The Future Species of Anthropocene Seas

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Summary

Averting extinctions in an increasingly affluent and populated world is the challenge of our generation. The defining features of geological epochs are the mass turnover and extinction of species, genera, and families. The oceans of the Anthropocene epoch face a multitude of problems, competing demands, and diagnoses of solutions. Here, we argue the most pressing problem is the risk of losing populations and species in the Anthropocene. A key challenge is that our interpretation of species' status depends on what we care about and value. The prevailing mindset has been unbelieving of the possibility of marine extinctions; indeed, only the local extinction of sawfishes in South Africa has been documented in real time. Unseen and unmanaged, more than a hundred local, regional, and global extinctions have been detected retrospectively half a century after the fact. Looking to the future, we need to develop approaches to diagnose and manage marine species, recognizing a wider range of perspectives on what our future oceans could look like. To this end, we show that we can prioritize populations and species for intervention using simple rules-of-thumb grounded in evolutionary ecology. Finally, we conclude that a pressing, but overlooked, need is to protect species to avoid extinctions, thus securing the full portfolio of biodiversity.

Key words: Aichi target, bycatch, CITES, CMS, defaunation, life history, Marine Protected Area, Red List, trade-off, traits

Introduction

We know to the nearest minute when the last Passenger Pigeon died $(1 \text{ pm on } 1^{\text{st}})$ September 1914). While not all terrestrial extinctions can be so precisely timed, it is clear that identifying extinction is vastly more difficult in the oceans than on land. The demise of a marine species cannot be seen. This does not mean that marine extinctions do not occur, but rather that their detection is exceedingly difficult.

The recent global marine extinctions that have been detected mainly have been airbreathing mammals and birds, such as Caribbean Monk seal (*Neomonachus tropicalis*; McClenachan & Cooper 2008). As far as we know there has only been one global extinction of a fully marine fish – that of the Galapagos Damselfish (*Azurina eupalama*; Dulvy et al. 2009). Yet leading indicators of extinction risk caution that large numbers of other marine populations and species may disappear. For example, few people realize that two species of sawfishes were once found in in US waters – the last Largetooth Sawfish (*Pristis pristis*) sighting was in Texas in 1961, and it is 99% certain that this species is extinct from US waters (Fernandez-Carvalho et al. 2014). Only a fragmented population of Smalltooth Sawfish (*P. pectinata*) in Florida and the Bahamas remains, occupying less than 5% of its historic range (National Marine Fisheries Service 2009).

A survey of local and regional marine extinctions showed that 133 populations of a wide array of taxa ranging from algae through to mammals have disappeared, including 28 populations of sawfishes, skates, and angel sharks (Dulvy et al. 2003; Dulvy & Forrest 2010). Such local extinctions reflect the loss of behaviorally, morphologically, and ecologically distinct segments of biological population diversity (Dulvy et al. 2003). This

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** among-population within-species biocomplexity and response diversity underpins species resilience and ecosystem services (Hilborn et al. 2003; Anderson et al. 2013, 2015).

A countervailing view is that these local disappearances represent natural metapopulation patch-dynamics -- the winking out of edge-of-range populations that will eventually be rescued as abundance increases and hence range occupancy expands (Del Monte-Luna et al. 2007). Since the global survey of marine extinctions (Dulvy et al. 2003), each year that elapses without recolonization strengthens the case for the local extinction hypothesis. With very few exceptions, the volume of evidence confirming the former presence of species and their continued absence grows – with sawfishes being a case in point (Dulvy et al. 2016).

Marine species face multiple threats, but the overwhelming causes of extinction risk are overexploitation, habitat loss and degradation, and climate change (McClenachan et al. 2012). This problem is acute for intrinsically sensitive species with large geographic ranges, such as large-bodied predators, and high value species, for which intense fishing is driven by globalized trade demand (McClenachan et al. 2016). It is now obvious to many that oceans aren't inexhaustible and some marine species can be driven to collapse. Therefore, our challenge is to predict and prevent marine species' extinctions before the opportunity passes us by.

Our understanding of the status of our oceans and their inhabitants is deeply intertwined with our values and perceptions, which can differ based on education, upbringing, and experience (Mace et al. 2014; Mace & Hudson 1999). Our epistemology – our way of

knowing or understanding the world – shapes our view of conservation solutions and goals. Diverse perspectives on ocean conservation thus span fisheries-focused and conservation-focused worldviews (Salomon et al. 2011). A survey of shark and ray biologists found that people with measurable fisheries expertise viewed sustainable fisheries management as a viable goal (Simpfendorfer & Dulvy 2017); by contrast those with no prior fisheries experience eschewed fisheries solutions and viewed a complete ban on elasmobranch fishing as the ultimate conservation goal (Shiffman & Hammerschlag 2016). At a larger scale, international policy demands that we confront trade-offs on the fisheries-focused versus conservation-focused axis (Veitch et al. 2012). These trade-offs directly affect whether governments agree to policies affording species protection.

