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17

Life Histories, Population Dynamics, and Extinction Risks in Chondrichthyans

Nicholas K. Dulvy and Robyn E. Forrest

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17.1 Introduction

The greatest threat to chondrichthyan (sharks, rays, and chimaeras) populations and species is fishing mortality. This can come from directed fisheries targeting sharks (Bonfil 1994; T.I. Walker 1998; Punt et al. 2005), mortality imposed as bycatch in more valuable crustacean fisheries (Stobutzki, Miller, and Brewer 2001), demersal fish trawling (Graham, Andrew, and Hodgson 2001; Ellis et al. 2005), pelagic trawling (Zeeberg, Corten, and de Graaf 2006), pelagic line fishing (Gilman et al. 2008), recreational fisheries (Anderson 2002) or through finning of sharks captured, mainly 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 to 42 months), egg hatching period (1 to 27 months), ovum diameter (0.5 to 600 mm), reproductive mode (egg-laying, live-bearing), maternal investment (yolk-only versus uterine milk, oophagosity, uterine cannibalism, placentation), fecundity (1 to 400 offspring), offspring size (20 to 1800 cm long), age at maturity (1.5 to 30+ years), and longevity (5 to 50+ years) (Compagno 1990; Dulvy and Reynolds 1997; Cortés 2000; Goodwin, Dulvy, and Reynolds 2002, 2005).

Such 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*), which are 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).

There have been a large number of studies in recent years, linking life history to risk of overexploitation and extinction in chondrichthyans (Hoenig and Gruber 1990; Kirkwood, Beddington, and Rossouw 1994; Cortés 1998, 2002; S.E. Smith, Au, and Show 1998; Heppell, Crowder, and Menzel 1999; Musick 1999; Gedamke et al. 2007; Au, Smith, and Show 2008; Forrest and Walters, in press). 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; T.I. 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.

17.2 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 modeled 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 that 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 exploited species, there is a theoretical constant long-term harvest rate (U) 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. 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 17.1).

In the following sections, we first 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.

17.3 Life History Strategies

The logistic growth equation underlies the concept of an r - K life history continuum (MacArthur and Wilson 1967; Pianka 1970). Under this scheme, species living in highly

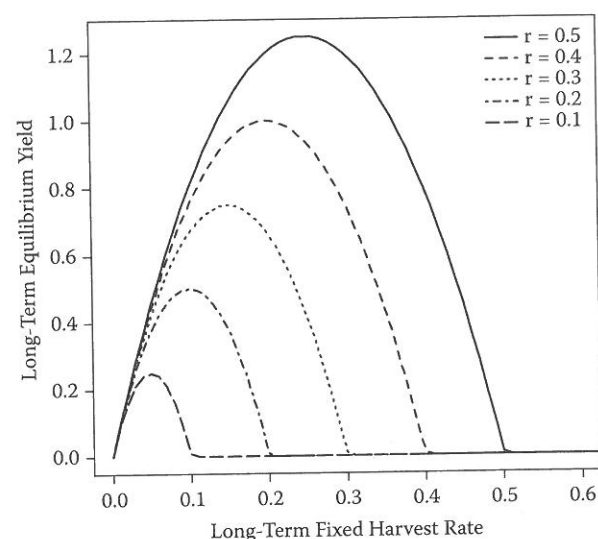


FIGURE 17.1

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 $r/2$. In reality, these curves tend to be asymmetric with peak yield occurring to the left of center at less than $r/2$ (Fowler 1981; Sutherland and Gill 2001).

variable, unpredictable environments and suffering repeated catastrophic mortality events (hence unlikely to reach carrying capacity) were termed r -selected species. These r -selected species tended to be characterized by frequent colonization and recolonization, 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 energized 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 (Stearns 1977; Reznick, Bryant, and Bashey 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 and Rose 1992; Winemiller 2005). In this realm, opportunistic strategists are categorized 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 characterized by long generation time, large body size, and moderate reproductive output, with large batch size and low investment per offspring. Finally, equilibrium strategists are characterized 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 on strong iteroparity (repeated breeding events), as in many teleosts (Roff 1984; Heppell, Crowder, and Menzel 1999) or high juvenile survival rates, as in many chondrichthyans (Branstetter 1990; Hoenig and Gruber 1990; Gruber, de Marignac, and Hoenig 2001).

17.4 Life Histories and the Intrinsic Rate of Population Increase r

Life history traits are static measures of fishes' life history that 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_m), lifespan (a_{max}), and natural mortality rate (M) or survival rate (e^{-M}). These traits form the backbone of the demography and population dynamics, 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. It is commonly said that there is no "free lunch," that is, 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 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: $M = K \cdot 1.65$ to 2

The faster you grow, the smaller your maximum size: $L_{\infty} = K^{-0.33}$

The quicker you die, the shorter your lifespan: $M \approx 1/a_{max}$ or a_{max}^{-1}

The shorter your lifespan, the earlier you must breed: $L_{\alpha} = L_{\infty} \cdot 0.66$ to 0.73 and $M = 1.65/a_{\alpha}$

where L_{∞} is the asymptotic maximum length and L_{α} 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 and 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 and Dulvy 2008). These ratios appear to be robust across a wide range of taxa and are now known as dimensionless ratios or life history invariants, which form the foundations of life history theory (Beverton 1987, 1992; Charnov 1993). Despite their widespread acceptance and use, there have been relatively few estimates of life history invariant ratios for elasmobranchs (see Chapter 6), although this gap has recently been addressed by Frisk, Miller, and Fogarty (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: $L_{\alpha} \sim 0.70 \cdot L_{\max}$

