “dramatic fall-off” in the numbers caught from 1977 onward: “in the five year period 1987-91, 320 angel sharks were tagged whereas in the period 1997-2001 only 16 individuals have been tagged despite the angling effort being relatively constant” (Fitzmaurice & Green 2009). In 2006, this species was taken off the official listings of the Irish Specimen Fish Committee as a precautionary measure, in recognition that they “are under serious threat due to commercial fishing pressure” (Anonymous 2009).

Further details of the decline come from a retrospective comparison of historic and recent trawl surveys, standardized by swept area, in two locations around the British Isles (West central Irish Sea and Start Bay in the western English Channel) (Rogers & Ellis 2000). Historically, moderate catch rates of between 2 (Irish Sea) and 19 (English Channel) individuals were captured per 24h of trawl survey between 1901 and 1907. More recently, none were caught in comparable modern surveys from 1989-1997; although the modern survey must undoubtedly have had higher fishing power (Rogers & Ellis 2000). Angel shark comprised 2% of the catch in Start Bay, English Channel prior to the First World War and angel shark was as abundant, at least in Start Bay, as adult North Sea cod (*Gadus morhua*) are presently!

It is possible that some angel sharks might remain in the Mediterranean Sea however this is looking increasingly unlikely. The MEDITS trawl survey, which consists of around 1000 hauls each year in depths ranging from 10 to 800 m in the West, North and Eastern Mediterranean captured angel sharks only in two out of a total of 9095 hauls carried out between 1994 and 1999 (Baino *et al.* 2001). These angel sharks were caught around the Balearic Islands in the Western Mediterranean in depths between 50-100m. However, a more recent and comprehensive trawl survey of the Balearic Islands, consisting of 143 hauls from 46 – 1713 m from 1996 to 2001, failed to capture a single angel shark. Consequently, this species has been listed as Critically Endangered globally by the IUCN Red List in 2006 (Cavanagh & Gibson). Remaining hope for the continued existence of this species lie with unsurveyed habitats in the southern North African coast of the Mediterranean and possibly in the Canary Islands where there are reports that individuals can be observed while SCUBA diving (S. Fowler pers. comm.). Without

urgent action to uncover and protect any remaining viable populations of this species, we are concerned that the angel shark could become one of the first species of fish to be driven to global extinction (Cavanagh & Gibson 2007).

19.3.6 Regional extinctions of guitarfishes and sawfishes

In addition to angel shark and skates, other coastal shark species have declined and / or disappeared from large parts of their former geographic range. Guitarfishes (Rhinobatidae) and sawfishes (Pristidae) are highly sensitive to fishing pressure as they are large-bodied, and presumably have a low intrinsic rate of population increase. They are also highly exposed to fishing mortality and have relatively high catchability. Sawfishes are easily entangled in nets. They tend to be restricted to shallow depths and consequently most of their depth range lies within reach of inshore and coastal fisheries. The Brazilian guitarfish (*Rhinobatos horkelli*) is endemic to the SW Atlantic and has undergone severe declines >80% since 1986 following intensive exploitation by fisheries and is consequently listed as Critically Endangered (Lessa & Vooren 2007).

Similarly, sawfishes appear to be in trouble worldwide – all are listed as Critically Endangered on the IUCN Red List. Sawfishes were once common in the Mediterranean Sea but are now absent. None had been captured within the living memory of the Mediterranean Scientists present at the IUCN Red List Mediterranean Sea workshop in San Marino in September 2003 (Cavanagh & Gibson 2007) and none have been caught in the Mediterranean-wide MEDITS annual trawl survey. It seems highly likely that two species, common sawfish (*Pristis pristis*) and large-tooth sawfish (*P. pectinata*) are regionally extinct from the Mediterranean Sea and NE Atlantic (Cook & Compagno 2000, Cavanagh & Gibson 2007). These sawfishes may also be close to global extinction. They were formerly found along the West African coast. Large specimens were regularly captured by Russian trawl surveys in the 1950-1960s, but none were observed in more recent surveys in the 1970s and 1980s (F. Litvanov pers. comm.). This anecdotal evidence is corroborated by Norwegian surveys conducted by RV *Fritjov Nansen*, over the last decade these surveys have failed to capture a single individual sawfish. The most recent catches of sawfishes occurred in Guinea-Bissau and Sierra Leone according to questionnaire surveys (Robillard & Seret 2006). Possibly the last remaining population of common and largetooth sawfishes in the eastern Atlantic, remains around the Bijagos Islands, Guinea-Bissau (Mika Diop, CSRP, SICAP AMITIE 3, VILLA 4430, BP 25485, Dakar Sénégal; Personal Communication). Here the sawfish is revered as totem of the indigenous people and recent landings surveys and questionnaire surveys hint that sawfishes are still present and occasionally captured (Robillard & Seret 2006). However, only three catches of individuals of either common or large-tooth sawfishes have been caught there since early 2008. While the Bijagos Islands are a UNEP Biosphere reserve, Guinea-Bissau is the fifth poorest country in the world and is politically highly unstable – the President and Head of the army were assassinated while this chapter was being written - making the conservation of the last populations of large sawfishes in the eastern Atlantic a major challenge.

The largetooth sawfish was the subject of pioneering biological studies by Thomas Thorson in the 1960s and 1970s (Thorson 1982). It was distributed in the western Atlantic Ocean and previously found in large numbers in Lake Nicaragua. This

migratory lake-dwelling population is now close to extinction as are any adjacent Caribbean and Meso-American populations due to capture, probably as bycatch, in commercial and artisanal fisheries. The most likely location for the remnant populations may be in the Northern coastal region of South America (Charvet-Almeida *et al.* 2007)

The smalltooth sawfish (*Pristis pectinata*) was similarly formerly widely distributed in the western central Atlantic. Large catches of large individuals were historically taken by US recreational fishers in the 1930s-1950s. Their distribution is currently over a small fraction (<5%) of their former range (Anonymous 2000). Large numbers were known from the Gulf of Mexico, but this species is locally extinct along the eastern US coast, mainly due to incidental capture in commercial fisheries and recreational fisheries (Anonymous 2000, Simpfendorfer 2005a). Habitat loss may have contributed to the decline and may hamper recovery efforts as mangroves and other shallow coastal habitats are used as a juvenile nursery habitat (Simpfendorfer 2007). A small population of smalltooth sawfishes remains in coastal Florida, which is currently monitored and protected by the US Endangered Species Act (Simpfendorfer 2005b, Carlson *et al.* 2007). Anglers in this region now return sawfishes alive (Anonymous 2000, Simpfendorfer 2005b)

19.3 Global threat status of chondrichthyans

19.3.1 A brief summary of IUCN Red List process

The Shark Specialist Group, under the auspices of the World Conservation Union for Nature and Natural Resources (www.iucnredlist.org), has undertaken a comprehensive evaluation of the threat status of all chondrichthyans since 1991. Global threat evaluations will have been completed for all species by the end of 2009. This collaborative effort has drawn upon the vast expertise of elasmobranch researchers, fisheries scientists and the staff of non-governmental organizations worldwide – and includes many of writers and readers of this book.

19.3.2 The global status of chondrichthyans

By the end of 2007, almost half (591) of all chondrichthyans had been evaluated at a global scale and 126 species or 21.3% of the known chondrichthyans were threatened. A small proportion has been assigned the highest threat status (Critically Endangered). Two species (3.7%) were Critically Endangered, 29 (4.9%) Endangered, and 75 (12.7%) Vulnerable (Dulvy 2008). A further 117 species (18%) were listed as Near Threatened, largely on the basis of the ongoing or increasing degree of potential threat faced by these species. It may or may not be a surprise that there are a large number of species for which little is known – 201 species (34%) were listed as Data Deficient.

19.3.3 Regional variation in chondrichthyan threat status

This global picture does not capture considerable regional variation in the degree of threat faced by chondrichthyans. To date, regional Red List assessments have been published for three regions, the Northeast Atlantic Ocean, the Mediterranean Sea and

Australia and Oceania (Cavanagh et al. 2003, Cavanagh & Gibson 2007, Gibson et al. 2008). The greatest proportion of threatened species is found in the Mediterranean Sea, followed by the Northeast Atlantic then Australia and Oceania. In the Mediterranean 30 species (42%) are Threatened (Critically Endangered, Endangered, Vulnerable) and 42 species (60%) are Threatened or Near Threatened. The same number of species are threatened in the Northeast Atlantic (30 species or 25%), and 53 species (45%) are Near Threatened.