The signatory Parties of the Convention on Biological Diversity committed to meeting the 2020 Aichi targets, including Target 6, specifying that all fish and invertebrate stocks and aquatic plants are managed and harvested legally and sustainably and Target 11, mandating the prevention of species' extinctions and the sustained improvement of threatened species, and the related Sustainable Development Goal 14 to "Conserve and sustainably use the oceans, seas and marine resources for sustainable development" (Brooks et al. 2015). Accomplishing these targets requires consensus on what qualifies as sustainable, or conversely, threatened. How do we reach consensus regarding relative extinction threat? The IUCN (International Union for the Conservation of Nature) Red List assessments place species into one of three threatened categories (Critically Endangered – CR, Endangered – EN or Vulnerable VU), or classify them as Near Threatened – NT, Least Concern – LC, or Data Deficient – DD. In the worst case, assessors must determine if the species is Extinct – EN or Extinct in the Wild – EW

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** (IUCN 2014). This global standard has been widely accepted as the definitive index of extinction risk. To date, 7,563 marine fishes (Actinopterygii, Chondrichthyes & Sarcopterygii) have been assessed using IUCN Red List Categories and Criteria. Of these 20% (1,511) are Data Deficient (http://www.iucnredlist.org/search/link/5808c733 ca6b5fe0). By comparison only around 200 species have been fisheries assessed for commercial and recreational management (Ricard et al. 2011). Furthermore, there are few species-specific measures of fisheries catch – for example only around one-third of the global catch of chondrichthyans is identified to species level (Davidson et al. 2016). A major impediment to developing international conservation policy is meeting the shortfall in knowledge and monitoring of our seas.

Marine conservation in the Anthropocene needs to (i) avoid extinctions, (ii) recover threatened species, and (iii) sustain abundance of species that play functional roles or ecosystem services. Our focus here is on identifying, predicting, and preventing species extinctions. We show when and why marine extinctions have been unbelievable, unseen and unmanaged. Finally, we summarize the scientific and policy tools needed to prevent further declines.

Why is understanding mindsets important to understand the state of the seas?

Our ability to identify and predict potential marine extinctions will depend on our mindset. An evidentiary mindset has dominated the scientific discourse and policy surrounding the diagnosis of marine extinctions. The bar for accepting a hypothesized extinction is high, and false alarms – where a marine species is incorrectly declared extinct – are rare (Peterman and M'Gonigle 1992, Dayton 1998). There is an analogy to the Type I error rate in statistical hypothesis testing. Tolerance of Type I error is commonly set to an α of

0.05, meaning that the risk of accepting an alternative hypothesis – a false alarm – is 1 in 20. By contrast a precautionary mindset requires tolerating a greater risk of Type I error in order to minimize the risk of missing extinction – a true emergency, or Type II error. Failing to diagnose a marine extinction even when it has occurred is easily done, because our power (in statistical terms, $1 - \beta$) is limited by our ability to detect and measure population trajectories in the marine realm. We will show that the evidentiary mindset that has prevailed in marine management has led to Type II errors (Dayton 1998). To avoid further extinctions – and protect the future species of Anthropocene seas – tolerance of higher Type I error rates is required to minimize the risk of missing true emergencies.

1. Are marine extinctions are unbelievable?

Local extinctions have happened, but our mindset and capacity to detect them is limited. Thus marine extinctions can be overlooked, and in hindsight it is clear we failed to take a sufficiently precautionary approach to their prevention. There are two reasons why a species might be absent at a location within its expected geographic range: either it is now extinct or it is undetected by the census method or sampling gear. Very often historical records show what was caught where, on what date. Until the discovery of shifting baseline syndrome (Pauly 1995), there has been little consideration of what was not caught.

We saw a shifting baseline unfold in Fiji in 2002 while searching in vain for the Bumphead Parrotfish (*Bolbometopon muricatum*). Dulvy & Polunin (2004) asked islanders if they ever catch *kalia* (the indigenous name for this large parrotfish), to which they always answered affirmatively. Eventually we thought to ask, "when did you last catch *kalia*?" --

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** this question sparked discussion leading to the villagers' self-realization that this species had disappeared unnoticed and had not been caught for decades (Dulvy & Polunin 2004). Historians, archaeologists, palaeontologists, and now ecologists, use expedition reports, cookbook recipes, and other non-traditional sources to demonstrate the role of shifting baselines in masking species extinctions, mainly at local and regional scales (Jackson 1997, Wolff 2000, Levin and Dufault 2010, Thurstan et al. 2015).

This historical ecological information was always present – why have we been blind to it? Marine science and especially fisheries science has traditionally had a highly evidentiary mindset where the absence of data could not be considered as evidence of absence (Diamond 1987; del Monte-Luna et al. 2009). Following lessons from terrestrial conservation, those with a conservation-focused mindset have shifted toward the precautionary approach in risk assessments (IUCN 2014, page 20). However, those with the fisheries-focused mindset can still demand an evidentiary approach to identifying extinctions at local, regional, and global scales. The higher evidentiary bar required to enact conservation measures for exploited marine species is well documented (Cooke 2011). A review of terrestrial species listed under CITES (the Convention on International Trade in Endangered Species) revealed highly precautionary judgments: many terrestrial species were listed without qualifying under the criteria for extinction risk or trade (Cooke 2011). Until recently, few exploited marine fishes were listed despite abundant evidence showing the criteria were met – the result of the unrealistically high bar for evidence required to list marine fishes (Cooke 2011).

2. Marine extinctions are unseen

The evidentiary mindset has led to the false assumption that marine fishes are safe from

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** extinction. An increasing number of local and regional extinctions have proven this assumption wrong. Therefore, we next discuss the problem of identifying marine extinctions when taxonomic uncertainty and observation error lead to false negatives and positives.