Age at maturity occurs at around 38% of maximum age: $a_{\alpha} \sim 0.38 \cdot a_{\max}$

Natural mortality rate is 42% of the growth rate: $M \sim K \cdot 0.42$

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 $r' = \ln(\text{fecundity})/t_{\text{mat}}$ (Jennings, Reynolds, and Mills 1998; Frisk, Miller, and Fogarty 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 -0.53 ± 0.13 SE (see Figure 17.2 and Frisk, Miller, and Fogarty 2001). This slope was slightly steeper than expected from metabolic theory of ecology that 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, Jennings, and Reynolds 2002; Maxwell and 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 in chondrichthyans. Studies such as these illustrate the role of constraints and trade-offs in producing predictable negative relationships between

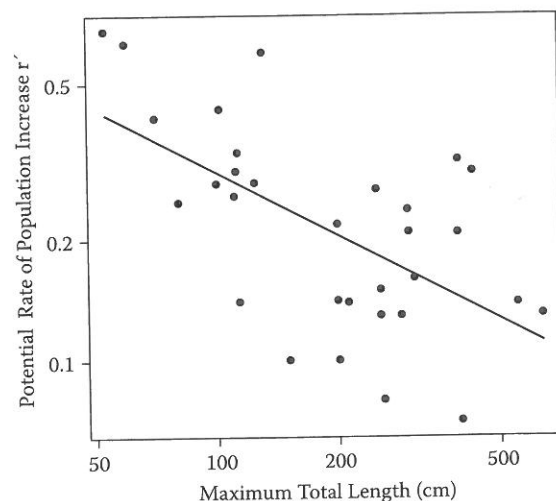


FIGURE 17.2

The potential rate of population increase is negatively related to maximum body size in elasmobranchs. Body size is measured as total length in centimeters. The tiger shark *Trianodon obesus* outlier was removed; however, this does not affect the overall result. The significance of the fit is improved but the estimated parameters change little. The line is a robust regression model, $r^2 = 0.34$, $F_{1,29} = 16.1$, $P < 0.001$, $\ln(r') = 0.54 + 0.533 \cdot \ln(\text{maximum length})$.

intrinsic rate of population increase and body size (see also Jensen 1996). Further analytical and empirical evidence suggests that smaller elasmobranch species may have greater resilience to fishing and/or rebound faster from depleted states than larger species (van der Elst 1979; Dulvy et al. 2000; Myers et al. 2007; Au, Smith, and Show 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 (S.E. Smith, Au, and Show 1998; Cortés 2002; Braccini, Gillanders, and Walker 2006b; Forrest and Walters, in press). 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, Stevens, and Graham 2002; Forrest and Walters, in press).

17.5 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 and Bradshaw 2006; Goodwin et al. 2006).^{*} 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 and 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, 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, Ketchen, and Beamish 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, Ketchen, and Beamish 1979; Brander 1981; Hoenig and Gruber 1990; Gruber, de Marignac, and Hoenig 2001; Gedamke et al. 2007).

Mechanisms for improved juvenile survival at lower population sizes include decreased territorial behavior, reduced competition for resources, and decreased vulnerability to predation or cannibalism at lower densities (Branstetter 1990; Walters and Korman 1999; Gruber, de Marignac, and Hoenig 2001; Rose et al. 2001; Heupel and Simpfendorfer 2002). 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, de Marignac, and Hoenig 2001; Heupel and Simpfendorfer 2002). At least one study has shown that juvenile sharks in nursery areas

^{*} 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.

may have difficulty capturing enough food to satisfy metabolic requirements, suggesting that food limitation may also be a source of juvenile mortality affected by density in some populations (Bush and Holland 2002).

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 and 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 and 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 and 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 Figure 17.3). 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, Mertz, and Fowlow 1997; Myers, Brown, and Barrowman 1999). The strength of density dependence can be measured as the compensation ratio (CR), 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, Brown, and Barrowman 1999). The equilibrium unfished juvenile survival rate (shown as line (ii) in Figure 17.3) can be calculated from life history data alone, as it occurs in the absence of fishing. It is given by the inverse of the equilibrium eggs per recruit summation across ages, i.e.,

$$\left(\sum_{a=1}^{amax} e^{-M(a-1)} f_a \right)^{-1}$$

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 being 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 that reflect the rate of change of population growth over a wide range of population densities (Hilborn and Walters 1992). The key challenge is that there are few such datasets available for chondrichthyans. We are aware of only five published stock-recruit relationships—all populations of spurdog or piked dogfish (*Squalus acanthias*) and the barndoor skate (da Silva 1993; Myers, Bridson, and Barrowman 1995; Gedamke et al. 2009). However,

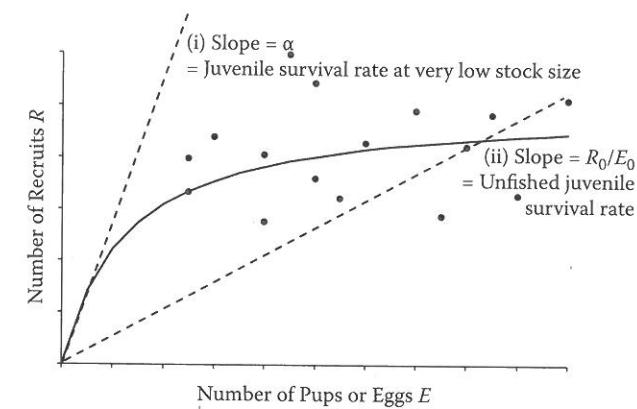


FIGURE 17.3

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, that is, 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 1993; Myers RA, Brown KG, Barrowman NJ (1999) Can J Fish Aquat Sci 56:2404–2419) 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 , where SPR_0 is unfished spawners per recruit.