A similar number of species (34) are threatened in Australia and Oceania as in the other two regions; however the higher regional diversity brings down the percentages. The Australia Oceania region has around a third of the world’s chondrichthyan diversity with an estimated 350 species and a large number of endemic species – 118, comprising 94 endemic sharks and 14 endemic batoids (Last & Stevens 1994, Cavanagh et al. 2003). So far 175 have been assessed in this region, and 34 species (16%) are Threatened with a total of 86 species (40%) classed as Threatened or Near Threatened.

Scientific knowledge of a large proportion of the chondrichthyan faunas of the three regions remains poor - around a quarter of the chondrichthyans from all three regions were listed as Data Deficient (Cavanagh et al. 2003, Cavanagh & Gibson 2007, Gibson et al. 2008). The true lack of knowledge may be underestimated because the majority of Australian & Oceania species have yet to be evaluated at the regional scale. A large number of species have recently been described, but many remain to be named (Last et al. 2008b, 2008a, 2008c). Many of these Data Deficient species may be threatened at smaller spatial scales. For example, the manta ray (*Manta birostris*) is Vulnerable in the South China Sea and Sulu Seas but Data Deficient regionally. Conversely there are regionally Data Deficient species which are locally Least Concern: this pertains particularly to Australia, where there is considerably higher scientific capacity for monitoring and management than in the rest of the region. This includes some large carcharhiniformes such as great hammerhead (*Sphyrna mokarran*), silvertip (*Carcharhinus albimarginatus*), nervous (*C. cautus*) and bignose sharks (*C. altimus*) (Cavanagh et al. 2003).

19.3.4 The distribution of threat is evolutionarily and ecologically non-random

The ecological and taxonomic distribution of threat across chondrichthyans also appears to be non-random. The most threatened ecological guild of species appears to be the oceanic pelagic sharks – species which are mainly found on the high seas and rarely come within the Exclusive Economic Zones and shelf seas (Compagno 2007, Gilman et al. 2008). Three-quarters of the 21 species of oceanic pelagic sharks have been listed as threatened or near threatened (Dulvy et al. 2008a). Consequently, this group of large oceanic predators may well constitute the most threatened group of animals in the world. They are more threatened, in the sense that a greater proportion of this ecologically-distinct group faces an elevated risk of extinction, than maybe even primates or whales or Amazonian frogs or freshwater turtles. These species are threatened because they are caught mainly as bycatch of the exploitation of tunas and billfishes and also because of their high intrinsic sensitivity to exploitation, particularly for lamniform sharks (Garcia et al. 2008). Their fins are removed, dried and sold to SE Asia to support the demand for

shark fin soup. An analysis of the sharkfin trade in Hong Kong – the main port of entry for shark fins – has estimated that an average of 38 million (range = 26-73) sharks are killed each year (Clarke *et al.* 2006). Retrospective analyses of fisheries observer logbooks in the North Atlantic suggests oceanic pelagic sharks have declined rapidly in the last few decades (Baum *et al.* 2003). While there are some challenges in guaranteeing the taxonomic identity of these observer data (Burgess *et al.* 2005), these declines appear robust in the face of such uncertainties (Baum *et al.* 2005) and appear consistent with the other available evidence such as the rise in estimated catches of pelagic sharks over the past 15 years (Shelley 2008) and a 30% decline in the catch per unit effort over the last 50 years of one of the most productive species - the blue shark (*Prionace glauca*) (Aires-da-Silva *et al.* 2008).

In addition to the high rates of threat in oceanic pelagic sharks and deepwater sharks (Dulvy *et al.* 2008a, Garcia *et al.* 2008), freshwater chondrichthyans are poorly known and face high rates of threat. The distributions of many freshwater species are poorly known, particularly in Australasian regions, such as Indonesia and Papua New Guinea, e.g. the Critically Endangered Bizant river shark (*Glyphis* sp. A) and Northern River shark (*Glyphis* sp. C) (Compagno 1997, Thorburn & Morgan 2005). The Northern river shark is known to science from only 18 individuals (Thorburn & Morgan 2005). Many species have relatively restricted ranges and tend to suffer from the impacts of habitat degradation and destruction and heavy exploitation. Many of the watersheds these species live in, particularly in Asia, are densely populated, for example the giant river stingray (*Himantura chaophraya*) inhabits the Chao Phraya river basin which runs through the centre of Bangkok.

19.4 Future threats to sharks and rays due to climate change

The widespread scale and intensity of fishing on coastal shelves in deeper waters and across the full extent of the high seas worldwide is increasingly evident (Worm *et al.* 2005, Morato *et al.* 2006). Fishing is the main cause of marine population extinctions and threat in North American marine fishes (55-60%), followed closely by habitat loss (32-26%) (Musick *et al.* 2000, Dulvy *et al.* 2003, Reynolds *et al.* 2005). However there is increasing concern of the role of climate change on marine communities (Brander 2006, Brander 2007, Dulvy *et al.* 2009a), particularly since climate change can interact with the effects of fishing and habitat loss both in temperate and tropical systems (Blanchard *et al.* 2005, Wilson *et al.* 2008). So far only one chondrichthyan has been listed on the IUCN Red List due to the impending threat of climate change – the New Caledonia catshark (*Aulohaelurus kanakorum*). This species was listed as Vulnerable largely on the basis that it is known from only a single type specimen, within an area that is biologically relatively well-known and it is presumed to be endemic to New Caledonia (Fowler & Lisney 2003). Like other species in this genus and family it is likely to be rare within a relatively small geographic range and it is likely to be distributed within a narrow depth band centered on coral reef habitat, which is highly vulnerable to degradation due to the projected increase in the frequency and intensity of coral bleaching (Fowler & Lisney 2003).

Many elasmobranchs are large-bodied and feed near the top of food chains (Cortés 1999), and hence one might expect that they are less sensitive to the impacts of

climate change. Climate change impacts are readily detectable in the primary producers and near the base of food webs, notably in plankton communities and on coral reefs. Marked impacts have also been noted in predatory species feeding directly on the herbivorous species. Notably fledging success of some North Sea seabirds has been linked to the effect of climate variability on the abundance and food quality of planktivorous fishes (Frederiksen et al. 2006). Similarly in the North Pacific the recent decline of Stellar sea lions (*Eumetopias jubatus*) is at least partially attributed to climate change mediated impacts on the quality of their fish prey (Guénette et al. 2006, Trites et al. 2007). For other higher trophic level fishes, including elasmobranchs, there is concern that the northward movement and deepening of their preferred isotherms will lead to smaller geographic distributions and poleward range shifts (Perry et al. 2005, Dulvy et al. 2008b). It is therefore worth considering the state of scientific understanding of the impact of climate change on sharks and rays. Here we summarize two studies that have considered the impact of climate change on chondrichthyans.

19.4.1 Climate change, fishing and extinction risk in the Australian grey reef shark

The grey nurse shark (*Carcharius taurus*) is globally Vulnerable and Critically Endangered in Eastern Australia mainly due to recreational and commercial fishing which is estimated to kill 12 sharks year⁻¹ and mortality from beach netting which kills 2-6 sharks per year. A recent study has considered the relative effect of fishing, climate change and demographic stochasticity on the grey nurse shark (Bradshaw *et al.* 2008). The current population size has been estimated at between 162-766 individuals and there is a 35% chance of quasi-extinction (<50 females) within three generations or 50 years, unless fishing mortality is underreported, in which case there is an almost certain (~100%) chance of quasi-extinction within this timeframe. Presently there are two disjunct east and west Australian populations of grey nurse shark, restricted to areas where winter sea surface temperatures are >14°C for nine or more months a year (Fig. 19.6). The most conservative Australian climate projections predict a 1°C SST rise by 2030, which is sufficient to eliminate the cool water separating these populations by 2030. There will be 10+ months each year when SSTs are >14 °C throughout the currently unoccupied region south to Victoria and full connectivity and panmixia of east and west populations is likely to occur soon after 2050. Assuming demographic rates are unchanged by climate change, the risk of extinction was reduced by 69% from a 35% to an 11% risk of quasi-extinction within fifty years. This outcome was sensitive to the potential immigration rates, the relative size of the western Australian population and the local details of how climate change affects this species - which all remain unknown.