A. The challenges of counting marine species extinctions

Marine extinctions have been underestimated because they are discovered long after the fact. A review of the status of 29 terrestrial and marine lineages reveals the proportion of threatened species tends to increase with assessment effort. In the best-studied lineages, the percentage of threatened species converges at around 20-25% in both terrestrial and marine realms (Webb & Mindel 2015). This is likely because the median lag between the local or regional extinctions of 133 marine populations and the reporting date was 55 years (Dulvy et al. 2003). Thus scientific knowledge and capacity are critical to understanding the state of the oceans and extinction risk (McClenachan et al. 2012; Miloslavich et al. 2016). Identifying extinctions requires accounting for uncertainty due to taxonomic uncertainty, observation error, and process error, all of which can generate false positives and false negatives.

A (i) Taxonomic uncertainty, false positives and negatives

False positives (Type I error) in extinction estimates can arise from updated taxonomy. For example, taxonomic reconsideration means that the 'extinct' Green Wrasse (*Anampses viridus*) in Mauritius never was a species, and hence there is one fewer global species extinction on the tally than reported in 2009 (Dulvy et al. 2009). The 'extinction' of this 'species' was first identified in an early summary of marine extinction risk (Roberts & Hawkins 1999). The authors stated, "The wrasse *Anampses viridis* was

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** described from Mauritius in 1839 (Randall 1972) but has not been seen in recent years despite intensive sampling. It may now be extinct, possibly a victim of sedimentation and nutrient pollution that has been degrading the reefs of Mauritius since the nineteenth century" (Hawkins et al. 2000). This paper, and subsequent propagation of this reported extinction (Dulvy et al. 2009; Dulvy et al. 2003) were based on a continual review of the evidence. Russell and Craig (2013) resolved this 180-year-old case of mistaken identity by showing that the Green Wrasse is actually the adult male terminal phase color form (and junior synonym) of the common species *A. caeruleopunctatus* Rüppell 1829.

Clearly, if the Green Wrasse was not a valid species then it should never have been declared extinct. Thus precautionary warning of the scale of the biodiversity crisis must be balanced against the cost of declaring a species extinct. Falsely categorizing a species as 'extinct' undermines the credibility of scientists in the public eye (Del Monte-Luna et al. 2007). The conservation status of each species must be reviewed and revised continually to account for retrospective changes in taxonomy and underscores the vital role of taxonomy in understanding the Anthropocene (Keith and Burgman 2004; Butchart et al. 2007).

A taxonomic false negative (Type II error) arises when one extinct or near extinct species turns out to be a species complex -- instead of one extinction, the tally increases by two or more. While not a global extinction, the Common Skate complex (*Dipturus batis* spp) provides a notable example. These large skates disappeared from the NE Atlantic shelf seas after decades of retained secondary take (bycatch; Rogers and Ellis 2000). Their depletion went unnoticed as their catch biomass was stabilized by a portfolio effect due to the serial depletion of smaller, more productive members of the skate assemblage

(Dulvy et al. 2000). Prescient and credible warnings of the disappearance of the largest 'species' (Brander 1981) went largely unheeded by managers (Holden 1992). By the early 1990s, Common Skate had all but disappeared from the North and Irish Seas (Walker and Hislop 1998). However, the expansion of the French deepwater trawl fleet to the West of Scotland led to new catches of Common Skate. This allowed savvy taxonomist, Samuel Igésias, to compare skate specimens side-by-side, revealing taxonomic identification issues. It turned out that this skate is in fact two species: a smaller species that reaches maturity at 120 cm, and another maturing at 200 cm. When 'common skate' landings from 2005 were reassigned to the correct species, less than 2% were of the larger species (Iglésias et al. 2010). Overlooking a new large vertebrate species is understandable in less well-studied areas of the world, but it was shocking when a new skate species was described on the doorstep of the UK, given the nation's long and proud natural history tradition (Dulvy & Reynolds 2009). This underscores the difficulty of 'seeing' marine extinctions. Furthermore, emerging taxonomic science suggests sibling species and complexes in marine fishes are more common than previously thought (Bickford et al. 2007).

A (ii) Observation error and Lazarus species

A false positive (Type II error) in extinction risk can also occur if insufficient effort has been expended to find the species presumed extinct (Diamond 1987). In the oceans, the broad scale and depth range of species' ranges, which may encompass several political jurisdictions, make this a persistent concern. Hence, the classification of extinctions requires a balance of two risks: (1) that a species is extinct and has gone undetected and unreported, and (2) that a Lazarus species is categorized as extinct at some scale when it is still present and, embarrassingly, is sighted at a later date (Keith and Burgman

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** 2004). For example, the Barndoor Skate (*D. laevis*) was declared near extinct based on its absence in Atlantic shelf trawl surveys (Casey & Myers 1998), yet significant numbers were subsequently discovered on the continental slope, preventing its listing under the US Endangered Species Act (Kulka et al. 2002).

In the tropics, observation and monitoring is a persistent challenge, even in nearshore waters. A recent paper suggested sawfishes may be extinct in Mexico (del Monte-Luna et al. 2009). This seemed plausible, as the last Largetooth Sawfish was landed in 1997 at Mujeres Island, Quintana Roo, Mexico. However, in 2016 the scientific world was stunned and relieved when a Largetooth Sawfish was reported in Veracruz, rewarding recent efforts to raise awareness, and providing hope that all is not lost for this species in the Gulf of Mexico (Bonfil, R Personal Communication).