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 and Gruber 1990; Gruber, de Marignac, and Hoenig 2001; Heupel and Simpfendorfer 2002). Gruber, de Marignac, and Hoenig (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 and Holt 1957; Walters and Korman 1999; Walters and Martell 2004). The equilibrium unfished juvenile survival rate for lemon sharks has been estimated from a demographic model to be 39% (Hoenig and 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).

In a recent simulation study, 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 and Walters, in press). Many of these species have been depleted by fishing (Graham, Andrew,

and Hodgson 2001), and are believed to have very low fecundity and late maturity (Daley, Stevens, and Graham 2002), resulting in mean estimates of unfished juvenile survival rates ranging from between around 0.05 to 0.2 for the different species (Forrest and Walters, in press). 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 20 and 5.

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, Brown, and Barrowman 1999; Goodwin et al. 2006). The low fecundities and high juvenile survival rates exhibited by many shark species have 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 and Gruber 1990; Cortés 2007; Gedamke et al. 2007). Also many smaller or more fecund shark species may have unfished juvenile survival rates more comparable with large teleosts (Au, Smith, and Show 2008) and, therefore, greater potential scope for compensatory effects that it would be unwise to ignore.

17.6 Comparative Demographic Studies of 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 and Gruber 1990; Au and Smith 1997; Cortés 1998, 2002, 2008; S.E. Smith, Au, and Show 1998; Heppell, Crowder, and Menzel 1999; McAllister, Pikitch, and Babcock 2001; Mollet and Cailliet 2002; Frisk, Miller, and Dulvy 2005; Gedamke et al. 2007; Au, Smith, and Show 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 and Smith 1997; Smith, Au, and Show 1998; Gedamke et al. 2007; Au, Smith, and Show 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: (1) life tables and (2) 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 r

to changes in individual parameters (Heppell, Crowder, and Menzel 1999; Simpfendorfer 2005a). They can therefore be used to identify which part of the life cycle has the greatest contribution to r and, therefore, where best to direct data-collection and management efforts (Heppell, Crowder, and Menzel 1999; Cortés 2002; Frisk, Miller, and Dulvy 2005; Braccini, Gillanders, and Walker 2006b). From these studies, the population growth rate appears to be relatively insensitive to fecundity (in agreement with Wood, Ketchen, and Beamish 1979; Brander 1981; Bonfil 1996). Instead, the most sensitive part of the life history tends to be the survival of juveniles to maturity rather than the survival of neonates (age 0 to 1), particularly for longer-lived sharks (Cortés 2002; Frisk, Miller, and Dulvy 2005; Kinney and Simpfendorfer 2009).

There are five advantages of demographic approaches: (1) they incorporate the best biological information available; (2) they can be used to develop biological characteristics compared to those obtained from alternative stock assessment approaches (e.g., aggregated surplus production models); (3) they allow examination of constraints imposed by life history traits; (4) they can be used to evaluate the effects of harvesting; and (5) they allow for species-specific assessment and management (Cortés 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 (Cortés 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, Pikitch, and Babcock 2001). For example, McAllister, Pikitch, and Babcock (2001) found that 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 (Heppell, Crowder, and Menzel 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 because the resulting estimate of r 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 (Cortés 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 and Smith 1997; Smith, Au, and Show 1998; Au, Smith, and Show 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, Smith, and Show 2008; Cortés 2008; Smith, Au, and Show 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, Au, and Show (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; that is, those with the lowest expected resilience to fishing were those that matured late.

17.7 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 and Walters, in press). 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 press) showed that the range of plausible hypotheses for 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 Figure 17.4, which shows the relationship between the CR and U_{MSY} for Harrison's dogshark (*Centrophorus harrissoni*) under three different ages at 50% first capture. Figure 17.4 illustrates that the maximum possible U_{MSY} 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 at around 18 years old). Application of this model to 12 species of Australian dogshark suggested that the maximum possible hypothesis for U_{MSY} for deepwater dogfishes is very low (5% to 10%), especially when individuals are caught at very young ages (Forrest and Walters, in press). 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 17.5). 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 knowledge of 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