19.4.2 Vulnerability of Australian sharks and rays to climate change

Vulnerability analyses developed by the social science community have emerged as a promising strategic planning tool with which to evaluate the impact of climate change particularly on data-poor socio-ecological systems (Williams et al. 2008, Allison et al. 2009). Vulnerability is defined as the combination of intrinsic sensitivity to, and extrinsic exposure to a threatening process, such as climate change, and the degree to which the

potential impact (sensitivity x exposure) can be offset or mitigated against by the adaptive capacity of the system (Figure 19.7). In this study, exposure and sensitivity were defined as having a negative impact on vulnerability, while adaptive capacity could offset and decrease vulnerability (Chin & Kyne 2007).

The key trick in such an analysis is to develop hypotheses of plausible pathways through which the extrinsic exposure to climate change is likely to affect species as determined by their intrinsic sensitivity to the driver (in this case climate change). Three plausible direct climate impacts on the physiology of Australian chondrichthyans were hypothesized: (1) rising air and sea temperatures; (2) increasing ocean acidification; and (3) increased variability in salinity resulting from greater variability in precipitation and riverine run-off into coastal zones, along with a further nine indirect impacts of climate on Australian sharks. The indirect impacts were hypothesized to be mediated through the effects of climate change on habitat distribution and quality and prey availability (Chin & Kyne 2007).

The exposure of six chondrichthyan functional groups to climate change was evaluated and ranked (low, medium, high). Biological attributes were ranked to provide sensitivity and adaptive capacity scores. The overall vulnerability was based on the rankings of all three components. Exposure was defined in terms of: (1) the degree of overlap between species geographic and depth range and the scale of the climate driver and (2) the extent to which the climate driver was likely to affect the habitats and ecological process upon which the functional group of chondrichthyans depends. Sensitivity was defined based on (1) rarity and (2) habitat-specificity, with rare species and species with highest habitat specificity scoring the highest sensitivity. Adaptive capacity was defined in four terms: (1) trophic specificity, which is the breadth of the diet; (2) physical or chemical tolerance – for example the bull shark is tolerant to a wide range of salinities; (3) immobility, or the degree to which species are site attached or cannot surmount physical barriers, e.g. species on seamounts; and (4) latitudinal range – which was used as a proxy for thermal range.

Temperature change, freshwater input and oceanic circulation are likely to have higher impacts on elasmobranchs, than, say, ocean acidification, particularly through the effect on prey availability. The freshwater and estuarine and coral reef functional groups were predicted to have the highest vulnerability due to high exposure to the widest range of climate drivers, and the strong direct linkage between climate drivers, such as freshwater flows and sea level rise, and coastal habitat quality. Coral reef species are highly exposed due to the effects of climate change on coral bleaching and, in the longer-term, ocean acidification. In contrast shelf, pelagic and bathyal species were predicted to have low to moderate exposure to projected climate change (Chin & Kyne 2007).

19.5 Prioritization for action: which sharks and rays require most urgent attention?

Many populations and species of shark, ray and chimaera have either suffered local and regional extinction or are threatened and face an elevated risk of extinction – as measured by IUCN Red List status. By the time the first IUCN Red List assessment is complete (anticipated by early 2009) it is likely that more than 300 species will require action to halt and reverse their decline and guarantee their future. However there is

limited scientific capacity to manage and conserve the large number of threatened species: there were only 407 registered members of the American Elasmobranch Society in 2007 (C. McCandless pers comm.) – this means we have to save at least one species per society member! Clearly we need to prioritize our limited scientific and financial capacity (Marris 2007).

There are a wide range of criteria for prioritizing species for conservation and management effort. To gain an insight into priority species one of us (NKD) conducted a straw poll of AES members and other scientists involved in marine conservation. A total of 50 people were asked, “if you had the chance to save five species of chondrichthyans, which five would you choose?”. No selection criteria were imposed and some respondents freely volunteered their criteria and rationalized their choices. A broad range of criteria were cited, many of which have been considered and subject to debate in the terrestrial conservation literature. For example, one selection criterion, evolutionary distinctness, prioritizes species that represent large amounts of unique evolutionary history (Redding & Mooers 2006, Isaac et al. 2007). All taxonomic orders were represented by the species voted for by the respondents. One approach to examine biases in preference with respect to the taxonomic distribution of species is to compare the proportion of votes cast for each order relative to the proportion of species within each order. The null expectation is that votes will be cast in proportion to the number of species in each order. Unsurprisingly voting was biased. Outcomes are, however, and possibly provide insights into the taxonomic distribution in the interests and research capacity of chondrichthyan biologists (Fig. 19.8). There were a greater proportion of votes for ground sharks (Carcharhiniformes) and mackerel sharks (Lamniformes) than expected, given the proportion of species in these orders. This may reflect the charismatic nature of many of these predatory species, but also the diverse unique morphological and physiology diversity typified, for example, by hammerheads, *Sphyrna* spp. and the filter-feeding basking shark (*Cetorhinus maximus*). There was considerable underrepresentation of batoids, particularly skates (Rajiformes) and torpedo rays (Torpediniformes). Clearly, our motivations and scientific capacity are biased toward a few favored groups and these could be the focus of initial conservation efforts. However, the underrepresentation of other taxa, particularly batoids may suggest that we need to be aware of our potential biases in our interests and scientific capacity when partitioning our limited management and conservation resources.

19.6 Research required to manage and conserve chondrichthyans

There has been rapid emergence of an awareness of the plight of chondrichthyans among scientists, policy makers and the public and a burgeoning of scientific literature on life histories, demography and population trends over the past decade. We can now make statements on the global and regional status of species and we now have an increased awareness of the wide variety of data from which inferences can be drawn of the former distribution and population trends. The range of data employed is remarkable and includes but is not restricted to fisheries observer logbook records (Baum *et al.* 2003), market surveys (Clarke *et al.* 2006, Clarke 2008), historical research vessel surveys (Rogers & Ellis 2000), newspaper reports and sightings data (Ferretti *et al.* 2008, Sims 2008, Mcpherson & Myers in press) and taxonomies, museum records and species lists

(Dulvy *et al.* 2000). The range of demographic and population models that cope with data limitations by using short cuts such as life history invariants (Frisk *et al.* 2001) incorporating uncertainty in parameter estimates (McAllister *et al.* 2001, Cortés 2002) or robust to uncertainty in density-dependence (Forrest *et al.* 2008, Forrest & Walters in review) is remarkable. A new opportunity for assessing the risk of fishing upon populations that incorporates less formal data and evidence includes the development of risk evaluation frameworks (Braccini *et al.* 2006b, Smith *et al.* 2007, Pilling *et al.* 2008). Such frameworks have the capacity to bridge the gap between formal stock assessments and IUCN Red List-style threat assessments and provide prioritization of the species, habitats and fishing processes for more rigorous assessment and management.

In addition there are clear taxonomic and geographic gaps and limited capacity within the scientific community to tackle these gaps. We have little knowledge of the detail of the fate and status of coastal and oceanic chondrichthyans in the Indian Ocean and South Atlantic and of the population substructure, movements and connectivity of deepwater chondrichthyans (Kyne & Simpfendorfer 2007). It is unclear whether severe declines in on part of the narrow depth range of some species have occurred throughout the full geographic range of these species. Increasing evidence of population substructuring suggests some of these apparently widespread species may actually comprise a species complex. We are fortunate that there are a large number of highly active chondrichthyan taxonomists. The rate of description of new chondrichthyans is in the region of 20-50 species each year! So training and support for chondrichthyan taxonomy and systematics would also be a priority.

There are clear biases in the species we value and hence are most likely to study. The charismatic megafauna of the Carcharhiniformes and Lamniformes - rightly or wrongly - attract the greatest attention of the public and the scientific community. Because of the compelling images and elaborate behaviors of these charismatic species many of us have been attracted to chondrichthyan science. There are hundreds of active white shark and manta ray biologists. Yet for many skates, rays, freshwater and deepwater chondrichthyans there are many more species that there are active scientists. The point is not that we should reduce white shark or manta ray science, but instead, alongside these efforts, we should encourage scientific capacity and knowledge of the other species occupying the diverse and complex chondrichthyan underworld.

