



Future Directions in *Eubalaena* spp.: Comparative Research to Inform Conservation

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All three extant right whales [*Eubalaena australis* (Southern; SRW), *glacialis* (North Atlantic; NARW), and *japonica* (North Pacific; NPRW)] were heavily exploited, and the status of the two northern hemisphere species remains precarious. Recently, limited gains made by the NARW have been reversed and urgent changes to management approaches are needed if extinction is to be averted. By contrast, some SRW populations are recovering. Given their close phylogenetic relationship, morphological, demographic, and ecological similarities, the contrasting recovery rates between populations and species provide an opportunity to apply a comparative approach to inform the differences in recovery as follows. (1) Recovery: All right whale species were internationally protected in 1931, but NARW, eastern NPRW and some SRW populations have barely recovered from whaling, while others are doing so at maximal rates. Are these differences a legacy of extreme depletion (e.g., loss of genetic diversity and cultural knowledge) or primarily due to anthropogenic factors (e.g., high mortality from ship strike and fisheries entanglement)? If modern anthropogenic threats are not affecting remote SRW populations, can these serve as baseline populations for comparison with NARW and NPRW? (2) Linking individuals to population-level responses: In wild mammals, strong links exist between reproductive indices and environmental conditions within the context of life-history strategies. Individual identification of whales provides the ability to track survival, reproduction and other demographic parameters, and their population-level consequences, providing the tools with which to uncover these links. Robust life-history analyses are now available for NARW and several SRW populations, linking demography with environmental conditions, providing the potential for teasing out important influencing factors. (3) Adapting to shifting resources: Recent reproductive declines in NARW appear linked to changing food resources. While we know some large-scale movement patterns for NARW and a few SRW populations, we know little of mesoscale movements. For NPRW and some SRW populations, even broad-scale movements are poorly understood. In the face of climate change, can methodological advances help identify *Eubalaena* distributional and migratory responses? (4) Emergent diseases and the vulnerability of populations under stress: Marine mammals are vulnerable to infectious diseases,

particularly when subjected to stressors such as fishing gear entanglements, acoustic disturbance, and prey shortages. New tools to assess large whale health include body condition imaging, viromes, microbiomes, as well as metabolic and stress hormones. Comparative analysis of the three *Eubalaena* spp. could identify causes of varying recovery. (5) Comparative synthesis and cumulative effects: The lack of a good analytical approach for cumulative effects is an urgent bio-statistical problem in conservation biology. Without such a framework every stressor is managed in isolation, limiting efficacy. We propose a comparative synthesis to inform future cumulative effect analyses and outline future research priorities to achieve these goals.

Keywords: right whale, conservation, cumulative effects analysis, conservation technology, threats, recovery