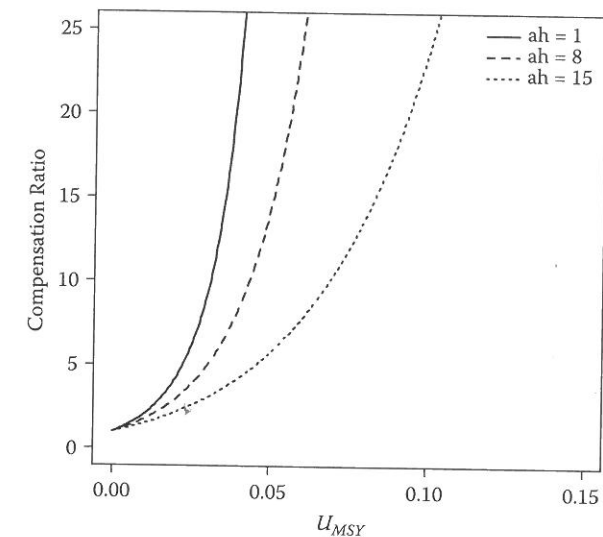
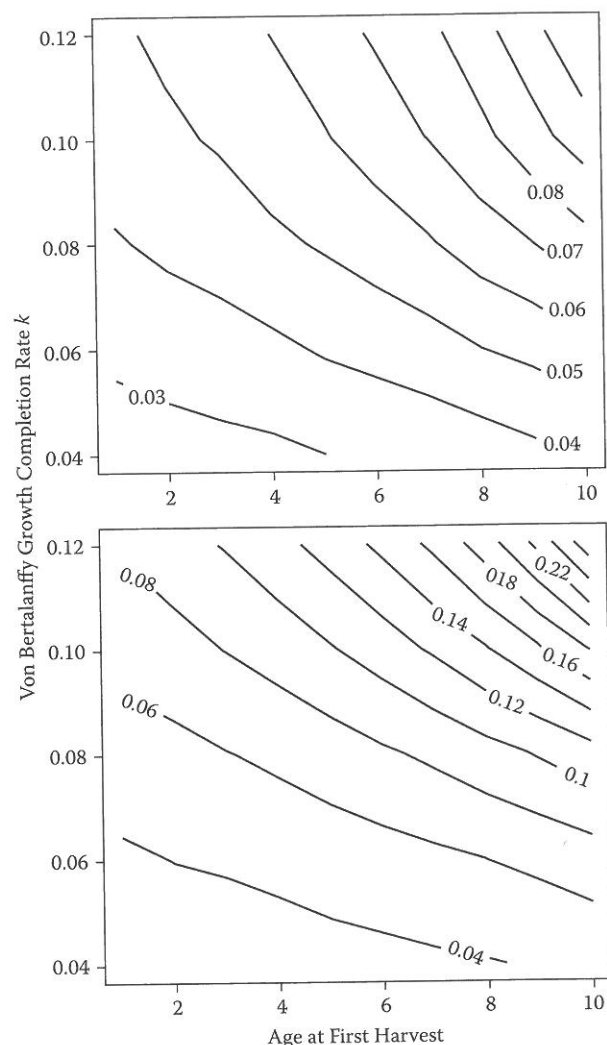


FIGURE 17.4

Curves showing relationship between the long-term sustainable catch rate U_{MSY} and the compensation ratio CR for Harrison's dogshark (*C. harrissoni*), under three hypothesized 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 press). 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 press). 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 age at entry to the fishery. All density-dependent mortality is therefore assumed to occur at age 0.

and selectivity data alone, this approach is appropriate for data-limited species. However, the method estimates the upper limit of U_{MSY} , not U_{MSY} itself, because 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 and 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 (T.I. 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, that is, as a threshold to fishing mortality that should not be exceeded (Mace 2001; Punt and Smith 2001). It represents a biologically valid threshold to exploitation that will prevent both growth and recruitment overfishing if successfully implemented (Sissenwine and Shepherd 1987; Mace 1994; R.M. Cook, Sinclair, and Stefansson 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.

**FIGURE 17.5**

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 k , for two fecundity scenarios—litter size of one (upper panel) and ten (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 17.3). Here we assume a maximum age of 30 years and an age at maturity of 10. (Adapted from Forrest RE, Walters CJ (in press) Can J Fish Aquat Sci. See their paper for detailed methods.)

17.8 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 similar arguments could apply to egg-laying species (e.g., Frisk, Miller, and Dulvy 2005; Gedamke et al. 2007). Over the last

decade, a number of innovative modeling approaches 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 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, Smith, and Show 2008). In coastal species, this may be achievable by creation of reserves where juveniles are known to occur, although a recent review has shown that protection of juvenile nursery areas alone will likely be insufficient and management plans must also include older age classes (Kinney and Simpfendorfer 2009). 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 [i.e., gauntlet fisheries (Prince 2005; Kinney and Simpfendorfer 2009)]. T.I. 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 only to be employed when there were legislative disincentives to catch sharks. Shark-repellent technologies, involving magnets or chemicals, may also be effective in the future (Gilman et al. 2008; Kaimmer and Stoner 2008).

A key lesson from recent modeling 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 shark species imply that even very strong compensatory responses in recruitment would not be enough to offset high harvest rates (Heppell, Crowder, and Menzel 1999; Forrest and Walters, in press). Therefore high harvests of low-productivity species achieved in the initial years of a fishery are analogous to the mining of a nonrenewable resource; that is, large biomass reserves are fished down but are not replaced at 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 (Ripley 1946; Holden 1979; Koslow and Tuck 2001). In fisheries where low-productivity species are bycatch (many of which catch chondrichthyans), it is an inevitability that these species simply cease to form a significant part of the catch or become extremely rare (Brander 1981; Dulvy et al. 2000; Graham, Andrew, and Hodgson 2001). In sum, 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.

17.9 Decline, Extirpation, and Extinction of Sharks and Rays

17.9.1 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 oceanic sharks and rays. Increasing scientific awareness of elasmobranch

vulnerability and high rates of fishing mortality are leading scientists to develop innovative methods to infer population trends. For example, a combination of sightings records, and commercial and recreational catch data was used to reconstruct nine time series of abundance indices for parts of the Mediterranean Sea (Ferretti et al. 2008). 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% and 99.99% relative to former abundance (Ferretti et al. 2008). 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 the 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 and 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).

17.9.2 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 and Pollard 2003). Its congeners, *C. zeehaani** and *C. moluccensis*, are listed as Data 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, Stevens, and Graham 2002; Forrest and Walters, in press). 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 one or two pups every two years (Daley, Stevens, and Graham 2002). Growth parameters are not available, but other dogsharks have been reported to grow very slowly (C.D. Wilson and Seki 1994; Braccini, Gillanders, and Walker 2006a; Irvine, Stevens, and Laurenson 2006). Like other dogsharks, *C. harrissoni* 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, Stevens, and Graham 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

* 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, Ebert, and Compagno 2008).

and 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 and 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 to 1977 and were not fully replicated until 20 years later in 1996 to 1997. This allowed for some striking comparisons of the abundance of many species (Andrew et al. 1997; Graham, Wood, and Andrew 1997; Graham, Andrew, and Hodgson 2001). In the 20 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, Andrew, and Hodgson 2001).