Finally we conclude that there have been numerous losses of populations of chondrichthyans which may represent the permanent loss of some unique, behavioral, morphological and genetic diversity. There is increasing concern for the Threatened or Near Threatened status of a large proportion of at least three regional faunas and across the globe. However, we have the benefit of a firm theoretical foundation for modeling and predicting the relative risk of extinction of chondrichthyans and fisheries sustainability. The key challenge for the future will be to prioritize species for intervention and to implement effective conservation and fisheries management.

Acknowledgements

We thank Mika Diop, Peter Kyne, Cami McCandless, Corey Bradshaw, and Willie Roache for providing reports, preprints and other invaluable information. Carl Walters, Ken Graham and Ross Daley were valued advisors during development of RF's research

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

on chondrichthyan population dynamics. We are particularly indebted to the fifty people who responded to NKD’s *ad hoc* questionnaire at the 2008 AES meeting in Montreal: Aleks Maljkovic, Amanda Vincent, Andrea Marshall, Andrew Clark, Andrew Percy, Aaron MacNeill, Bill Duffy, Brooke Flammang, Christina Walker, Christine Bedere, Christine Ward-Paige, Colin Simpfendorfer, Cyrena Riley, Dovi Kacev, Erin Standen, Fiona Hogan, Francesco Ferretti, Heather Marshall, Isabelle Côté, Ivy Baremore, Jeremy Vando, Jim Ellis, John Carlson, John Foronda, John Froeschke, John Reynolds, Jon Walsh, Julian Dickenson, K. Parsons, Ken Goldman, Lewis Barnett, Luis Lucifora, Lynda Dirk, Marta Calosso, Matt Kolmann, Michelle Heupell, Mike Heithaus, Mike McAllister, Mike Stratton, Neil Ascheilman, Peter Kyne, Simon Brown, Tanya Brunner, Toby Daly-Engel, Tom Kashiwagi, Veronica Garcia & Yannis Papastamatiou and three other anonymous respondents.