RECOVERY

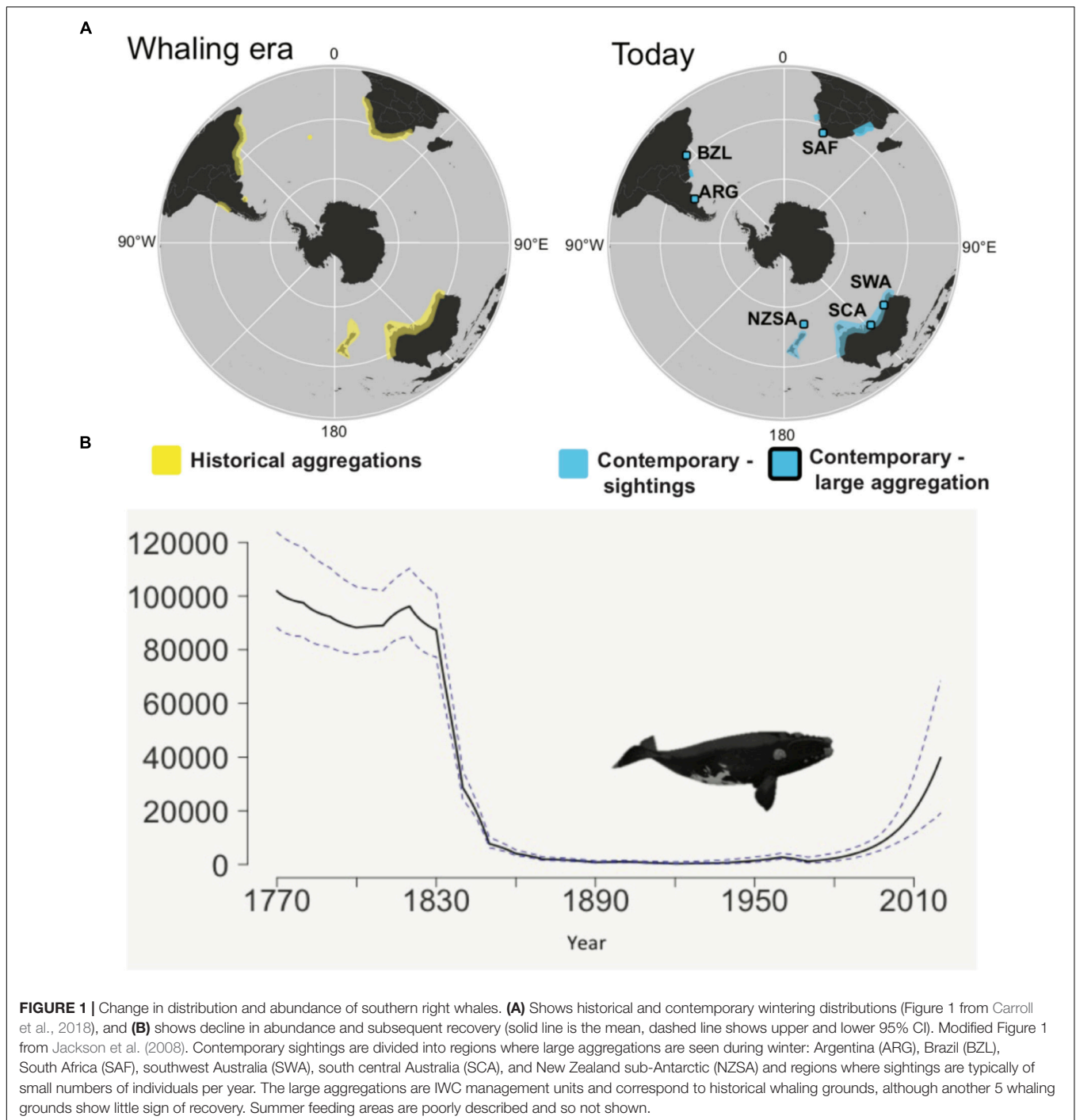
Introduction – Exploitation/Devastation

The *Eubalaena* genus comprises three species of right whale that have the dubious honor of being named by whalers for their desirability: North Atlantic (*Eubalaena glacialis*), North Pacific (*E. japonica*), and southern (*E. australis*) right whales (Braham and Rice, 1984; Rosenbaum et al., 2000). The ‘right’ whale to kill, these species are large baleen whales that tend to float when dead and yielded long baleen plates (known as whalebone historically), and much valuable oil that was used in industries from cosmetics to commercial lubricant (Allen, 1916; International Whaling Commission [IWC], 2001). The family (Balaenidae) also includes a fourth member, the bowhead whale (*Balaena mysticetus*), which was also heavily exploited but the Pacific population has had a major recovery and numbers more than the combined populations of the other three species (Givens et al., 2016). Exploitation of right whales began in earnest in the eastern North Atlantic with Basque shore and Basque pelagic whaling as early as 1000 AD (Reeves and Smith, 2006). The Basque shore-whaling techniques were exported to the South Atlantic by 1603. In the North and South Pacific, following the decline of Basque whaling, American shore and pelagic whaling methods predominated, appearing in the southern Indo-Pacific by 1805. Within 20 years the French whaling vessel *Gange* became the first pelagic whaling vessel to venture north of 50°N where it harpooned the first NPRW in 1835 (Reeves and Smith, 2006).

Shore whaling targeted right whales on their wintering grounds, as these are generally in sheltered coastal waters. Shore stations set up in these regions routinely killed calves as a way to secure the larger, more valuable, female, as this description from 1844 shows; “the object is to harpoon the calf ... the maternal affection of the whale causes it to follow the calf till it gets ashore” (New Zealand Blue Book, 1841). Females show fidelity to nursery grounds, frequently returning to the same bay to calve, so shore stations were successful for several years until they had wiped out those whales philopatric to a particular region. Offshore whaling, although termed Basque or American (“Yankee”) whaling due to its origins, was in fact conducted by many nations, including British, French, Norwegian and Dutch, and was indiscriminate in its killing of right whales (Reeves et al., 1999; Richards, 2009; Smith et al., 2012).

The decline of the SRW is the best understood of all the right whales. It is estimated that prior to whaling there were approximately 120,000 SRW found in 12 wintering grounds (Figure 1, International Whaling Commission [IWC], 2001, 2012; Jackson et al., 2008). However, between 1790 and 1971 up to 150,000 SRW were killed, leading to a hemispheric decline to as few as 400 whales around 1920 (International Whaling Commission [IWC], 2001, 2012; Jackson et al., 2008). Full protection from commercial whaling was provided for all right whale species under the Convention for Regulation of Whaling (CRW) in 1931 under the League of Nations. Japan did not accede to the CRW, but the CRW provided the framework for the future regulation of whaling that continues until today as the 1946 International Convention for the Regulation of Whaling (ICRW). Both the Soviet Union and Japan acceded to the ICRW. However, like the CRW, the ICRW was not perfect and even as the various species recovered from historical whaling, they were targeted illegally by the Soviet whaling fleet in the 1960s and 1970s. For the SRW, this killed half the extant population at the time (Tormosov et al., 1998; Jackson et al., 2008). Today, the SRW is estimated to have recovered to 12,000–15,000 individuals across its circumpolar distribution (Figure 1; International Whaling Commission [IWC], 2012).