Commercial trawling on the slope began with two vessels in 1968, followed by rapid expansion of the fishery during the 1980s (Graham, Andrew, and Hodgson 2001). Most vessels fishing in dogshark habitat (300 to 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, Volkman, and Davenport 1990; Daley, Stevens, and Graham 2002). At its peak, the price obtained for *Centrophorus* livers was around \$7 per kilogram, although the price has fallen in recent years due to declining catches, improvements in the profitability of synthetic squalene, and other economic factors affecting the cosmetics industry (Daley, Stevens, and Graham 2002). Despite dogsharks being caught and marketed in southeastern Australia for more than three decades, large gaps exist in the catch and effort data that limit their usefulness for assessment purposes (Daley, Stevens, and Graham 2002; T.I. Walker and 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 assessments to determine threatened species status for three species of *Centrophorus* under consideration (DEWHA 2008). Recent work has placed credible limits on productivity parameters for these species, showing that extremely low fecundity, slow growth, and late maturity imply very low sustainable harvest rates (Forrest and Walters, in press). Demographic analyses of *Squalus* species have come to similar conclusions (Cortés 2002; Braccini, Gillanders, and Walker 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, that is, how much of the population is protected from fishing and how far outside the refuge do individuals move on foraging or mating excursions (Gerber and Heppell 2004; Gerber et al. 2005). Very little is known about Australian deepwater dogsharks in these respects, although a recently launched tagging program, in collaboration with the fishing industry, may provide some answers (R. Daley, CSIRO, personal communication).

17.9.3 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, Sadovy, and Reynolds 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. Numerous populations of sharks and rays have become locally extinct and have not recovered or returned to the area even after several decades (Dulvy, Pinnegar, and Reynolds 2009). 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 financial 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 this patrol boat was fitted with a forward-pointing, large-curved blade and the intention was to ram and kill the shark. On April 24, 1956, the newly modified vessel put to sea, whereupon it rammed and killed 34 basking sharks in Pachena Bay, Vancouver Island (Wallace and 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 to 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 and Gisborne 2006). A single gill-netter 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 and Keogh 1994; Wallace and 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 others were killed with harpoons, and by shooting and ramming.

“For many coastal residents, harassing basking sharks was simply a way of life in the 1950s and 1960s” (Wallace and 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 and 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 British Columbia. 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 extirpated population is currently being considered for legal protection under the Canadian Species at Risk Act.

17.9.4 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 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 Seas. 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) 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 (P.A. Walker and 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 (P.A. Walker and 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 southwest North Sea (Rogers and Ellis 2000; Ellis et al. 2005; Hunter et al. 2006). 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 (P.A. Walker and 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 northwest Atlantic shelf seas a large skate had also disappeared (Casey and 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, Miller, and Fogarty 2002; Kulka, Frank, and Simon 2002; Simon, Frank, and Kulka 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.

17.9.5 Regional Extinction of the Angel Shark

The angel shark (*Squatina squatina*) is a large benthic sit-and-wait predator, and in the northeast 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*) that 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 modern 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 northeast 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 program of *Squatina squatina* captured by recreational anglers was carried out in Tralee and Clew Bays on the Atlantic coast of western Ireland (Fitzmaurice and Green 2009). A total of 1107 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, and five recaptured in French waters, two 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 gillnets, 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 1987–1991, 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 and 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" (Irish Specimen Fish Committee 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 and Ellis 2000). Historically, moderate catch rates of between 2 (Irish Sea) and 19 (English Channel) individuals were captured per 24 hours of trawl survey between 1901 and 1907. More recently, none were caught in comparable modern surveys from 1989 to 1997, although the modern survey must undoubtedly have had higher fishing power (Rogers and 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 and 100 meters. However, a more recent and comprehensive trawl survey of the Balearic Islands, consisting of 143 hauls from 46 to 1713 meters 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 and Gibson 2007). Remaining hope for the continued existence of this species lies with unsurveyed habitats in the southern North African coast of the Mediterranean and possibly in the Canary Islands where there are reports that they have been observed by individuals while SCUBA diving (S. Fowler, personal communication). 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 and Gibson 2007).

17.9.6 Regional Extinctions of Guitarfishes and Sawfishes

In addition to angel shark and skates, other coastal shark species have declined 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 southwest Atlantic and has undergone severe declines >80% since 1986 following intensive exploitation by fisheries and is consequently listed as Critically Endangered (Lessa and 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 and 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 smalltooth sawfish (*P. pectinata*), are regionally extinct from the Mediterranean Sea and northeast Atlantic (S.F. Cook and Compagno 2000; Cavanagh and 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 to 1960s, but none were observed in more recent surveys in the 1970s and 1980s (F. Litvanov, personal communication). 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 undertaken at fisheries landing sites (Robillard and Seret 2006). Possibly the last remaining population of common and smalltooth sawfishes in the eastern Atlantic is found 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 and Seret 2006). However, only there have been only three catches of individuals of either common or smalltooth sawfishes 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 (*Pristis perotteti*) 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 U.S. recreational fishers in the 1930s to 1950s. Their distribution is currently over a small fraction (<5%) of their former range (National Marine Fisheries Service 2000). Large numbers were known from the Gulf of Mexico, but this species is locally extinct along the eastern U.S. coast, mainly due to incidental capture in commercial fisheries and recreational fisheries (National Marine Fisheries Service 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 U.S. Endangered Species Act (Simpfendorfer 2005b; Carlson, Osborne, and Schmidt 2007). Anglers in this region now return sawfishes alive (National Marine Fisheries Service 2000; Simpfendorfer 2005b).