DRAFT

References

- Aires-da-Silva, A.M., J.J. Hoey & V.F. Gallucci. 2008. A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. *Fisheries Research* 92: 41-52.
- Allison, E.H., A.L. Perry, W.N. Adger, M.-C. Badjeck, K. Brown, D. Conway, A. Halls, G.M. Pilling, J.D. Reynolds & N.K. Dulvy. 2009. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries*.
- Andrew, N.L., K.J. Graham, K.E. Hodgson & G.N.G. Gordon. 1997. Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. pp. 109, NSW Fisheries Research Institute, Cronulla, Australia.
- Anonymous. 2000. Status review of smalltooth sawfish (*Pristis pectinata*). pp. 71, National Marine Fisheries Service, Office of Protected Resources, Silver Springs, Maryland.
- Anonymous. 2009. Irish Trophy Fish. Irish Specimen Fish Committee, Dublin. <http://www.irish-trophy-fish.com/trophies/species.htm>. Accessed on 4th February 2009
- Au, D.W. & S.E. Smith. 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Canadian Journal of Fisheries and Aquatic Sciences* 54: 415-420.
- Au, D.W., S.E. Smith & C. Show. 2008. Shark productivity and reproductive protection and a comparison with teleosts. pp. 298-308. *In*: M.D. Camhi, E.K. Pikitch & E.A. Babcock (ed.) *Sharks of the Open Ocean. Biology, Fisheries and Conservation*, Blackwell Publishing, Oxford.
- Baino, R., F. Serena, S. Ragonese, J. Rey & P. Rinelli. 2001. Catch composition and abundance of elasmobranchs based on the MEDITS program. *Rapp. Comm. int. Mer Medit* 36: 234.
- Baum, J.K., D. Kehler & R.A. Myers. 2005. Robust estimates of decline for pelagic shark populations in the northwest Atlantic and Gulf of Mexico. *Fisheries* 30: 27-30.
- Baum, J.K., R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley & P.A. Doherty. 2003. Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299: 389-392.
- Beverton, R.J. 1987. Longevity in fish: some ecological and evolutionary considerations. *Basic life sciences* 42: 161-185.
- Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* 41: 137-160.
- Beverton, R.J.H. & S.J. Holt. 1957. *On the dynamics of exploited fish populations*. Chapman & Hall, London. 533 pp.
- Beverton, R.J.H. & S.J. Holt. 1959. A review of the life-spans and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquia on Aging* 5: 142-180.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Blanchard, J.L., N.K. Dulvy, S. Jennings, J.E. Ellis, J.K. Pinnegar, A. Tidd & L.T. Kell. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? ICES Journal of Marine Science 62: 405-411.
- Bonfil, R. 1994. Overview of world elasmobranch fisheries, Food and Agriculture Organisation of the United Nations, Rome.
- Bonfil, R. 1996. Elasmobranch Fisheries: Status, Assessment and Management, University of British Columbia, Vancouver. 301 pp.
- Braccini, J.M., B.M. Gillanders & T.I. Walker. 2006a. Determining reproductive parameters for population assessments of chondrichthyan species with asynchronous ovulation and parturition: piked spurdog (*Squalus megalops*) as a case study. Marine and Freshwater Research 57: 105-119.
- Braccini, J.M., B.M. Gillanders & T.I. Walker. 2006b. Hierarchical approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in southeastern Australia. Canadian Journal Of Fisheries and Aquatic Sciences 63: 2456-2466.
- Bradshaw, C.J.A., V.M. Peddemors, R.B. Mcauley & R.G. Harcourt. 2008. Population viability of eastern Australia grey nurse sharks under fishing mitigation and climate change, Final Report to the Commonwealth of Australia, Department of the Environment, Water, Heritage and the Arts.
- Brander, K. 1981. Disappearance of Common skate *Raia batis* from Irish Sea. Nature 290: 48-49.
- Brander, K. 2006. Assessment of possible impacts of climate change on fisheries. pp. 30, German Advisory Council on Global Change, Berlin.
- Brander, K. 2007. Global Fish Production and Climate Change. Proceedings of the National Academy of Sciences 104: 19709-19714
- Branstetter, S. 1990. Early life-history implications of selected carcharhinid and lamnoid sharks of the northwest Atlantic. pp. 17-28. In: H.L. Pratt, S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries., NOAA Technical Report NMFS 90.
- Brewer, D., N. Rawlinson, S. Eayrs & C. Burrige. 1998. An assessment of bycatch reduction devices in a tropical Australian prawn trawl fishery. Fisheries Research 36: 195-215.
- Brook, B.W. & C.J.A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87: 1445-1451.
- Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage & G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85: 1771-1789.
- Burgess, G.H., L.R. Beerkircher, G.M. Cailliet, J.K. Carlson, E. Cortes, K.J. Goldman, R.D. Grubbs, J.A. Musick, M.K. Musyl & C.A. Simpfendorfer. 2005. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries 30: 19-26.
- Carlson, J.K., J. Osborne & T.W. Schmidt. 2007. Monitoring the recovery of smalltooth sawfish, *Pristis pectinata*, using standardized relative indices of abundance. Biological Conservation 136: 195-202.
- Casey, J. & R.A. Myers. 1998. Near extinction of a large, widely distributed fish. Science 281: 690-692.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Cavanagh, R. & C. Gibson. 2007. Overview of the Conservation Status of Cartilaginous Fishes (Chondrichthyans) in the Mediterranean Sea. pp. 42, IUCN, Gland, Switzerland and Malaga, Spain.
- Cavanagh, R.D., P.M. Kyne, S.L. Fowler, J.A. Musick & M.B. Bennett. 2003. The conservation status of Australasian chondrichthyans: Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop. pp. 170, The University of Queensland, School of Biomedical Sciences, Brisbane, Australia.
- Charnov, E.L. 1993. Life history invariants. Oxford University Press, Oxford. 167 pp.
- Charvet-Almeida, P., V. Faria, M. Furtado, S.F. Cook, C.L.J. V. & M.I. Oetinger. 2007. *Pristis perotteti*. IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed on Downloaded on 05 February 2009
- Chin, A. & P.M. Kyne. 2007. Vulnerability of chondrichthyan fishes of the Great Barrier Reef to climate change. pp. 393-425. *In*: J.E. Johnson & P.A. Marshall (ed.) Climate Change and the Great Barrier Reef, Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Australia.
- Clarke, S. 2008. Use of shark fin trade data to estimate historic total shark removals in the Atlantic Ocean. pp. 373-381.
- Clarke, S.C., M.K. McAllister, E.J. Milner-Gulland, G.P. Kirkwood, C.G.J. Michielsens, D.J. Agnew, E.K. Pikitch, H. Nakano & M.S. Shivji. 2006. Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* 9: 1115–1126.
- Compagno, L.J.V. 1990. Alternative life-history styles of cartilaginous fishes in time and space. *Environmental Biology of Fishes* 28: 33-75.
- Compagno, L.J.V. 1997. Threatened fishes of the world: *Glyphis gangeticus* (Muller & Henle, 1839) (Carcharhinidae). *Environmental Biology of Fishes* 49: 400-400.
- Compagno, L.J.V. 2007. Checklist of oceanic sharks and rays. *In*: M.A. Camhi & E.K. Pikitch (ed.) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*, Blackwell Publishing, Oxford.
- Cook, R.M., A. Sinclair & G. Stefansson. 1997. Potential collapse of North Sea cod stocks. *Nature* 385: 521-522.
- Cook, S.F. & L.J.V. Compagno. 2000. *Pristis pristis*. IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed on Downloaded on 05 February 2009
- Cortes, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research* 39: 199-208.
- Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. International Council for Exploration of the Seas, *Journal of Marine Science* 56: 707-717.
- Cortés, E. 2000. Life history patterns and correlations in sharks. *Reviews in Fisheries Science* 8: 299-344.
- Cortés, E. 2002. Incorporating uncertainty into demographic modelling: application to shark populations and their conservation. *Conservation Biology* 18: 1048-1062.
- Cortés, E. 2007. Chondrichthyan demographic modelling: an essay on its use, abuse and future. *Marine and Freshwater Research* 58: 4-6.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Cortés, E. 2008. Comparative life history and demography of pelagic sharks. pp. 309-322. *In*: M.D. Camhi, E.K. Pikitch & E.A. Babcock (ed.) Sharks of the Open Ocean. Biology, Fisheries and Conservation, Blackwell Publishing, Oxford.
- da Silva, H.M. 1993. The cause of variability in the stock-recruitment relationship of spiny dogfish, *Squalus acanthias*, in the NW Atlantic, ICES.
- Daley, R., J. Stevens & K.J. Graham. 2002. Catch analysis and productivity of the deepwater dogfish resource in southern Australia, CSIRO, Hobart.
- Darling, D.J. & K. Keogh. 1994. Observations of basking sharks, *Cetorhinus maximus*, in Clayoquot Sound, British Columbia Canadian Field-Naturalist 108: 199-210.
- Denney, N.H., S. Jennings & J.D. Reynolds. 2002. Life history correlates of maximum population growth rates in marine fishes. Proceedings of the Royal Society of London, B 269: 2229-2237.
- Deprez, P.P., J.K. Volkman & S.R. Davenport. 1990. Squalene content and neutral lipid-composition of livers from deep-sea sharks caught in Tasmanian waters. Australian Journal of Marine and Freshwater Research 41: 375-387.
- DEWHA. 2008. Finalised Priority Assessment List for the Assessment Period Commencing 1 October 2008. <http://www.environment.gov.au/biodiversity/threatened/nominations-fpal.html>. Accessed on March 12, 2009.
- Dulvy, N.K., J.K. Baum, S. Clarke, L.V.J. Compagno, E. Cortés, A. Domingo, S. Fordham, S. Fowler, M.P. Francis, C. Gibson, J. Martínez, J.A. Musick, A. Soldo, J.D. Stevens & S. Valenti. 2008a. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks. Aquatic Conservation - Marine and Freshwater Ecosystems 18: 459-482.
- Dulvy, N.K., K. Hyde, J.J. Heymans, E. Chassot, D. Pauly, K. Sherman & T. Platt. 2009a. Climate change, ecosystem variability and fisheries productivity. *In*: T. Platt, M.-H. Forget & V. Stuart (ed.) Remote Sensing in Fisheries and Aquaculture: The Societal Benefits, International Ocean-Colour Coordinating Group, Dartmouth, Canada.
- Dulvy, N.K., S.J. Jennings, N.B. Goodwin, A. Grant & J.D. Reynolds. 2005. Comparison of threat and exploitation status in Northeast Atlantic marine populations. Journal of Applied Ecology 42: 883-891.
- Dulvy, N.K., J.D. Metcalfe, J. Glanville, M.G. Pawson & J.D. Reynolds. 2000. Fishery stability, local extinctions and shifts in community structure in skates. Conservation Biology 14: 283-293.
- Dulvy, N.K., J.K. Pinnegar & J.D. Reynolds. 2009b. Holocene extinctions in the sea. pp. 129-150. *In*: S.T. Turvey (ed.) Holocene extinctions, Oxford University Press, Oxford.
- Dulvy, N.K. & J.D. Reynolds. 1997. Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. Proceedings of the Royal Society of London, B 264: 1309-1315.
- Dulvy, N.K., S.I. Rogers, S. Jennings, V. Stelzenmüller, S.R. Dye & H.R. Skjoldal. 2008b. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of regional warming. Journal of Applied Ecology 45: 1029-1039.
- Dulvy, N.K., Y. Sadovy & J.D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4: 25-64.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Ellis, J.R., N.K. Dulvy, S. Jennings, M. Parker-Humphreys & S.I. Rogers. 2005. Assessing the status of demersal elasmobranchs in UK waters: a review. *Journal of the Marine Biological Association, U.K.* 85: 1025-1047.
- FAO. 2000. Fisheries management. 1. Conservation and management of sharks, Food and Agriculture Organisation of the United Nations, Rome.
- Ferretti, F., R.A. Myers, F. Serena & H.K. Lotze. 2008. Loss of Large Predatory Sharks from the Mediterranean Sea. *Conservation Biology* 9999.
- Fitzmaurice, P. & P. Green. 2009. Monkfish Migrations. Central Fisheries Board, Ireland. http://www.cfb.ie/fisheries_research/tagging/monkfish.htm. Accessed on 2/2/2009
- Forrest, R.E., S.J.D. Martell, M.C. Melnychuk & C.J. Walters. 2008. An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 286-296.
- Forrest, R.E. & C.J. Walters. in review. Estimating thresholds to optimal harvest rate for long-lived, low-fecundity sharks accounting for selectivity and density dependence in recruitment. *Canadian Journal of Fisheries & Aquatic Sciences*.
- Fowler, S.L. & T.J. Lisney. 2003. *Aulohalaelurus kanakorum*. 2008 IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed on 09 February 2009
- Frederiksen, M., M. Edwards, A.J. Richardson, N.C. Halliday & S. Wanless. 2006. From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* 75: 1259-1268.
- Frisk, M.G., T.J. Millar & N.K. Dulvy. 2005. Life histories and vulnerability to exploitation of elasmobranchs: Inferences from elasticity, perturbation and phylogenetic analyses. *Journal of the North Atlantic Fisheries Organisation* 35: 27-45.
- Frisk, M.G., T.J. Miller & M.J. Fogarty. 2001. Estimation of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 969-981.
- Frisk, M.G., T.J. Miller & M.J. Fogarty. 2002. The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. *ICES Journal of Marine Science* 59: 576-586.
- Garcia, V.B., L.O. Lucifora & R.A. Myers. 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society of London, B* 275: 83-89.
- Gazey, W.J., B.J. Gallaway, J.G. Cole & D.A. Fournier. 2008. Age composition, growth and density-dependent mortality in juvenile red snapper estimated from observer data from the Gulf of Mexico penaeid shrimp fishery. *North American Journal of Fisheries Management* 28: 1828-1842.
- Gedamke, T., J.M. Hoenig, W.D. DuPaul & J.A. Musick. 2008. Total mortality rates of the barndoor skate, *Dipturus laevis*, from the Gulf of Maine and Georges Bank, United States, 1963-2005. *Fisheries Research* 89: 17-25.
- Gedamke, T., J.M. Hoenig, J.A. Musick, W.D. DuPaul & S.H. Gruber. 2007. Using demographic models to determine intrinsic rate of increase and sustainable fishing