In South Africa, by contrast, extensive long-term sampling bolsters our confidence that sawfishes are regionally extinct. South Africa has long time-series of elasmobranch abundance from netting programs designed to protect bathers from sharks. These data show that sawfishes were formerly common in KwaZulu-Natal, but that numbers declined (likely due to incidental mortality in trawl fisheries and degradation of juvenile habitat; (Everett et al. 2015). The last reported observation of any sawfish species in South Africa was in 1999 (Figure 1). While this fish was released alive, no sawfish has been recorded since, despite the presence of survey gear though 2012. Both sawfish case studies illustrate that our confidence in species' disappearance depends on 'observation error' – a rather prosaic term that encompasses awareness, search effort, and continued monitoring using appropriate methods and gears.

A (iii) False alarms depend on process error and risk tolerance

The likelihood of detecting meaningful declines – the precursor to raising the alarm on an impending extinction – depends on both observation error and process error. Observation error stems from our ability to measure population abundance or range, while process error is the inherent "noise" in population dynamics that comes from natural environmental variation. Both present challenges for detecting population trends: process error can increase the chance a population randomly winks out, while observation error limits our power to determine the true population trend. There is no way to entirely eliminate either risk and again, risk tolerance depends on the mindset of the audience. Fisheries-focused scientists might try to minimize false alarms (false positives), in case they lead to unnecessary fisheries closures. Conservation scientists fear false negatives because, at best, the species' chances of recovery are diminished and costly; at worst extinctions are irreversible (Mace & Hudson 1999; Matsuda et al. 1997; Reynolds and Mace 1999). In reality neither risk can be eliminated entirely without elevating the risk of the other error (Punt 2000). The choice of balancing risks may not just be a scientific one (Datyon 1998, Peterman and M'Gonigle 1992). However, science can contribute by quantifying when a precautionary approach (minimizing false negatives) is warranted, based on life-history traits and irreversibility of consequences.

Species' life history traits and population ecology affect the risk of false positives and negatives. Species with more variable dynamics are more likely to be misclassified in a recent study where both risks were estimated for the terrestrial species represented in the Global Population Dynamics database (Connors et al. 2014). This study determined the characteristics of the population time-series associated with two outcomes (i) incorrectly detecting a decline (Type I error) and (ii) failing to detect a true decline (Type

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** II error) (Connors et al. 2014). Shorter time-series (< 10 years) and shallow decline thresholds (< 30%) lead to a moderate frequency of false alarms (45%) and true emergencies (60%) for populations with variable population dynamics. For populations with more predictable dynamics due to stronger density-dependence, such as long-lived birds and exploited long-lived fishes, the frequency of false alarms and true emergencies was much lower (15 and 55% respectively for 10 year-long time-series) (Connors et al. 2014; Keith et al. 2015).

Only recently have we been able to quantify the risks and trade-offs between false negatives and positives (Figure 2; Porszt et al. 2012, d'Eon-Eggertson et al. 2015). If a strong fisheries-focused ethic prevailed – adverse to a false positive – one might set the triggering threshold (at which one might declare a species to be threatened) to a 90% decline (grey diamond; Figure 2A). This would guarantee zero false positives, but would result in a species being falsely classified as non-threatened at least 20% of the time (end of downward grey arrow; Figure 2C). If a strong conservation-focused ethic prevailed then one might lower the triggering threshold to 40% to eliminate the false negative risk of overlooking a threatened species (grey dot; Figure 2B). This would mean false positives in at least half of the status assessments (end of upward grey arrow; Figure 2C). Historically, the tendency has been to call for raised thresholds, indicating a fisheries-focused mindset. For example, in 1999 the American Fisheries Society proposed raising the threatened threshold from 70% to 99% decline to eliminate false positives. The empirically measured False Negative Rate (the rate of failing to detect true emergencies) of this decision was 62% when AFS criteria were applied to EU fish stocks (Dulvy et al. 2005).

There are profound conservation costs to the fisheries-focused mindset. The lack of recognition of the tradeoff in these risks has led to "too little, too late" conservation measures, as well as extreme management. *Too little, too late* occurred in South Africa, where sawfishes were protected only two years before the last sawfish capture in 1999 (Fig. 1) (Everett et al. 2015). By contrast, extreme management measures occurred in EU fisheries, but only after decades of alarms raised by fisheries scientists were ignored, including the disappearance of the Common Skate (Brander 1981) and the very steep declines of Spiny Dogfish (called the Spurdog in Europe; *Squalus acanthias*) (Hammond & Ellis 2005; Holden 1974). Instead of gradually reducing take of these species using the quota management system, a zero Allowable Catch was set prohibiting take (Clarke 2009). Hence, these species went from no management to prohibition almost overnight – a huge management challenge for a bycatch species! This type of management is *too much, too late.* While such extreme measures could be appropriate in some cases, successful marine conservation requires policy makers, fisheries scientists, and conservation biologists to proactively navigate a middle road.

B. Predicting species' risk of extinction

Until now we have focused on the challenges and trade-offs that come with identifying extinctions in the ocean. How then can one identify, or even better, predict species' risk of extinction before it causes a management crisis? In other words, what actions can be taken to prevent both *too little, too late,* and heavy-handed *too much, too late* measures?