17.10 Global Threat Status of Chondrichthyans

17.10.1 A Brief Summary of the 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 nongovernmental organizations worldwide—and includes many of the writers and readers of this book.

17.10.2 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 et al. 2008a). 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.

17.10.3 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 and 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 there are 80 known chondrichthyan species, 30 out of the 71 assessed species (42%) are Threatened (Critically Endangered, Endangered, Vulnerable) and over half of all species 42 (60%) are Threatened or Near Threatened. In the Northeast Atlantic all 116 chondrichthyan species were assessed and a similar 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 and 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 and Gibson 2007; Gibson et al. 2008). The true lack of knowledge may be underestimated because the majority of Australian and 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, White, and Pogonoski 2008a, 2008b; Last et al. 2008). 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 that 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). It should be borne in mind that species that are protected or Least Concern at local scales may be threatened by large-scale migrations and vulnerability to fisheries over wider spatial scales (Bonfil et al. 2005; Heithaus et al. 2007).

17.10.4 The Distribution of Threat Is Evolutionarily and Ecologically Nonrandom

The ecological and taxonomic distribution of threat across chondrichthyans also appears to be nonrandom. The most threatened ecological guild of species appears to be the

oceanic pelagic sharks, species that are found mainly 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, Lucifora, and Myers 2008). Their fins are removed, dried, and sold to southeast Asia to support the demand for shark fin soup. An analysis of the shark fin trade in Hong Kong, the main port of entry for shark fins, has estimated that an average of 38 million (range = 26 to 73 million) sharks are killed each year (Clarke et al. 2006; see Chapter 15). 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, Kehler, and Myers 2005) and appear consistent with the other available evidence such as the rise in estimated catches of pelagic sharks over the past 15 years (Clarke 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, Hoey, and Gallucci 2008).

In addition to the high rates of threat in oceanic pelagic sharks and deepwater sharks (Dulvy et al. 2008a; Garcia, Lucifora, and Myers 2008; Kyne and Simpfendorfer 2007), 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, for example, the Critically Endangered Bizant river shark (*Glyphis glyphis*; previously known as *Glyphis* sp. A) and Northern River shark (*Glyphis garricki*) (Compagno 1997; Thorburn and Morgan 2005; Last and Stevens 2009). The Northern river shark is known to science from only 18 individuals (Thorburn and 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 that runs through the center of Bangkok.

17.11 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; Bailey et al. 2009). Fishing is the main cause of marine population extinctions and threat in North American marine fishes (55% to 60%), followed closely by habitat loss (32% to 26%) (Musick et al. 2000; Dulvy, Sadovy, and Reynolds 2003; Reynolds et al. 2005). However there is increasing concern regarding the effect of climate change on marine communities (Brander 2006, 2007; Dulvy et al. 2009), particularly since climate

change can interact with the effects of fishing and habitat loss both in temperate and tropical systems (Blanchard et al. 2005; S.K. 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 (*Aulohalaelurus 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 and 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 and 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 Steller sea lions (*Eumetopias jubatus*) is attributed at least partially 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.

17.11.1 Climate Change, Fishing, and Extinction Risk in the Australian Grey Reef Shark

The grey nurse shark (*Carcharias taurus*) is globally Vulnerable and Critically Endangered in eastern Australia mainly due to recreational and commercial fishing, which is estimated to kill 12 sharks per year, and mortality from beach netting, which kills 2 to 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 and 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 (Figure 17.6). The most conservative Australian climate projections predict a 1°C sea surface temperature (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 50 years. This outcome was sensitive to the potential immigration rates,