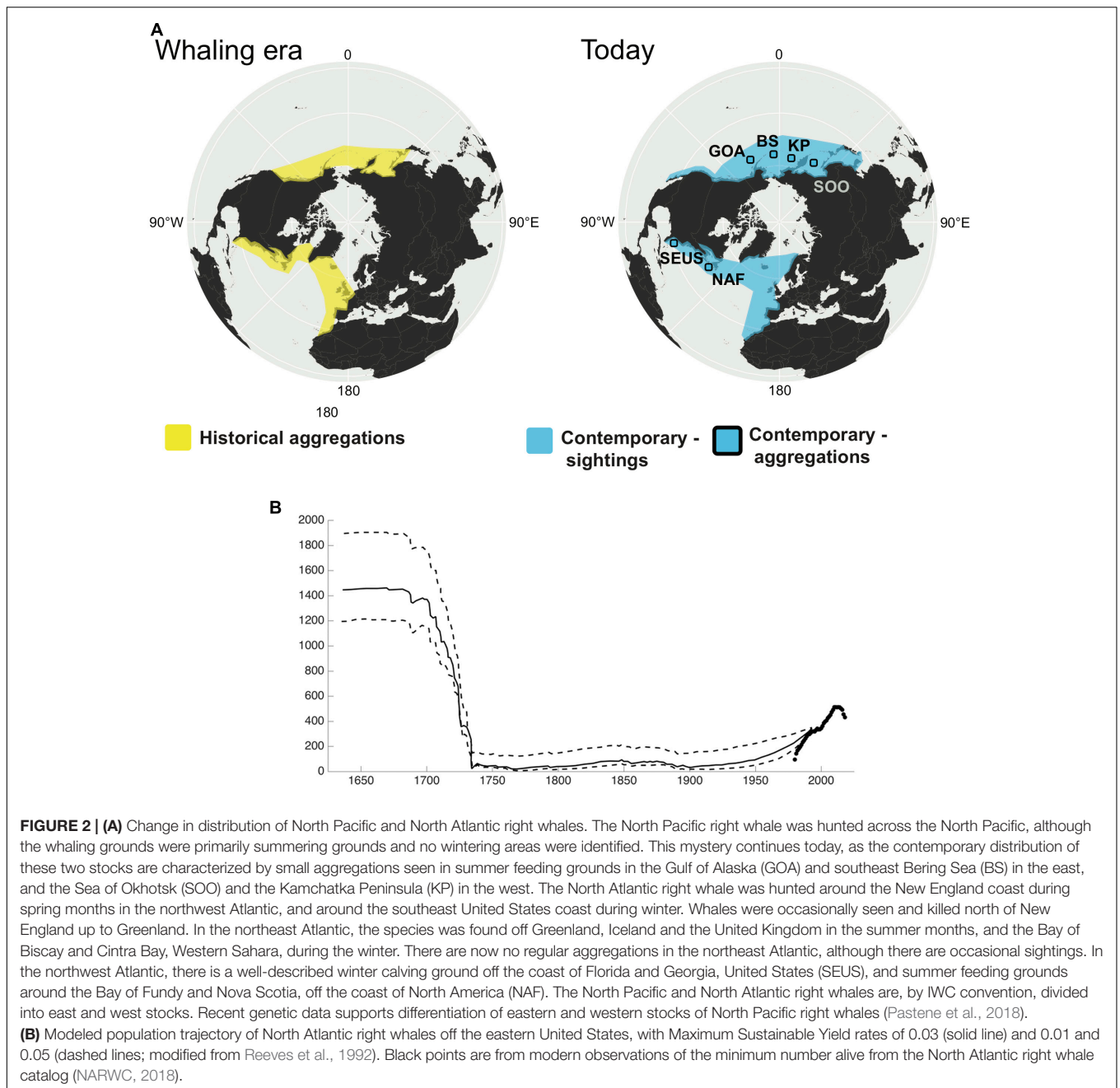
NARW have a much longer and poorly documented catch history, and the ability to estimate historical abundance for this species has proved challenging. Reeves et al. (2007) used catch records, whale oil, and baleen import records to estimate at least 5500 (and possibly twice that number) NARW were killed in the western North Atlantic between 1634 and 1950 and suggested a population of at least a few thousand whales in the mid-1600’s. Early studies indicating that Basque whalers took tens of thousands of NARW in the 1500’s from eastern Canada have been corrected by genetic analyses of bones from the Labrador whaling stations. These show that Basque whalers took primarily bowheads, and rarely caught right whales, leading to suggestions that small population size may be a long-term characteristic of this species (Rastogi et al., 2004; McLeod et al., 2008). Nevertheless, Reeves et al. (1992) suggested that fewer than 100 right whales were alive at the end of the 1700’s, and Katona and Kraus (1999) hypothesized that only a few dozen survived by the early 1900’s (Figure 2). As of 2015, there were an estimated



458 individuals in the western NARW population (Pace et al., 2017).

Two centuries of aboriginal, commercial, and then illegal Soviet whaling significantly reduced the NPRW (Scarff, 1991, 2001; Ivashchenko and Clapham, 2012; Ivashchenko et al., 2013). There are two distinct populations of NPRW, on the eastern and western sides of the Pacific (Gregg and Coyle, 2009), which are genetically distinct (Pastene et al., 2018). Early estimates based on sightings data suggested the species as a

whole totaled 100–200 whales (Wada, 1973; Sekiguchi et al., 2014; Ovsyanikova et al., 2015). For the western stock, surveys by Miyashita and Kato (1998) in summers of 1989, 1990, and 1992 in the Okhotsk Sea estimated abundance at 922 (95% CI 404–2108). More recently, surveys by Hakamada and Matsuoka (2016) suggest an abundance estimate of 1,147 individuals on the feeding ground off the southern end of the Kamchatka Peninsula in 2011 and 2012. In contrast, the eastern stock is on the order of 20–30 times smaller. Mark-recapture estimates for the eastern NPRW



stock from photographic (18 identified individuals) and genotype (21 identified individuals) data through 2008 were 31 (95% CI: 23–54) and 28 whales (95% CI: 24–42), respectively (Wade et al., 2011b) and the photo-ID and genetic catalogs have 20 and 23 unique individuals, respectively (1997–2011; LeDuc et al., 2012; Muto et al., 2017). Confirmed sightings since 1996 (Goddard and Rugh, 1998), and a recent increase in effort have led to more frequent detections in the region, including calves (Wade et al., 2006, 2011a; Zerbini et al., 2015; Ford et al., 2016).

All contemporary right whale populations reflect remnants of their pre-whaling populations. As such, they appear to occupy a portion of their historical ranges (Figures 1, 2). Whaling

logbooks have been useful in describing the distribution of the species prior to and during their exploitation (Dawbin, 1986; Du Pasquier, 1986; Reeves et al., 1992; Clapham et al., 2004; Reeves et al., 2007; Smith et al., 2012; Carroll et al., 2014; Rocha et al., 2014; Thomas et al., 2016) as well as identifying potential habitats that members of the modern populations may be re-exploiting.