The risk of a population or species extinction is a function of intrinsic sensitivity (biology) and exposure to an extrinsic threatening process. This risk can be offset by a species adaptive capacity (Turner et al. 2003; Allison et al. 2009), whereby it can mitigate its

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** sensitivity or exposure. This provides a conceptual framework that has great utility for framing species risk of decline and extinction:

Vulnerability ∝ Sensitivity + Exposure Adaptive capacity

For our purposes adaptive capacity might be an evolutionary response that rescues species by allowing adaptation to climate change (Bell & Gonzalez 2009) or to new habitats. While such responses are possible for organisms with faster generation times, evolutionary rescue will be too slow for large-bodied species currently at risk of disappearing within one or two generations (Vander Wal et al. 2013). Therefore, we do not consider evolutionary adaptive capacity further, although it remains a pertinent issue.

Vulnerability is the combination of intrinsic sensitivity and exposure to an extrinsic threatening process. A large body size, or a slow life history *per se* will not mean that a species is necessarily at greater risk, unless the species is exposed to a threat. Many large-bodied marine fishes are at risk because they are heavily fished; many smallbodied freshwater species are at risk from habitat degradation and loss because they have small geographic ranges (Arthington et al. 2016). Small-bodied freshwater fishes, however, aren't necessarily at risk from overfishing (Reynolds et al. 2005). In birds, the largest species are at risk from overhunting and the smaller species are threatened by habitat degradation (Bennett & Owens 1997). A species' response to one threat does not indicate its response or co-tolerance to other threatening processes (Isaac and Cowlishaw 2004; Vinebrooke et al. 2004; Graham et al. 2011); in addition where more than one threatening process is operating, cumulative impacts are likely (Selkoe et al.

B (i) Trait-based predictions of extinction risk

By comparison to habitat loss, our understanding of the importance of hunting and fishing mortality is hindered by a lack of data on population-level mortality (Reynolds 2003; Cowlishaw et al. 2009). Opportunities to understand mortality in marine species come from stock assessments, which in some cases estimate natural mortality and fishing mortality rates (*F*), as well as high-value species for which exposure to trade-driven extinction risk can be indexed by their market value (McClenachan et al. 2016). These species provide the best evidence for the interaction of exposure and sensitivity.

Traits related to exposure

Fish behavior, particularly aggregation, can increase exposure by increasing catchability. Reef fishes that form spawning aggregations, salmon that return to natal rivers to spawn, and migratory fishes that follow their food sources are predictably concentrated in a small area. Indeed, many of the world's most fished species (by weight) such as cod, pollock, mackerel, and herring migrate or aggregate to spawn, increasing their catchability (FAO 2016). In a survey of exploited marine fishes, Sadovy de Mitcheson (2016) showed that global IUCN Red List status depends on (1) if the spawning season is short or long (indicating how predictably concentrated they are in time) and (2) if they aggregate to spawn (Figure 3). The role of behavior in increasing exposure to threats like fishing is even more obvious when comparing two closely related, large-bodied Caribbean groupers: Nassau Grouper *Epinephelus striatus* and Red Grouper *E. morio.* Historically, Nassau Grouper formed brief, large, and predictable aggregations (many of which have Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** now vanished), while populations of Red Grouper remain viable in the Caribbean despite an ongoing fishery (Sadovy de Mitcheson 2016). There is little doubt that this difference is due to the increased exposure of Nassau Grouper to fishing during their spawning aggregations. Thus behavior plays a strong role in determining whether fishes are at risk of overexploitation and extinction.

Traits related to sensitivity

We now turn to the traits that predict intrinsic sensitivity, temporarily setting aside the issue of exposure. When fishing mortality is controlled for statistically, large-bodied species are the most likely to have declined steeply in temperate and coral-reef fish assemblages (Dulvy et al. 2000; 2004; Jennings et al. 1998; 1999). However, when analyzing the response of 21 tuna populations to fishing, body size was slightly less important than time-related or 'speed-of-life' traits such as growth rate or age at maturity (Juan-Jordá et al. 2013). Furthermore, environmental temperature sets the speed of life such that species with faster generation times are found in warmer habitats (Munch & Salinas 2009). The relationship between temperature and speed-of-life suggests that species in cooler habitats and higher latitudes are intrinsically more prone to decline for a given level of mortality. This hypothesis is borne out in tunas: species with slower life histories such as the cold-water temperate bluefin tunas and deeper, tropical Bigeye Tuna (*Thunnus obesus*) are largely overfished (Collette et al. 2011; Juan Jorda et al. 2011, 2015), whereas the tropical Yellowfin Tuna (*Thunnus albacares*) are more likely to be sustainable, despite their large body size. These patterns reveal an opportunity to understand the geographic patterning of intrinsic sensitivity. The connection between temperature and time-related traits suggests that biogeography provides the template for life-history evolution (Southwood 1977; Juan Jorda et al. 2013). A challenge is that

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** time-related traits – growth and maturation rates – can be more difficult to measure than morphological traits such as body size.

So far we have discussed of life histories in simplistic phenomenological terms of sizeand time-related traits. We need a deeper understanding of life history sensitivity and how it relates to population regulation if we are to evaluate and justify these simple 'ruleof-thumb' approaches. Variation in birth and death rates, which depend on life history, influences both the growth rate and the *compensatory capacity* of a population (its ability to compensate for additional mortality such as fishing; Kindsvater et al. 2016). Naturally, persistence of any population or species depends on the processes that regulate its population dynamics. Regulation arises from a combination of top-down processes, such as predation, and bottom-up processes, such as resources. Regulatory processes that depend on density can buffer populations against disturbance (the underlying principle enabling sustainable fisheries take). However, scientists have long understood that aquatic species have evolved multiple strategies for coping with their environment (Winemiller 2005), which affects their density-dependent regulation.