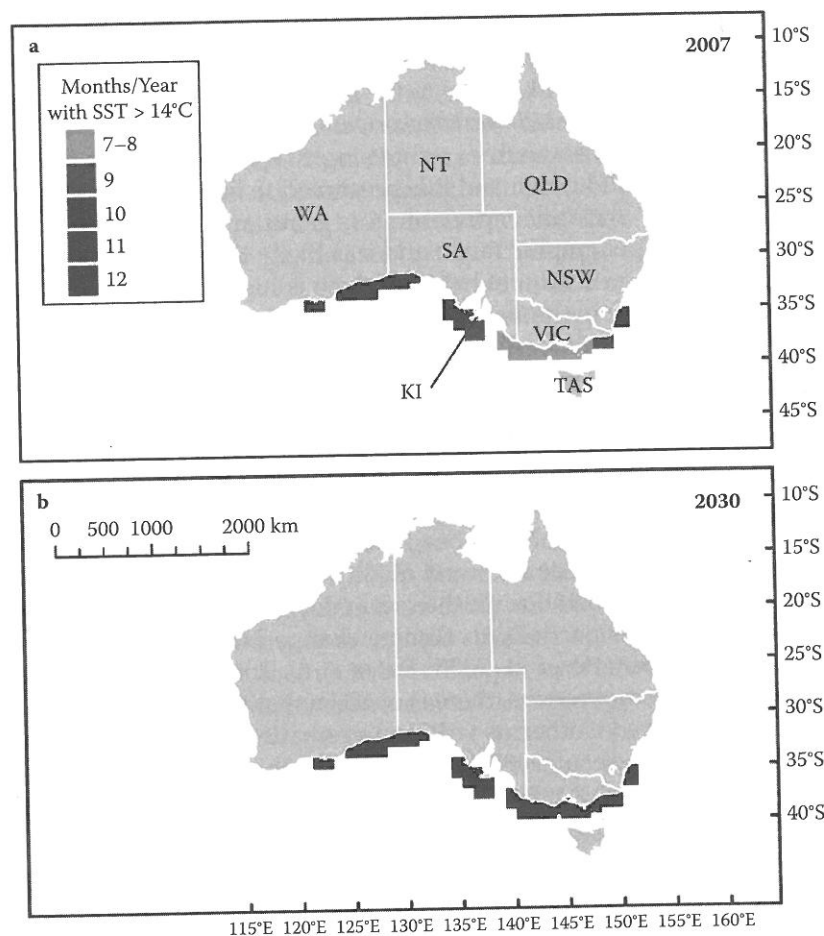


FIGURE 17.6

A color version of this figure follows page 336. 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 CJA, Peddemors VM, Mcauley RB, Harcourt RG (2008) Final Report to the Commonwealth of Australia, Department of the Environment, Water, Heritage and the Arts.)

the relative size of the western Australian population, and the local details of how climate change affects this species, which all remain unknown.

17.11.2 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 \times exposure) can be offset or mitigated against by the adaptive capacity of the system (Figure 17.7). In this study, exposure and sensitivity were defined

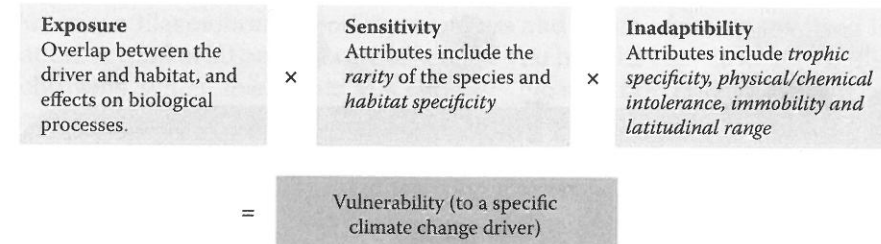


FIGURE 17.7

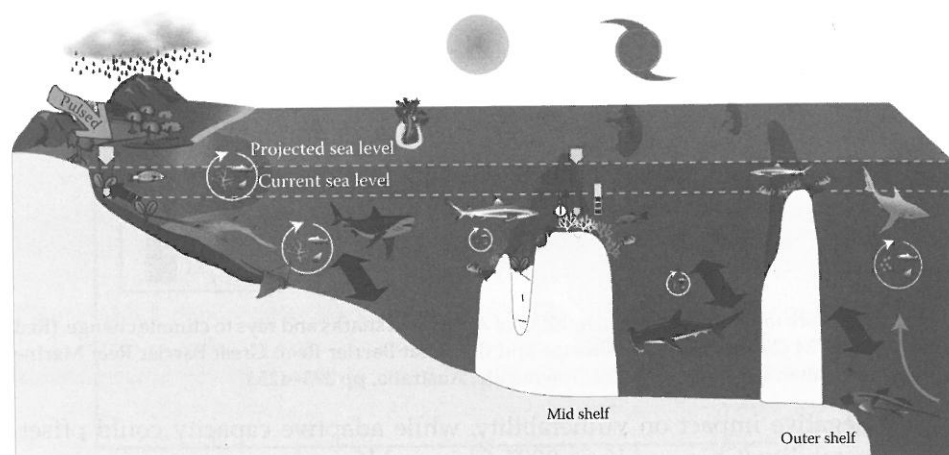
A conceptual framework to evaluate the vulnerability of Australian sharks and rays to climate change. (Redrawn from Chin A, Kyne PM (2007) In Climate Change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Australia, pp 393–425.)

as having a negative impact on vulnerability, while adaptive capacity could offset and decrease vulnerability (Chin and Kyne 2007; Chin and Kyne, in press).

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 (Figure 17.8). The indirect impacts were hypothesized to be mediated through the effects of climate change on habitat distribution and quality and prey availability (Chin and Kyne 2007).

The exposure of six chondrichthyan functional groups to climate change (Figure 17.8) 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. Ecological 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, for example, 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 and Kyne 2007).



Key climate change factors that affect shark and ray ecological groups

Freshwater/estuarine	Coastal/inshore	Reefal
<ul style="list-style-type: none"> Sea level rise and changed habitat distribution Productivity and prey abundance affected by runoff Storm disturbance of seagrass and loss of habitat for prey Increased temperatures, seagrass loss and loss of habitat for prey Light penetration to seagrass that supports prey 	<ul style="list-style-type: none"> Sea level rise and changed habitat distribution Productivity affected by runoff Storm disturbance of seagrass and loss of habitat for prey Increased temperatures, bleaching of inshore reefs and loss of habitat Currents that can affect migration and spawning of prey Light penetration to seagrass that supports prey 	<ul style="list-style-type: none"> Coral bleaching and physical disturbance affect habitat for prey Ocean acidification leading to loss of reef habitat Small effect of runoff on productivity Currents that can affect migration and spawning of prey Light penetration to benthic habitats that support prey Storm disturbance of seagrass and loss of habitat for prey
Shelf	Bathyal	Oceanic/pelagic
<ul style="list-style-type: none"> Small effect of runoff and upwelling on productivity Currents and water flow that can affect migration and spawning of prey Habitats potentially affected by temperature 	<ul style="list-style-type: none"> Productivity affected by upwelling Currents that can affect migration and spawning of prey 	<ul style="list-style-type: none"> Productivity affected by upwelling Currents that can affect migration and spawning of prey

FIGURE 17.8

Six functional groups of sharks and rays and the main climate change drivers that may affect the habitats and biological processes upon which they depend. (Redrawn from Chin A, Kyne PM (2007) In *Climate Change and the Great Barrier Reef*. Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Australia, pp 393–425.)