While this short summary demonstrates the dramatic impact of whaling, it does not capture the spatially variable patterns of decline and, in some cases, recovery. There are several aspects of right whale ecology, population dynamics, as well as anthropogenic impacts that need to be considered when

contemplating why there has not been uniform recovery across populations or stocks. Each of these are explored with the intent of providing an overarching discussion of the roles of intrinsic and extrinsic drivers of recovery in the different species of right whales.

Migratory Culture, Extirpation and Recovery

SRW have a circumpolar distribution and rates of recovery have varied from near maximum growth rates (r_m) in some populations (southwest Australia, South Africa, East South America, and subantarctic New Zealand), to poor or not measurable in others. We now know that SRW show a form of migratory culture, with females transmitting preferences for both winter calving/breeding areas and summer foraging areas to their calves during the 1st year of life (Valenzuela et al., 2009; Carroll et al., 2015, 2016). This has led to genetic structuring across the species' migratory network (Patenaude et al., 2007; Carroll et al., 2015; Carroll et al., 2018), and has been invoked to explain the species' patchy recovery (Clapham et al., 2008; Carroll et al., 2011). Essentially, when whales inhabiting a region were extirpated, the memory of that area as a good migratory destination was also lost. This loss of 'cultural memory', exacerbated by low density and loss of adjacent populations, mean it is unlikely that once-inhabited areas will be recolonized on a timeframe relevant to management (i.e., decades; Clapham et al., 2008). This may help explain the lack of recovery around mainland New Zealand and east Australia wintering grounds compared with the strongly recovering populations in the New Zealand sub-Antarctic Islands and southwest Australia (Carroll et al., 2011, 2015). Comparable findings from the NARW show female philopatry to summering grounds (Malik et al., 1999), and population structuring that is probably due to migratory patterns of behavior (Schaeff et al., 1993). NPRW also show significant differentiation in maternally inherited DNA markers between Eastern and Western stocks that are likely partially attributable to female philopatry and stock identity (Pastene et al., 2018). However, historical bottlenecks may have influenced population structuring and migratory behavior prior to major whaling impacts (Waldick et al., 2002).

While vertical transmission (cow to calf) of migratory destinations provides valuable information on suitable foraging and nursery areas in a vast ocean (Whitehead, 2007, 2010), decisions conserved across generations can become problematic in the face of environmental change (Keith and Bull, 2017). This is because of the potential for ecological or evolutionary traps; a behavior that originally increased fitness (e.g., fidelity to rich feeding ground) becomes a hindrance in the face of rapid environmental change (e.g., changes in distribution of food resources due to climate variation and/or anthropogenic activities; Schlaepfer et al., 2002; Keith and Bull, 2017).

This information is critical to understanding the variable rates of recovery of all right whales; foraging ground quality seems to be a strong determinant of the reproductive rate of SRW populations, and hence recovery rates (Leaper et al., 2006;

Seyboth et al., 2016). The Patagonian Shelf, and South Georgia, south of the Polar Front, are an important feeding ground for the Argentina SRW population based on stable isotope, photo-ID and satellite track data. This high productivity means that some of these foraging grounds are shared with whales that winter in South Africa (Table 1; Best et al., 1993; Moore et al., 1999; Rowntree et al., 2001; Valenzuela et al., 2009; Mate et al., 2011; Zerbini et al., 2016). Both of these populations are thriving; although the Argentinean population is now increasing at a slower rate (Crespo et al., 2018) and it has been subject to a recent die off (Rowntree et al., 2013). In the NARW, there are strong links between prey availability, condition, and fecundity: poor prey years lead to low population health and body condition, and longer inter-birth intervals (Hlista et al., 2009; Miller et al., 2011, 2012; Fortune et al., 2013; Rolland et al., 2016; Meyer-Gutbrod and Greene, 2018). NARW move between habitats, especially foraging grounds, many times within a season (Mate et al., 2011; Baumgartner et al., 2017). Connectivity to alternative feeding grounds could buffer a population against poor conditions in a single feeding ground, ensuring that some of the population had sufficient resources to reproduce.

However, some feeding grounds of the SRW appear to have been completely abandoned, and this may be due to a loss of cultural memory rather than resource quality. For example, New Zealand right whales historically used foraging grounds around the Chatham Rise and Louisville and Kermadec ridges (Smith et al., 2012; Jackson et al., 2016), but there are no contemporary records of the whales from this region (Carroll et al., 2014).

Fortunately, like NARW, there is evidence of mixed foraging strategies within populations of SRW with whales visiting multiple foraging grounds, both within and between years. Satellite tagging in Argentinean wintering grounds showed that some whales will visit both the Patagonian Shelf and South Georgia in a single season (Zerbini et al., 2016). This is consistent with findings reported by Rowntree et al. (2008), who used isotopic signals in baleen plates to suggest a mixture of foraging strategies. Some whales appeared to specialize in either low- or high-latitude foraging grounds but not both, while others exhibited a mixture of latitudes over the 6–8 years represented in the baleen record (Rowntree et al., 2008). It remains to be seen whether right whales are able to learn from each other, and horizontally transmit foraging-ground preferences. Horizontal transmission of behavior or information could facilitate spread of innovation; in this case, potentially new foraging grounds (Dautenhahn and Nehaniv, 2002; Keith and Bull, 2017); and could buffer right whales from changes in prey distribution and abundance driven by climate.

Inverse Density Dependence: Genetic Diversity and Stochastic Demographic Influences on Recovery

Standard density-dependent population theory, exemplified by logistic growth models (Tsoularis and Wallace, 2002), holds that populations reduced to low densities should in the absence of migration increase at close to the maximum biological rate.