To connect these insights to compensatory capacity, in Fig. 4 we introduce a conceptual framework to categorize species based on our knowledge of life history evolution. We categorize species as Precocial, Opportunistic, Survivor, and Episodic (which we refer to as the POSE framework; Kindsvater et al. 2016). Species such as forage fish mature early and capitalize on favorable conditions, attempting to reproduce before the environment changes (we call this an Opportunistic strategy). Alternatively, Episodic species such as cod grow slowly, mature late, and live a long time, allowing for a bethedging reproductive strategy. These species reproduce for many years, waiting for

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** favorable environmental conditions that will allow their progeny to survive. Both Opportunistic and Episodic species have relatively high fecundity, producing thousands

if not millions of progeny over their lifetime. Of the two, the slow-growing late-maturing Episodic species have lower compensatory capacity (Kindsvater et al. 2016), and they are much more likely to be overfished (Dulvy et al. 2014, Juan-Jorda et al. 2015). The relationship between fecundity and intrinsic sensitivity to extinction is weak (Dulvy et al. 2003, Hutchings 2012), because populations of highly fecund species (Episodic and Opportunistic) are more likely to have strong density-independent juvenile mortality (reviewed in Kindsvater et al. 2016).

At the other end of the spectrum are species that have evolved under strong densitydependent regulation. Density-dependent competition among juveniles selects for large relative offspring size when there is a size advantage among competitors. For example, elasmobranchs such as skates are Survivors – they mature late and grow large. Seahorses are Precocial, meaning they have extreme parental investment in offspring, which allows them to mature early. These clades have similar fecundities, despite differences in body size. Historically, it has been unclear whether skates or seahorses are most vulnerable to overfishing. Using simulations that factored in the different dimensions of each of these life histories, in Kindsvater et al. (2016) we found that for the same level of fishing mortality, seahorses have a much greater intrinsic capacity to compensate than skates (setting aside the fact that seahorses may have elevated exposure to fishing mortality due to their habitat). In fact, large relative offspring size, which enables early maturation in Precocial species, confers the strongest compensatory capacity of any POSE category. Yet policy and management do not necessarily reflect this difference in sensitivity. Because declines in heavily traded charismatic seahorse

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** species are more visible, their protection has received global support at CITES and they were listed under Appendix II before any other marine fish (Vincent et al. 2014). By stark contrast, measures to protect elasmobranchs have been absent or implemented only after their local extinction, as explained above. We shouldn't protect seahorses less, but we should protect skates.

These deeper insights connecting life history and sensitivity are essential for conserving marine species where little is known about their population biology. For example, we know very little about the population sizes, movement, and behavior of most sea turtle species. Much of the initial efforts to conserve sea turtles focused on improving survival of hatchlings, as they are the life history stage that humans can see. Yet from Figure 4 we can infer that sea turtles are Episodic species, as they mature late, yet produce hundreds or thousands of eggs in their lifetime. They have evolved under conditions with extremely low juvenile survival, while adult survival must be relatively high. Reducing incidental take of adult turtles was recognized to have more profound effect on their conservation in the long term (Crouse et al. 1993), and today there has been a large effort to reduce adult bycatch. This example underscores that the contributions of different life stages to population dynamics is a key component of optimizing conservation and management efforts.

How does the POSE framework relate to species conservation status? In Fig. 5 we categorize species into POSE categories according to their age at maturation and fecundity. Age at maturation is inversely related to adult mortality rates, as delayed maturation is an indicator of low natural mortality (Kindsvater et al. 2016). Fecundity is related to juvenile survival; species with lower fecundity tend to have greater survival.

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** We can then add the IUCN Red List Status, where available. The analysis in Fig. 5 highlights the disparity between life-history-driven sensitivity and conservation evaluation and status. Many, but not all Episodic species are Least Concern, even though they are both intrinsically sensitive and fished (meaning they are exposed), yet others are Endangered. The Extinct and Extinct in the Wild species in this analysis are both European whitefish endemic to estuaries with small natural ranges. Finally, many heavily fished species are Not Evaluated (NE), despite the availability of data from fisheries. We can infer that exposure is the missing link that can explain much of the variation in Red List Status.

With this framework in mind, we can return to the question of determining exposure. Accessibility to humans, proximity to centers of human population density, contributes to exposure to anthropogenic threats (Jennings and Polunin 1995). Marine species with the highest exposure are highly catchable species in shallow, nearshore habitat, such as the Bumphead Parrotfish in Fiji. Large-bodied species in these habitats are the strongest candidates for elevated risk (Dulvy & Polunin 2004). Species in inaccessible habitats, such as the deep ocean, far from port, will be protected regardless of their life history (Dulvy et al. 2014).

B (ii) Quantitative predictions of extinction risk

It is one thing to explain declines *post-hoc*; it is another to predict extinction risk *a priori*. While many paper titles claim to 'predict' risk, in reality they are fitting trait models to 'explain' risk. True prediction is an entirely different beast that again involves balancing the risks of true and false positives (Figure 2). There are two kinds of prediction: within and beyond sample prediction. The former is a form of cross-validation that simply

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** measures accuracy or the degree to which a model fit to a subset of data can explain the remaining data (Anderson et al. 2011). In the quest to assess the IUCN Red List Status of the world's animals, plants, and fungi, beyond-sample prediction is most useful. This is because the primary obstacle to the completion of this quest is the large number of Data Deficient (DD) species for which there are insufficient data to assess whether they are threatened or not, much less the specific IUCN Red List category.