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- for elasmobranchs: Pitfalls, advances, and applications. *North American Journal of Fisheries Management* 27: 605-618.
- Gerber, L.R. & S.S. Heppell. 2004. The use of demographic sensitivity analysis in marine species conservation planning. *Biological Conservation* 120: 121-128.
- Gerber, L.R., S.S. Heppell, F. Ballantyne & E. Sala. 2005. The role of dispersal and demography in determining the efficacy of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 863-871.
- Gibson, C., S.V. Valenti, S.L. Fowler & S.V. Fordham. 2008. The conservation status of Northeast Atlantic Chondrichthyans. pp. 76, IUCN Shark Specialist Group, Newbury, UK.
- Gilman, E., S. Clarke, N. Brothers, J. Alfaro-Shigueto, J. Mandelman, J. Mangel, S. Petersen, S. Piovano, N. Thomson, P. Dalzell, M. Donoso, M. Goren & T. Werner. 2008. Shark interactions in pelagic longline fisheries. *Marine Policy* 32: 1-18.
- Goodwin, N.B., N.K. Dulvy & J.D. Reynolds. 2002. Life history correlates of the evolution of live-bearing in fishes. *Philosophical Transactions of the Royal Society of London, B* 356: 259-267.
- Goodwin, N.B., N.K. Dulvy & J.D. Reynolds. 2005. Macroecology of live-bearing in fishes: latitudinal and depth range comparisons with egg-laying relatives. *Oikos* 110: 209-218.
- Goodwin, N.B., A. Grant, A. Perry, N.K. Dulvy & J.D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 494-509.
- Goodyear, C.P. (ed.). 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Canadian Special Publication in Fisheries and Aquatic Science*. 67-81 pp.
- Graham, K.J., N.L. Andrew & K.E. Hodgson. 2001. Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research* 52: 549-561.
- Graham, K.J., B.R. Wood & N.L. Andrew. 1997. The 1996-97 survey of upper slope trawling grounds between Sydney and Gabo Island (and comparisons with the 1976-77 survey). pp. 96, NSW Fisheries Research Institute, Cronulla, Australia
- Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250: 26-31.
- Gruber, S.H., J.R.C. de Marignac & J.M. Hoenig. 2001. Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. *Transactions of the American Fisheries Society* 130: 376-384.
- Guénette, S., S.J.J. Heymans, V. Christensen & A.W. Trites. 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2495-2517.
- Heppell, S.S., L.B. Crowder & T.R. Menzel. 1999. Life table analysis of long-lived marine species with implications for conservation and management. pp. 137-147. *In: J.A. Musick (ed.) Life in the slow lane: ecology and conservation of long-lived marine animals*, American Fisheries Society, Bethesda, Maryland.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Heupel, M.R. & C.A. Simpfendorfer. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Canadian Journal of Fisheries and Aquatic Sciences 59: 624-632.
- Hilborn, R. & C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York. 570 pp.
- Hoening, J.M. & S.H. Gruber. 1990. Life-history patterns in the elasmobranchs: Implications for fisheries management. pp. 1-16. In: H.L. Pratt, S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries., NOAA NMFS.
- Holden, M.J. 1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 164: 360-367.
- Holden, M.J. 1977. Elasmobranchs. pp. 117-137. In: J.A. Gulland (ed.) Fish population dynamics, J. Wiley & Sons, London.
- Holden, M.J. 1979. The migrations of tope, *Galeorhinus galeus* (L) in the eastern North Atlantic as determined by tagging. Journal du Conseil International de l'Exploration de la Mer 38: 314-317.
- Irvine, S.B., J.D. Stevens & L.J.B. Laurenson. 2006. Comparing external and internal dorsal-spine bands to interpret the age and growth of the giant lantern shark, *Etmopterus baxteri* (Squaliformes : Etmopteridae). Environmental Biology Of Fishes 77: 253-264.
- Isaac, N.J.B., S.T. Turvey, B. Collen, C. Waterman & J.E.M. Baillie. 2007. Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. PLoS ONE 2: e296.
- Jennings, S. & N.K. Dulvy. 2008. Beverton and Holt's insights into life history theory: influence, application and future use. In: A.I. Payne, A.J.R. Cotter & E.C.E. Potter (ed.) Advances in fisheries Science: 50 years on from Beverton and Holt, Blackwell Publishing, Oxford.
- Jennings, S., F. Mélin, J.L. Blanchard, R.M. Forster, N.K. Dulvy & R.W. Wilson. 2008. Global-scale predictions of community and ecosystem properties from simple ecological theory. Proceedings of the Royal Society B: Biological Sciences 275: 1375–1383.
- Jennings, S., J.D. Reynolds & S.C. Mills. 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London, B 265: 333-339.
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53: 820-822.
- Kaimmer, S. & A.W. Stoner. 2008. Field investigation of rare-earth metal as a deterrent to spiny dogfish in the Pacific halibut fishery. Fisheries Research 94: 43-47.
- Kirkwood, G.P., J.R. Beddington & J.A. Rossouw. 1994. Harvesting species of different lifespans. pp. 199-227. In: P.J. Edwards, R.M. May & N.R. Webb (ed.) Large-scale ecology and conservation biology, Blackwell Science, Oxford.
- Koslow, J.A. & G. Tuck. 2001. The boom and bust of deep-sea fisheries: Why haven't we done better? . pp. 10 Report Sci. Coun. Res. Doc. NAFO.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Kulka, D.W. 1999. Barndoor skate on the Grand Banks, Northeast Newfoundland, and Labrador shelves: distribution in relation to temperature and depth based on research survey and commercial fisheries data. pp. 15p, Department of Fisheries and Oceans, Canadian Science Advisory Secretariat Research Document.
- Kulka, D.W., K.T. Frank & J.E. Simon. 2002. Barndoor skate in the northwest Atlantic off Canada: distribution in relation to temperature and depth based on commercial fisheries data. pp. 17, Department of Fisheries and Oceans, Canadian Science Advisory Secretariat Research Document.
- Kyne, P.M. & C.A. Simpfendorfer. 2007. A collation and summarization of available data on deepwater chondrichthyans: biodiversity, life history and fisheries, IUCN SSC Shark Specialist Group.
- Last, P.R. & J.D. Stevens. 1994. Sharks and rays of Australia. CSIRO, Australia. 513 pp.
- Last, P.R., W.T. White & J. Pogonoski. 2008a. Descriptions of new Australian chondrichthyans pp. 368, CSIRO Marine and Atmospheric Research Paper, Hobart, Australia.
- Last, P.R., W.T. White & J. Pogonoski. 2008b. Descriptions of new dogfishes of the genus *Squalus* (Squaloidea: Squalidae). pp. 136, CSIRO Marine and Atmospheric Research Paper, Hobart, Australia.
- Last, P.R., W.T. White, J. Pogonoski & D.C. Gledhill. 2008c. Descriptions of new Australian skates (Batoidea: Rajoidea). pp. 187, CSIRO Marine and Atmospheric Research Paper, Hobart, Australia.
- Law, R. 1979. Ecological determinants in the evolution of life histories. pp. 81-103. *In*: R.M. Anderson, B.D. Turner & L.R. Taylor (ed.) Population dynamics, Blackwell Scientific Publications, Oxford.
- Lessa, R. & C.M. Vooren. 2007. *Rhinobatos horkelii*. 2008 IUCN Red List of Threatened Species, Cambridge. www.iucnredlist.org. Accessed on 16 March 2009
- Mace. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries* 2: 2-32.
- Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 110-122.
- Manire, C.A. & S. Gruber. 1990. Many sharks may be headed toward extinction. *Conservation Biology* 4: 10-11.
- Manire, C.A. & S.H. Gruber. 1993. A preliminary estimate of natural mortality of Age-0 lemon sharks, *Negaprion brevirostris*. pp. 65-71.
- Marris, E. 2007. Conservation priorities: What to let go. *Nature* 450: 152-155
- Maxwell, D.L. & S. Jennings. 2005. Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *Journal of Applied Ecology* 42: 25-37.
- McAllister, M.K., E.K. Pikitch & E.A. Babcock. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1871-1890.
- Mcpherson, J.M. & R.A. Myers. in press. How to infer population trends in sparse data: examples with opportunistic sighting records for great white sharks. *Diversity and Distributions*.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Mollet, H.F. & G.M. Cailliet. 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Marine and Freshwater Research* 53: 503-516.
- Morato, T., R. Watson, T.J. Pitcher & D. Pauly. 2006. Fishing down the deep. *Fish and Fisheries* 7: 24-34.
- Musick, J.A. 1999. Life in the slow lane: ecology and conservation of long-lived marine animals. *American Fisheries Society Symposium* 23: 1-10.
- Musick, J.A., M.M. Harbin, S.A. Berkeley, G.H. Burgess, A.M. Eklund, L. Findley, R.G. Gilmore, J.T. Golden, D.S. Ha, G.R. Huntsman, J.C. McGovern, S.J. Parker, S.G. Poss, E. Sala, T.W. Schmidt, G.R. Sedberry, H. Weeks & S.G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25: 6-30.
- Myers, R.A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *International Council for Exploration of the Seas, Journal of Marine Science* 58: 937-951.
- Myers, R.A. 2002. Recruitment: understanding density-dependence in fish populations. pp. 123-148. *In: P.J.B. Hart (ed.) Handbook of fish and fisheries*, Blackwell Science, Oxford.
- Myers, R.A., J.K. Baum, T.D. Shepherd, S.P. Powers & C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315: 1846-1850.
- Myers, R.A., J. Bridson & N. Barrowman. 1995. Summary of worldwide stock and recruitment data. *Canadian Technical reports of Fisheries and Aquaculture Science* 2024: iv + 327.
- Myers, R.A., K.G. Brown & N.J. Barrowman. 1999. The maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2404-2419.
- Myers, R.A. & G. Mertz. 1998. The limits of exploitation: A precautionary approach. pp. S165-S169.
- Myers, R.A., G. Mertz & P.S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. *Fishery Bulletin* 95: 762-772.
- Perry, A.L., P.J. Low, J.R. Ellis & J.D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* 308: 1912-1915.
- Pianka, E.R. 1970. On r & K selection. *American Naturalist* 104: 592-597.
- Pilling, G.M., P. Apostolaki, P. Failler, C. Floros, P.A. Large, B. Morales-Nin, P. Reglero, K.I. Stergiou & A.C. Tsikliras. 2008. Assessment and management of data-poor fisheries. pp. 547. *In: A.I. Payne, A.J. Cotter & E.C.E. Potter (ed.) Advances in Fisheries Science. 50 years on from Beverton and Holt*, Blackwell, Oxford.
- Pogonoski, J. & D. Pollard. 2003. *Centrophorus harrissoni*. 2008 IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed on Downloaded on 02 March 2009.
- Pratt, H.L. & J.G. Casey. 1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. pp. 97-111. *In: H.L. Pratt, S.H. Gruber & T. Taniuchi (ed.)*