TABLE 1 | Tools for monitoring right whale occurrence and movements.

Method	Scale	North Atlantic right whale	Southern right whale	North Pacific right whale
Satellite tags	10s–1000s km	Mate et al., 1997; Baumgartner et al., 2003; Baumgartner and Mate, 2003, 2005; Schick et al., 2009	Childerhouse et al., 2010; Mate et al., 2011; Zerbini et al., 2016	Zerbini et al., 2015
Passive acoustic monitoring	10s–1000s km	Davis et al., 2017 and studies cited therein	Webster et al., 2016; Jacobs et al., 2018; Rayment et al., 2018	Waite et al., 2003; Mellinger et al., 2004; Rone et al., 2012; Širović et al., 2015; Wright et al., 2018
Autonomous vehicles with on-board acoustics	10s–100s km	Baumgartner, 2014; Davis et al., 2016		
Stable isotopes	100s–1000s km	Lysiak, 2009; Lysiak et al., 2018	Best and Schell, 1996; Rowntree et al., 2001, 2008; Valenzuela et al., 2009, 2010, 2018; Carroll et al., 2015	
Genetics	100s–1000s km	Schaeff et al., 1993; Malik et al., 1999; Frasier et al., 2007	Baker et al., 1999; Patenaude et al., 2007; Valenzuela et al., 2009; Carroll et al., 2011, 2014, 2015, 2018	Pastene et al., 2018
Shore-based tracking	10s–1000s km	Hain et al., 2013	Payne, 1986; Barendse and Best, 2014	
Time-depth recorders	1–1000s km	Winn et al., 1995; Goodyear, 1996; Nowacek et al., 2001, 2004; Baumgartner and Mate, 2003; Parks et al., 2012; Nousek-McGregor et al., 2013; van der Hoop et al., 2013b, 2017b; Baumgartner et al., 2017	Argüelles et al., 2016	
High-resolution orientation, kinematics	1–10s km	Nowacek et al., 2001, 2004; Parks et al., 2012; Nousek-McGregor et al., 2013; van der Hoop et al., 2013b, 2017b		

There is some evidence from the whaling era to support density-dependent changes in growth curves and fecundity in sperm whales (Kasuya, 1991) and other cetacean species (Fowler, 1984), but these data may be erroneous (NOAA, 2017) and cannot be relied upon. However, the lack and/or slow recovery of many populations of SRW, has led to speculation about the role of inverse density dependence at low densities or the Allee effect (Baker and Clapham, 2004). There are generally three primary categories of Allee effects; inbreeding, or a loss of heterozygosity; demographic stochasticity; and the reduction in cooperative interactions when there are fewer individuals (Allee, 1931; Courchamp et al., 1999).

Loss of genetic diversity due to demographic bottlenecks depends on the severity of the event, in terms of effective population size, and its duration, in terms of generations (Nei, 1975; Allendorf, 1986). Genetic erosion can lead to inbreeding, maladaptation, and loss of adaptive potential, increasing the risk of population extinction (Leroy et al., 2017). Simulation studies suggest that the centuries-long demographic bottleneck due to whaling did reduce mitochondrial genetic diversity in SRW (Jackson et al., 2008), with Indo-Pacific populations showing significantly lower mtDNA diversity than their South Atlantic counterparts (Carroll et al., 2018). However, it is not yet resolved whether this has impacted nuclear DNA diversity, as microsatellite studies show high levels of heterozygosity in the extant SRW wintering grounds (Carroll et al., 2018). In the North Pacific, LeDuc et al. (2012) analyzed 49 biopsy samples from 24 right whales, of which all but one were from the eastern North Pacific. The analysis revealed a male-biased sex

ratio and a loss of genetic diversity that appeared to be midway between that observed for right whales in the North Atlantic and the Southern Hemisphere. The analysis also suggested a degree of separation between eastern and western populations, a male:female ratio of 2:1, and a low effective population size for the Eastern North Pacific stock, which LeDuc et al. (2012) considered to be at “extreme risk” of extirpation. In contrast, the NARW has long been recognized as having low levels of genetic diversity, although genetic erosion does not seem to have coincided with 19th century whaling (Waldick et al., 2002; McLeod et al., 2010). It is possible that the NARW historically had a lower effective population size and hence harbored lower genetic diversity than its more numerous southern counterpart. Today, the high variability in male reproductive success seen in NARW, less prominent in SRW, could contribute to further lowering effective population size by limiting genetic input from all apart from those few successful males (Frasier et al., 2007; Carroll et al., 2012).

Demographic stochasticity in inverse density dependent effects are most likely to enact through sex ratio fluctuations in very small populations and this may be impeding the recovery of the eastern NPRW. Wade et al. (2011b) estimated the eastern NPRW population contained only eight females (95% CI: 7–18) and 20 males (95% CI: 17–37). Fujiwara and Caswell (2001) suggested that demographic stochasticity was less likely to impact the NARW population, but Pace et al. (2017) have shown a strong trend to a male biased sex ratio that is worrisome. The current estimate of breeding females is 105, in a population of 458. Equivalent data for SRW is lacking for the

smallest sub-populations where demographic stochasticity might be enacted.