The simplest approach to this challenge is to model the binomial probability that a species is safe (Least Concern = 0) versus threatened (CR, EN or VU = 1) in a mixedeffects modeling framework (Dulvy et al. 2014; Field et al. 2009). Using linear models incorporating maximum body size and geographic distribution traits (representing exposure to fishing mortality), Dulvy et al. (2014) estimated that 68 of 396 DD chondrichthyan species are potentially threatened. The prediction accuracy can be calculated as the Area Under the Curve (AUC) of the relationship between false positive rates (α or p-value) and true positive rates (β). The estimated AUC were in the range of 77% with moderate explanatory power $R^2 = 0.3$, which is a good start but better statistical tools are available (Dulvy et al. 2014).

Two more-sophisticated approaches hold promise for predicting IUCN status of Data Deficient species, but require considerably more data. The 'simplest' requires a phylogeny and distribution maps of all species – including the DD species. The premise of the approach is that sensitivity-related traits are phylogenetically clustered, whereas exposure is likely to be geographically clustered. By this reasoning, extinction risk depends on the combination of phylogenetic and geographic proximity. Data Deficient species that are related to and geographically near to Critically Endangered species are Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** also likely to be in the same IUCN category. Using this approach, scientists found that 331 of the 483 Data Deficient mammals might be in one of the IUCN threat categories; AUC was 0.9 and R^2 = 0.4 (Jetz & Freckleton 2014).

In the second approach, new hierarchical statistical tools offer the opportunity to spread information from data-rich to Data Deficient taxa according to their shared characteristics, such as evolutionary lineage. This is most useful when quantifying population trajectories (i.e., fitting time-series models) in the case where *some* members of a given clade are data-rich, meaning they are assessed regularly. These statistical methods can then fit model parameters from both direct information (e.g., Bayesian priors based on life history traits) and indirect information (e.g., abundance indices that are underpinned by interacting demographic processes; New et al. 2012, Matthiopoulos et al. 2014). Rather than fitting models to each species separately, data from multiple species may be used simultaneously (hierarchically), accounting for similarity among species based on their phylogeny, habitat, or geography (Maunder et al. 2015). This approach can capture dimensions of sensitivity and exposure that are not obvious to the naked eye, potentially predicting the risk of extinction of marine species that have so far escaped assessment. By leveraging multiple types of evolutionary, biogeographic, and socio-economic information to predict species' extinction risk, this approach offers the chance to predict the looming threat of extinction in a more comprehensive way than has ever been accomplished.

3. Marine extinctions are unmanaged

Much of the attention on the state of the world's fishes are focused on large-scale industrial fisheries and their effects on species that live in the waters of wealthy, Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** developed nations, where there is increasing evidence of fishery sustainability in developed nations (Branch et al. 2011; Worm et al. 2009). Yet small-scale fisheries – an ambiguous category that can also include aquaculture – are far more important resources for the food security and livelihoods of developing nations (FAO 2016). Half of the world's fish, and 98 out of every 100 fishers, are part of small-scale fisheries that are far removed from national or global fisheries governance (FAO 2016). Recent surveys have documented widespread unsustainability of fisheries of this type (Costello et al. 2012; Davidson et al. 2016).

A. Preventing species' extinctions

The primary tool we have to prevent extinction is a <u>focus</u> on saving species – this may sound circular but the reality is that most marine conservation efforts do not have the explicit aim of saving species! With few exceptions, many current conservation actions improve habitat quality or protect locations, but there has been little policy action to ensure that marine species do not go extinct (Redford et al. 2013). For example, the rapid rise in super-sized marine protected areas is viewed as a conservation win (Lubchenco & Grorud-Colvert 2015), but it is far from clear what the specific species conservation objectives are or which species will benefit (Edgar 2011, Wilson 2015). A focus on ecosystem function and services is important, but it does not save species. Ecosystem services are driven by numerical abundance and biomass and hence the most abundant species, including invasive species, provide the bulk of function and services (Solan et al. 2004). While monetizing ecosystems and biodiversity will unlock greater awareness of their value to governments, this does little to directly prevent extinction. To reiterate, to avoid extinctions we actually need to focus on saving species.

A focus on meeting the area coverage target of Marine Protected Areas is important but this focus *alone* currently does not save species. We are currently protecting the areas left over after industries have been allocated fishing and other extraction rights, which distracts from protected areas that are most valuable to biodiversity (Barnes 2015; Devillers et al. 2015). The phenomenon of protecting areas, not saving species, has been described as the appearance that the naked emperor has clothes (Pressey 2013). This is nowhere more prevalent than in the creation of "shark sanctuaries" that have borne few measurable benefits for sharks (Davidson 2012). Almost one-third of the world's marine protected areas were designated for sharks by 2015, yet they do little to save those species most at risk of extinction – only 10 imperiled sharks and rays had more then 10% of their geographic range within a protected area (Davidson and Dulvy 2017). The solution is to focus MPA expansion toward the outcome of avoiding extinctions (Aichi target 11), which would involve protecting those places that harbor the most endangered species, especially their most sensitive life stages (Devitt et al. 2015). Ideally the next wave of MPAs and associated CBD targets out to 2030 will capture a significant fraction of the remaining range of the most endangered marine species and set appropriate goals for their recovery (Venter et al. 2014).