17.12 Prioritization for Action: Which Sharks and Rays Require Most Urgent Attention?

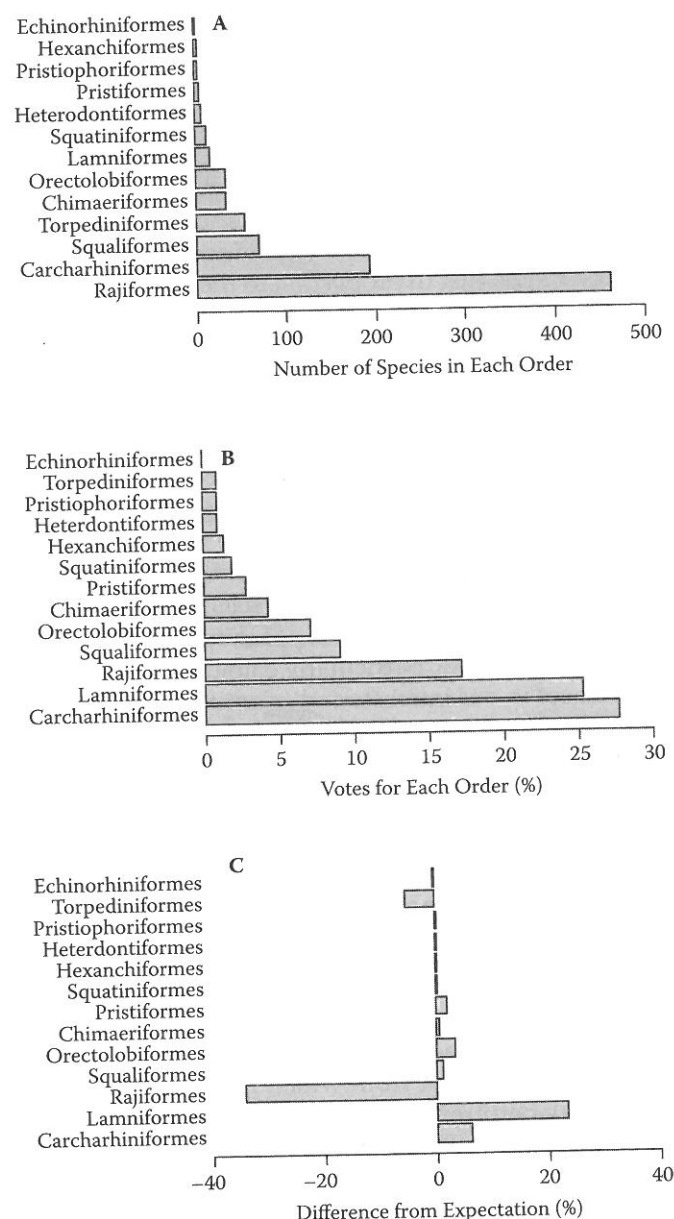
Many populations and species of shark, ray, and chimaera have either suffered local and regional extinction or are threatened and face an elevated risk of extinction, as measured by IUCN Red List status. By the time the first IUCN Red List assessment is published (anticipated in 2010) it is likely that 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! 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 American Elasmobranch Society 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 was 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 and 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. However, the findings are valid and provide insight into the taxonomic distribution in the interests and research capacity of chondrichthyan biologists (Figure 17.8). Four orders comprise almost 90% of all elasmobranchs: Rajiformes, Carcharhiniformes, Squaliformes, and Torpediniformes (Figure 17.9A). The most votes were cast for species in the Carcharhiniformes, Lamniformes, Squaliformes, and Rajiformes (Figure 17.9B). There were a greater proportion of votes for mackerel sharks (Lamniformes) and, to a lesser extent, ground sharks (Carcharhiniformes) than expected, given the proportion of species in these orders (Figure 17.9C). There was considerable underrepresentation of batoids, particularly skates (Rajiformes) and torpedo rays (Torpediniformes) (Figure 17.9C). Clearly, our motivations, values, 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.

17.13 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 and Ellis 2000), newspaper reports and sightings data (Ferretti et al. 2008; Sims 2008; McPherson and Myers 2009), 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, Miller, and Fogarty 2001) incorporating uncertainty in parameter estimates (McAllister, Pikitch, and Babcock 2001; Cortés 2002) or are robust to uncertainty in density dependence (Forrest et al. 2008; Forrest and Walters, in press) is remarkable. A new opportunity for assessing the risk of fishing on populations that incorporates less formal data and evidence includes the development of risk evaluation frameworks (Braccini, Gillanders, and Walker 2006b; A.D.M. Smith et

**FIGURE 17.9**

If you had a choice to save five chondrichthyan species, which five would you choose? A. The distribution of 903 elasmobranch species across the 13 taxonomic orders. B. The proportion of votes for species grouped by taxonomic order. C. The overrepresentation (positive values) or underrepresentation (negative values) of votes compared to the proportion of species in each order.

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 combined with limited capacity within the scientific community to tackle these gaps. We have little knowledge of the details 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 and Simpfendorfer 2007; see Chapter 2). It is unclear whether severe declines in part of the narrow depth range of some species have occurred throughout their geographic range. 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; however, the rate of description of new chondrichthyans is in the region of 20 to 50 species each year (Last 2007). Thus 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, and freshwater and deepwater chondrichthyans there are many more species than 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 that 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.

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