Anthropogenic Impacts on Recovery

The role of anthropogenic impacts on right whale recovery is best understood in the NARW, due to comprehensive population monitoring over the last four decades (Pettis, 2009; Rolland et al., 2016) and consistent necropsy effort (Moore et al., 2004, 2013; van der Hoop et al., 2013a). The toll of human-induced mortality is, and continues to be, high; from 1970 to 2009, 44% (38/87) of detected and diagnosed NARW mortalities were due to ship strikes and 35% (31/87) were due to entanglements (van der Hoop et al., 2013a), despite widespread regulations attempting to reduce these threats. Entanglement has now surpassed vessel strike as the leading cause of death to the population (van der Hoop et al., 2014): from 2010 to 2015, 15% of diagnosed mortalities were due to ship strikes and 85% were due to entanglements (Pettis and Hamilton, 2015; Hayes et al., 2017). Demographic models emphasize the importance of individual reproductive females in the population (e.g., Fujiwara and Caswell, 2001) and suggest that a loss of 4–6 females per year will lead the population to extinction (Meyer-Gutbrod and Greene, 2018). In 2017, at least 17 NARW mortalities were detected, including five diagnosed vessel-strike mortalities, and four entanglement mortalities, leading to the declaration of an Unusual Mortality Event (NOAA, 2017). As of 2009, 83% of NARW showed evidence of entanglement; 26% showed new entanglement scars every year, and 59% had been entangled more than once (Knowlton et al., 2012a). Rates of serious injury from entanglement (i.e., those that will likely lead to death, NOAA, 2008) have increased from on average 0.7/year (2000–2009) to > 3/year (2010–2017) (van der Hoop et al., 2014; Hayes et al., 2017). The sublethal effects of entanglements have been quantified with respect to individual energetic cost (van der Hoop et al., 2016a; van der Hoop et al., 2017a), stress (Hunt et al., 2016; Pettis et al., 2017; Rolland et al., 2017; Lysiak et al., 2018) and reproductive output (Knowlton et al., 2012b), as is their role in combination with fluctuations in prey availability on population level health (Rolland et al., 2016).

The situation is comparatively positive for SRW populations. At its best, <1% of SRW in New Zealand show anthropogenic scarring (W. Rayment, pers. comm.) compared with the 83% for the NARW. Nevertheless, particularly for the smaller, more vulnerable populations there may still be critical impacts. While there have been ten ship-strikes with at least four mortalities and 28 entanglements with two deaths in Australian waters, the fatalities include mother and calf pairs from the small, remnant southeast population (Kemper et al., 2008; Carroll et al., 2015; Lanyon and Janetzki, 2016; Peel et al., 2018; Tulloch et al., unpublished). Vessel strikes to the Brazilian population still occur at low levels (<0.5 per year) but between 1999 and 2014, 38 entanglement cases were reported (Figueiredo et al., 2017; Groch, 2018). In Argentina, 6% of whales identified in 2007, 2008, 2009 seasons in Golfo Nuevo showed evidence of vessel interactions via scarring (International Whaling Commission [IWC], 2011). The potential for increased negative interactions between recovering right whale populations and increased human development has

been identified as an issue of concern in Brazil (Figueiredo et al., 2017), New Zealand (Suisted and Neale, 2004), and eastern Australia (Carroll et al., 2015).

The level of human-induced mortality to NPRW is currently unknown, due to their rare occurrence and poorly known distribution (Muto et al., 2017); however, threats are assumed to be similar to other right whale populations and bowhead whales (Reeves et al., 2012) and their observed distribution does overlap heavy vessel traffic and fishing areas. The threats from vessels will only increase as Arctic shipping increase in the near future and the shipping lanes will be through the summer feeding habitat in the southeastern Bering Sea, as it will for their cousin the bowhead whale (Reeves et al., 2012; Pirota V. et al., 2018). Despite the low likelihood of observing anthropogenic mortality or serious injury to NPRW in the eastern population, some live individuals show scars as evidence of fisheries interactions (Ford et al., 2016). For the much larger western NPRW population, 25 whales have been reported entrapped in fishing gear or stranded from Japan, South Korea, and Russia since 1996 and at least 10 of these are confirmed fishing mortalities (Brownell et al., 2001; Burdin et al., 2004; Brownell and Mallette, 2018).

Synthesis

Whaling nearly extirpated all right whale species worldwide. Numerous factors have influenced the recolonization and recovery of species and populations. The lack of obvious differences in anthropogenic impacts and to date, climate change, between SRW wintering grounds has led to intrinsic factors, such as migratory culture, extirpation and Allee effects, being inferred as strong drivers and/or inhibitors of recovery. In what is potentially the world's smallest whale population, the eastern NPRW, demographic stochasticity could play a deciding role in population persistence if the proportion of females in the population does not increase. Finally, the NARW has been reduced to a single, small population that is highly susceptible to extrinsic factors influencing recovery. The combination of anthropogenic impacts, both lethal and sublethal, and environmental fluctuations, appear to shape health and reproductive success in the NARW (Corkeron et al., 2018). This has only been elucidated by long-term, scientific monitoring projects using a range of approaches combined with intensive necropsy efforts; next, we discuss how this has worked and how it may be applied elsewhere.

LINKING INDIVIDUAL TO POPULATION-LEVEL RESPONSES

Introduction

The predictable aggregations of right whales that once attracted whalers are now the foundation of some of the longest-running, continuous whale studies in the world. These long-term datasets began with pioneering work that used natural markings to identify individuals and follow them through time (Kraus et al., 1986; Payne, 1986), and have been extended into multi-disciplinary studies (e.g., genetics, health) to gain

a comprehensive understanding of population and individual status.