A focus on fisheries sustainability is important for food security and ecosystem services (but it does not necessarily save species). We have seen local and regional extinction can happen both as a result of directed fishing (as in the case of Nassau Grouper), or due to incidental take (as in the case of Common Skate or South African sawfishes). A primary challenge is to minimize the mortality of threatened species occasionally taken alongside more productive target species. Minimizing incidental take for endangered species through improved bycatch management is one of the most effective ways for

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** policy changes to prevent extinction. For example, the once-controversial 1994 law banning gillnets in Florida proved to be crucial in preventing the local extinction of the USA's remaining sawfish species, the Smalltooth Sawfish (Adams 2000). Similar legislation in 1990 in California protected the Pacific Angelshark (*Squatina californica*), now one of the few angelshark populations that is not Threatened according to IUCN criteria (its Atlantic counterpart, *S. squatina*, was once found throughout the North Sea and eastern Atlantic but has been reduced to an isolated population in the Canary Islands) (Ferretti et al. 2015).

Serious issues in bycatch management continue to threaten vulnerable marine species. For example, Yellowfin Tuna managed by the Western Central Pacific Fisheries Council are MSC certified, yet the Oceanic Whitetip Shark (*Carcharhinus longimanus*), retained as valuable secondary catch in the fishery, is unmanaged and declining at a rate of 5% per year (Clarke et al. 2013). Often, insufficient data (and an evidentiary mindset) impedes effective regulation of bycatch. Again, we need for an alternative method of assessment and a precautionary approach to preventing species extinctions. As a last resort, CITES listings have been used to force trade regulations of bycaught species. However, a diagnosis or listing does not mean action will be taken to recover populations to sustainable levels. Instead of waiting until a species qualifies for CITES listing, we need preventative action.

Conclusion

The global future of marine species depends on our ability to pick and chose what species we eat, instead of indiscriminately scooping up whatever is available. Early maturing, fast growing species hold the greatest promise for productive fisheries. Our

first challenge in protecting threatened species is the identification and assessment of those at greatest risk. The next step is cooperation between parties with conservationfocused and fisheries-focused perspectives (Figure 2C). Some progress in this direction has been made: fisheries agencies are no longer the sole custodians of ocean management; and Departments of Environment are expanding beyond terrestrial issues to confront marine conservation issues. The mandates of Multilateral Environmental Agreements, such as CITES and Convention of Migratory Species (CMS), and the need to deliver on the Convention of Biological Diversity's Aichi targets are measureable progress. Their broader remit and societal engagement has the power to drive fisheries improvements that can also help secure ecosystem services, alleviate poverty, and promote climate change adaptation, while also ensuring that species recover, rather than go extinct.

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Figure 1. Sawfish catch-per-unit-effort from South African bather nets from 1964 to 2012. Redrawn from Everett et al. (2015). Inset is the rostrum, probably of the Largetooth Sawfish *Pristis pristis*, of the last known captive South African sawfish, which was housed in the uShaka marine World, Durban (Photo credit Colin A. Simpfendorfer).

Figure 2. Choice of triggering threshold depends on the balance of two risks. (A) False Positive Rate is the risk that a species is listed as threatened when it is sustainably fished. (B) False Negative Rate is the risk that a species is classified as Least Concern when it is overfished and headed toward extinction. (C) A goldilocks point where both risks are equal, but the choice of threshold may be asymmetric depending on the relative costs and benefits of each risk. Extinction is forever; hence it could be argued that the 50% threshold (zero FNR, minimal FPR) should be used (redrawn from Figure S5 d'Eon-Eggertson et al. 2014)

Figure 3. Thirty-six species of fished aggregating and non-aggregating fishes. Shade indicates IUCN Red List Status. Size of point indicates body size: small points correspond to fish of less than 100 cm TL and large points are greater than 100 cm TL. Redrawn from Sadovy de Mitcheson (2016).

Figure 4. The POSE framework. Relative adult and juvenile mortality risk select for differences in age at maturation, offspring size, and number. We compared each species' ability to compensate for the same level of fishing mortality with simulation models of population dynamics, parameterized with demographic data from a representative

Please cite as: **Dulvy NK and Kindsvater HK. (2017) The Future Species of Anthropocene Seas. pp. 39-64 in M.R. Poe editor.** *Conservation for the Anthropocene Ocean.* **Academic Press.** species in each category (gray silhouettes). These analyses revealed that compensatory capacity increases with adult mortality (Redrawn from Kindsvater et al. 2016).

Figure 5. The relationship between life history and POSE category for 24 clades of marine fishes representing 204 species. The natural log of fecundity (x-axis) is assumed to correlated with juvenile mortality. The inverse of the age at maturity, standardized between 0 and 1, reflects adult mortality risk, as increased adult mortality leads to earlier maturation. Each point represents a species; color indicates most recent IUCN Red List status and character correspond to clade. Teleost life history data are species' means from FishBase (Froese and Pauly 2016) and were collated using rfishbase (Boettiger et al. 2012). Chondrichthyan life history data and all Red List status data are from the IUCN Red List website (www.iucnredlist.org; accessed 20 February 2016).

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