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries., NOAA NMFS.
- Punt, A.E. 2000. Extinction of marine renewable resources: a demographic analysis. *Population Ecology* 42: 19.
- Punt, A.E., F. Pribac, B.L. Taylor & T.I. Walker. 2005. Harvest strategy evaluation for school and gummy shark. *Journal of Northwest Atlantic Fisheries Science* 35: 387-406.
- Punt, A.E. & A.D.M. Smith. 2001. The gospel of maximum sustainable yield in fisheries management: birth crucifixion and reincarnation. pp. 41-66. *In*: J.D. Reynolds, G.M. Mace, K.H. Redford & J.G. Robinson (ed.) *Conservation of exploited species*, Cambridge University Press, Cambridge.
- Redding, D.W. & A.O. Mooers. 2006. Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* 20: 1670-1678.
- Reynolds, J.D., N.K. Dulvy, N.B. Goodwin & J.A. Hutchings. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society of London, B* 272: 2337–2344.
- Reznick, D., M.J. Bryant & F. Bashey. 2002. r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology* 83: 1509-1520.
- Ricker, W.E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11: 559-623.
- Ripley, W.E. 1946. The biology of the soupfin *Galeorhinus zygopterus* and biochemical studies of the liver. *California Fishery Bulletin* 64: 1–96.
- Robillard, M. & B. Seret. 2006. Cultural importance and decline of sawfish (Pristidae) populations in West Africa. *Cybium* 30: 23-30.
- Roff, D.A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Science* 41: 989-1000.
- Rogers, S.I. & J.R. Ellis. 2000. Changes in the demersal fish assemblages of British coastal waters during the 20th century. *International Council for Exploration of the Seas, Journal of Marine Science* 57: 866-881.
- Rose, K.A., J.H. Cowan, K.O. Winemiller, R.A. Myers & R. Hilborn. 2001. Compensatory density dependence in fish populations importance, controversy, understanding and prognosis. *Fish and Fisheries* 2: 293-327.
- Rothwell, D.R. & M. Haward. 1996. Federal and international perspectives on Australia's maritime claims. *Marine Policy* 20: 29-46.
- Savage, V.M., J.F. Goillooly, J.H. Bropwn, G.B. West & E.L. Charnov. 2004. Effects of body size and temperature on population growth. *American Naturalist* 163: 429-441.
- Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Inter-American Tropical Tuna Commission Bulletin* 127-56.
- Shelley, C. 2008. Use of shark fin trade data to estimate historic total shark removals in the Atlantic Ocean. *Aquatic Living Resources* 21: 373-381.
- Simon, J.E., K.T. Frank & D.W. Kulka. 2002. Distribution and abundance of barndoor skate *Dipturus laevis* in the Canadian Atlantic based upon research vessel surveys and industry/science surveys. pp. 67, Department of Fisheries and Oceans, Canadian Science Advisory Secretariat Research Document.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- Simpfendorfer, C.A. 2005a. Demographic models: life tables, matrix models and rebound potential. pp. 187–204. *In*: J.A. Musick & R. Bonfil (ed.) *Elasmobranch Fisheries Management Techniques*, Food and Agriculture Organisation of the United Nations, Rome.
- Simpfendorfer, C.A. 2005b. Threatened fishes of the world: *Pristis pectinata* Latham, 1794 (Pristidae). *Environmental Biology of Fishes* 73: 20.
- Simpfendorfer, C.A. 2007. The importance of mangroves as nursery habitat for smalltooth sawfish (*Pristis pectinata*) in South Florida. *Bulletin of Marine Science* 80: 933-934.
- Sims, D.W. 2008. Sieving a living: a review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus* *Advances in Marine Biology* 54: 171-220.
- Sissenwine, M.P. & J.G. Shepherd. 1987. An alternative perspective on recruitment over fishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 913-918.
- Smith, A.D.M., E.J. Fulton, A.J. Hobday, D.C. Smith & P. Shoulder. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. pp. 633-639.
- Smith, S.E., D.W. Au & C. Show. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* 49: 663-678.
- Smith, S.E., D.W. Au & C. Show. 2008. Intrinsic rates of increase in pelagic elasmobranchs. pp. 288-297. *In*: M.D. Camhi, E.K. Pikitch & E.A. Babcock (ed.) *Sharks of the Open Ocean. Biology, Fisheries and Conservation*, Blackwell Publishing, Oxford.
- Stevens, J.D. 1999. Variable resilience to fishing pressure in two sharks: the significance of different ecological and life history parameters. pp. 11-16. *In*: J.A. Musick (ed.) *Life in the slow lane: ecology and conservation of long-lived marine animals*, American Fisheries Society, Bethesda.
- Stevens, J.D., R. Bonfil, N.K. Dulvy & P. Walker. 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57: 476-494.
- Stobutzki, I., M. Miller & D. Brewer. 2001. Sustainability of fishery bycatch: a process for assessing highly diverse and numerous bycatch. *Environmental Conservation* 28: 167-181.
- Summers, G. 1987. Squalene—a potential shark byproduct. *Catch* 14: 29.
- Thorburn, D.C. & D.L. Morgan. 2005. Threatened fishes of the world: *Glyphis* sp C (Carcharhinidae). *Environmental Biology of Fishes* 73: 140-140.
- Thorson, T.B. 1982. The impact of commercial exploitation on sawfish and shark populations in Lake Nicaragua. *Fisheries* 7: 2-10.
- Tilzey, R.D.J. & K.R. Rowling. 2001. History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research* 52: 361-375.
- Trites, A.W., V.B. Deecke, E.J. Gregr, J.K.B. Ford & P.F. Olesiuk. 2007. Killer whales, whaling, and sequential megafaunal collapse in the North Pacific: A comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. *Marine Mammal Science* 23: 751-765.