Catalogs

The foundation of long-term monitoring projects is the identification of individuals, typically using natural markings, but also DNA profiles. In right whales, individuals are identified using callosity patterns, lip ridges, unusual color or patches, or scarring (Kraus et al., 1986), from both aerial and boat-based photographs (Patenaude et al., 1998). Photo-identification studies started on NARW in the United States in the 1960s (Kraus et al., 1986), on SRW in South Africa, southwest Australia, and Argentina in the 1970s (Payne et al., 1981; Best, 1990), in Brazil in the 1980s (Groch et al., 2005), in New Zealand in the 1990s (Patenaude et al., 1998), and in Chile in the 2000s (Vernazzani et al., 2014). NOAA/NMFS began compiling the NPRW catalog in 2008, and this now includes photos from 1979 to present (Kennedy et al., 2012). DNA profiles, constructed using a combination of hyper-variable microsatellite markers and sex-specific loci, have also been used to identify individuals primarily in NARW, NPRW and SRW in the Indo-Pacific region (Frasier et al., 2007; Carroll et al., 2011; Wade et al., 2011b; Carroll et al., 2012, 2015).

The strength of these catalogs is derived from the ability to use individual recognition to record all of the significant events that occur in an individual's life. This is best exemplified in the NARW where sightings locations, entanglement history, body condition, calving, tagging history and many other factors such as health and paternity can and are recorded. Having this detailed information provides us with immensely greater confidence in estimating demographic parameters and linking factors such as entanglement, environmental parameters, foraging success with reproductive output, health status and likelihood of survivorship.

Estimating Demographic Parameters

The ability to identify and track individuals across time is fundamental to assessments of population abundance and growth using open capture-recapture models for eastern NPRW and New Zealand SRW (Carroll et al., 2011, 2013; Wade et al., 2011b). These models are appropriate when heterogeneity in capture probability can be modeled by sex (i.e., genotype mark-recapture) or where there is no segregation by demographic class (e.g., feeding ground studies). Heterogeneity in female capture probability on wintering grounds is associated with reproductive cycles, i.e., females are more likely to be sighted in calving years, means that standard capture-recapture models cannot be used for estimating abundance or demographic trends in long-term photo-identification studies. Instead, stage-structured demographic models that estimate population parameters based on sightings of females in calving years are used to estimate abundance and trend in Argentina and South Africa (Cooke et al., 2015; Brandão et al., 2018). In southwest Australia, the total number of calving females seen in 3 years of aerial surveys has been assumed to represent the total number of reproductive females (see section "Linking Reproductive Success and Health to Environmental and Anthropogenic Factors"), which is then subject to a correction factor to estimate the total population size (Bannister, 2017). Population trends, estimated from the

mark-recapture or stage-structured models, or from the linear regression analyses of aerial count data, show that most of the recovering SRW populations have been growing at ~7% per annum (Table 1).

The NARW is one of the best-studied whale populations in the world, with concentrated survey efforts in the species' known habitats since 1979 producing a near-complete census of the entire population (Hamilton et al., 2007). Abundance estimates have typically been produced by calculating the total cataloged population minus the cumulative number of individuals detected or presumed dead (Kraus et al., 2001). However, habitat use patterns have changed in recent years, meaning that capture probabilities have declined. Therefore, Pace et al. (2017) conducted a mark-recapture estimate of abundance of NARW, and showed the population increased at ~2.8% from 270 whales in 1990 to 482 whales in 2010. Since then, however, there are strong indications that the population is declining, with abundance estimated to be 458 whales in 2015 (95% credible interval: 444-471, Pace et al., 2017).

Linking Reproductive Success and Health to Environmental and Anthropogenic Factors

Cataloging females through multiple calving events in SRW, and the ability to monitor almost all individual NARW, have provided powerful datasets from which to assess environmental and anthropogenic drivers of reproductive success and health. This, in turn, provides the ability to determine drivers of population growth and persistence. In particular, the low or negative growth rate of NARW stands in contrast to the higher growth rates of SRW (Table 1), and has been explicitly linked to changes in calving intervals between the two species (Corkeron et al., 2018).

Right whales typically have a 3-year reproductive cycle; 1 year gestation, 1 year calving and 1 year resting (Knowlton et al., 1994). Right whale calves grow extremely fast compared with other cetacean species, with SRW calves estimated to grow between 2.2 and 3.5 cm per day (Whitehead and Payne, 1978; Best and R  ther, 1992; Christiansen et al., 2018). During their typically fasting wintering period, lactating females are estimated to lose up to 3.4 cm of blubber thickness (Miller et al., 2011) or 25% of their body volume (Christiansen et al., 2018). NARW have significantly thinner blubber than SRW (Miller et al., 2011). Unsurprisingly these factors all demonstrate that female health and body condition are strong determinants of calving rates.

Since 1984, nearly all of the new calves in the NARW population have been observed due to aerial and ship surveys on calving grounds (Browning et al., 2010). Using this comprehensive dataset for years 1988–2008, Rolland et al. (2016) showed that females that transition from resting to pregnant had a significantly higher annual mean health score compared with those that did not calve (Rolland et al., 2016). This and other work shows that the greatest fluctuations in NARW body condition and health scores are linked to the cost of lactation in the calving cycle, with the lowest estimated health scores in resting and lactating females, and blubber thicknesses increasing with the years since the last calving event (Pettis et al., 2004; Miller

et al., 2011, 2012; Rolland et al., 2016). Recovery of condition post calving may, however, be impeded by external factors and chronic entanglement in fishing gear can result in the consumption of endogenous lipid energy reserves on the same order of magnitude as is consumed during lactation (van der Hoop et al., 2016a).

As foraging success helps determine body condition, work in SRW has investigated the link between foraging ground conditions and reproductive success. Leaper et al. (2006) showed a relationship between breeding success at the Argentinean wintering ground and sea surface temperature (SST) anomalies at their feeding ground in South Georgia. The SST anomalies in late summer to autumn prior to winter conception seemed to have the largest impact, and the authors hypothesized it was due to relationship between SST and krill biomass (Trathan et al., 2003). Variation in krill abundance and density, linked with the phase of the Antarctic Oscillation and El Niño events, were also found to be significantly correlated with the number of calves observed on the Brazilian wintering ground (Seyboth et al., 2016).