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

- van der Elst, R. 1979. A proliferation of small sharks in the shore-based Natal sport fishery. *Environmental Biology of Fishes* 4: 349-362.
- Walker, P.A. & H.J.L. Heessen. 1996. Long-term changes in ray populations in the North Sea. *International Council for Exploration of the Seas, Journal of Marine Science* 53: 1085-1093.
- Walker, T.I. 1998. Can shark resources be harvested sustainably? A question revisited with a review, of shark fisheries. *Marine and Freshwater Research* 49: 553-572.
- Walker, T.I. & A.S. Gason. 2007. Shark and other Chondrichthyan byproduct and bycatch estimation in the Southern and Eastern Scalefish and Shark Fishery. pp. 182 + vi, Primary Industries Research Victoria, Queenscliff, Victoria, Australia.
- Wallace, S. & B. Gisborne. 2006. Basking sharks: the slaughter of BC's gentle giants. New Star Books, Vancouver. 92 pp.
- Walters, C.J. & J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton–Holt recruitment model from a life history and multispecies perspective. *Reviews in Fish Biology and Fisheries* 9: 187–202.
- Walters, C.J. & S.J.D. Martell. 2004. *Fisheries Ecology and Management*. Princeton University Press, Princeton, New Jersey.
- White, W.T., D.A. Ebert & L.J.V. Compagno. 2008. Description of two new species of gulper sharks, genus *Centrophorus* (Chondrichthyes: Squaliformes: Centrophoridae) from Australia. pp. 1-21. *In*: P.R. Last, W.T. White & J.J. Pogonoski (ed.) *Descriptions of new Australian Chondrichthyans*, CSIRO Marine and Atmospheric Research Paper 022., Hobart.
- Williams, S.E., L.P. Shoo, J.L. Isaac, A.A. Hoffmann & G. Langham. 2008. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *PLoS Biology* 6: e325.
- Wilson, C.D. & M.P. Seki. 1994. Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central north Pacific Ocean. *Fishery Bulletin* 92: 851-864.
- Wilson, S.K., R. Fisher, M.S. Pratchett, N.A.J. Graham, N.K. Dulvy, R.A. Turner, A. Cakacaka, N.V.C. Polunin & S.P. Rushton. 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology* 14: 2796-2809.
- Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Science* 62: 872-885.
- Winemiller, K.O. & K.A. Rose. 1992. Patterns of life history diversification in North American fishes - implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196-2218.
- Wood, C.C., K.S. Ketchen & R.J. Beamish. 1979. Population dynamics of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *J. Fish Res. Board Can.* 36: 647-656.
- Worm, B., H.K. Lotze, R.A. Myers, M. Sandow & A. Oschlies. 2005. Global patterns of predator diversity in the open oceans. *Science* 309: 1365-1369.
- Zeeberg, J., A. Corten & E. de Graaf. 2006. Bycatch and release of pelagic megafauna in industrial trawler fisheries off Northwest Africa. *Fisheries Research* 78: 186–195.

DRAFT

Figure legends

Figure 19.1. Equilibrium yield curves predicted from the logistic surplus production model (Schaefer 1954) for five hypothetical species with different intrinsic rates of growth r . Note that maximum sustainable yield (MSY) occurs at the peak of each curve at a value of $r/2$.

Figure 19.2 The potential rate of population increase is negatively related to maximum body size in elasmobranchs. Body size is measured as total length in cm. The line is a robust regression model (which downweights outlying datapoints), $F_{2,30} = 11.1$, $P < 0.002$, $\ln(r') \sim 2.484 * 0.52 * \ln(\text{maximum length})$.

Figure 19.3. Stock recruitment relationship for a hypothetical fished population. Points represent observed number of recruits R plotted against number of pups/eggs E . The solid line shows a fitted Beverton-Holt stock recruitment curve. Dashed lines represent juvenile survival rate: (i) close to the origin; and (ii) at unfished (maximum) production of eggs (i.e., E_0 where the 0 subscript indicates fishing mortality $F = 0$). The maximum juvenile survival rate, i.e., slope of dashed line (i) is called α and occurs at the fishing mortality rate F_{ext} , which, if applied consistently, would cause extinction of the population. The ratio of slopes (i) and (ii) is called the recruitment Compensation Ratio, CR (Goodyear 1977; Myers *et al.* 1999) and represents the maximum possible improvement in juvenile survival as stock size is reduced.

Note that R_0/E_0 is the inverse of unfished eggs per recruit, and, therefore, $CR = \alpha (E_0/R_0)$ or αSPR_0 (Myers *et al.* 1999), where SPR_0 is unfished spawners per recruit.

19.4. Contour plots showing maximum possible U_{MSY} over a range of tested values of age at 50% first harvest ah and von Bertalanffy growth rate κ , holding all other parameter values constant. The two plots show the effect of increasing litter size, LS, on the maximum possible value of U_{MSY} , which occurs at the maximum possible hypothesis for α (i.e., 100% juvenile survival at very low stock size, $\alpha = 1$; see text and Figure 19.3). Here we assume a maximum age of 30 years and an age at maturity of 10, litter size is 1 (upper panel) and 5 (lower panel). Adapted from Forrest and Walters (in review), see their paper for detailed methods.

Figure 19.4. Curves showing relationship between U_{MSY} and the compensation ratio CR for Harrison's dogshark (*C. harrissoni*), under three hypothesised values of ah (age in years at 50% first harvest). Values were calculated using an analytical relationship between U_{MSY} and CR (Forrest *et al.* 2008) assuming a Beverton-Holt stock-recruit relationship. Parameter values for this species can be found in Forrest and Walters (in review). The parameters representing growth rate, age at maturity, maximum age, litter size and the ratio of the growth rate to natural mortality were treated as uncertain and drawn randomly from distributions given in Forrest and Walters (in review). The curves therefore represent the mean U_{MSY} -CR relationships from 100 Monte Carlo simulations. Curves are truncated at the average maximum possible compensation ratio for this species under this set of parameters (i.e., 100% juvenile survival at very low stock size, $\alpha = 1$; see text). Note that a recruit is here defined as an age 1 individual, regardless of the

Chapter 19 in “The Biology of sharks and their relatives”, by Carrier JC, Musick, JA & Heithaus, MR

age at entry to the fishery. All density-dependent mortality is therefore assumed to occur at age 0.

Figure 19.5. Life history, selectivity and maximum possible harvest rate U_{MSY} . Contour plots showing maximum possible U_{MSY} over a range of tested values of age at 50% first harvest and von Bertalanffy growth rate κ , for two fecundity scenarios - litter size of 1 (upper panel) and 5 (lower panel) and holding all other parameter values constant. The two plots show the effect of increasing litter size on the maximum possible value of U_{MSY} , which occurs at the maximum possible hypothesis for α (i.e., 100% juvenile survival at very low stock size, $\alpha = 1$; see text and Figure 19.3). Here we assume a maximum age of 30 years and an age at maturity of 10. Adapted from Forrest and Walters (in review), see their paper for detailed methods.

Figure 19.6 Climate change and the increasing distribution of suitable thermal habitat for the grey nurse shark. Present day (A) and predicted to 2030 (B) estimates of the number of months each year where annual minimum monthly sea surface temperature averages are greater than 14°C in 1-degree blocks are along the south Australian coast. Predictions for 2030 are derived from the CSIRO Mk3 model Redrawn from Bradshaw et al. (2008).

Figure 19.7 A conceptual framework to evaluate the vulnerability of Australian sharks and rays to climate change Redrawn from Chin & Kyne (2007).

Figure 19.8 If you had a choice to save five chondrichthyan species which five would you choose? A. The proportion of votes for species grouped by taxonomic order. B. The over- or underrepresentation of votes based on the number of species in each order. The asterisk represents significant deviation from the expectation (observed number of species in each order) at the $P < 0.01$ level.