A similar relationship has been found in the NARW, where calving success is strongly correlated with the abundance of its primary prey *Calanus finmarchicus*, which in turn is linked to the North Atlantic Oscillation (Greene and Pershing, 2004; Hlista et al., 2009; Meyer-Gutbrod and Greene, 2018). Recent analyses have sought to understand the relative contribution of anthropogenic impacts and food availability on NARW reproduction and population growth (e.g., Meyer-Gutbrod and Greene, 2018). This work offers an important example to understanding right whale population persistence and recovery more generally. It has become particularly relevant on a global scale as the strong population growth in some SRW's appears to have slowed in recent years, with lower counts since 2015 (Charlton, 2017; Brandão et al., 2018). In Australia this appears to be due to a redistribution of calving females to historical calving areas such as Fowlers Bay (Charlton, 2017). But in South Africa this has been attributed to an increase in the calving interval, with models suggesting females are resting longer than in the past (Brandão et al., 2018). Furthermore, major die offs of calves at the Argentinean wintering ground may reduce population growth in the future, and the drivers of these events remain as yet unknown (Rowntree et al., 2013; Marón et al., 2015).

Synthesis

Long-term monitoring studies have linked environmental factors such as prey availability and its proxies, as well as anthropogenic impacts, with right whale health, body condition and reproductive success. The analyses conducted in NARW using over three decades of detailed sightings histories of individually identified whales showcases the way forward for explaining the impact of environmental variation and human impacts on reproduction and population persistence. As some SRW populations begin to experience a decline in reproductive success with population-level implications, we suggest adopting a similar strategy and in particular targeting efforts toward monitoring those that appear most vulnerable. Given that SRW travel between feeding grounds shared by more than one population, we also recommend developing a unified catalog strategy between regions and research groups.

ADAPTING TO SHIFTING RESOURCES

The distribution of right whale species reflects evolutionary, demographic, ecological, habitat and anthropogenic processes that come together over various scales of space and time (e.g., Forcada et al., 2012). Within each species, individuals move through different habitats that provide appropriate conditions for specific ecological and physiological needs, often governed by life-history stages or characteristics (e.g., Corkeron and Connor, 1999). All three right whale species show some migratory tendency, though the identification of calving, breeding and foraging grounds varies for each species. Moving between these grounds can require multi-month migrations over thousands of kilometers (Figure 1). For the most part these migratory pathways between grounds remain only partially defined and may indeed be very diffuse. Within grounds, individuals will move to fulfill their needs of foraging, socializing, courtship (Best et al., 1993; Kraus and Hatch, 2001) and calving (Patenaude and Baker, 2001; Elwen and Best, 2004; Torres et al., 2013; Rayment et al., 2015). As reported above, within a season, some (though emphatically not all) individuals may move between different habitats that support the same needs (e.g., movement between different foraging grounds), depending on proximity and suitability (Vanderlaan, 2010; Schick et al., 2013), and perhaps, experience or cultural knowledge.

Factors Driving Distribution

The single most important habitat feature for the NARW is the occurrence of concentrated patches of copepod prey (Murison and Gaskin, 1989; Wishner et al., 1995; Mayo et al., 2001; Baumgartner and Mate, 2003). Similarly, the probability of detecting NPRW in the Southeastern Bering Sea is strongly associated with the abundance of their primary prey, *Calanus marshallae*, with patch densities around right whales as high as 10^5 copepods m^{-3} (Baumgartner et al., 2013b). Copepod patches result from a combination of physical (supply, removal, and resuspension) and biological (diapause and density) mechanisms occurring across scales. Together, these factors can lead to predictable and persistent, high-energy food sources, or can cause high inter-annual variability in the abundance, concentration, and energy density in the same foraging habitat (Zakardjian, 2003; Jiang et al., 2007; Davies et al., 2013; Davies et al., 2014). The same features that tend to concentrate NARW prey (*Calanus* spp.) have not necessarily been shown to concentrate NPRW or SRW prey, nor have NPRW or SRW been associated with similar foraging-type environments (Baumgartner et al., 2013b). The latter do not appear to be obligative frontal foragers (Reid et al., 2000), although Mate et al. (2011) reported that some SRW tagged in South Africa were associated with the Subtropical Convergence. There is limited information on foraging behavior or prey in NPRW and SRW (Hamner et al., 1988), though current efforts are underway. For example, D'Agostino et al. (2018) describe seasonal phytoplankton and mesozooplankton dynamics along with environmental factors in the northern Patagonian gulfs in addition to mesozooplankton composition and abundance measured close to foraging SRW.

Calving areas share many features between SRW and NARW. Mother-calf pairs select shallow areas closer to shore (Winn et al., 1986; Elwen and Best, 2004; Keller et al., 2012; Rayment et al., 2012; Rayment et al., 2015), with calm waters (Winn et al., 1986; Rowntree et al., 2001), protection from ocean swell and seasonal winds (Elwen and Best, 2004), and soft substrates, when compared to unaccompanied or non-calving individuals. Historical and contemporary calving grounds for either NPRW stock remain a mystery.

Changes in distribution of different demographic classes have been linked with changes in density in multiple SRW populations. Increases in the number of cow-calf pairs displaces social groups and solitary individuals to other habitat in Argentina (Rowntree, 2001; Arias et al., 2018) New Zealand (Carroll et al., 2014; Torres et al., 2017), and Australia (Charlton, 2017).

Studies of social and cultural drivers remain in their infancy, currently restricted to SRW (Valenzuela et al., 2009; Carroll et al., 2015). Application to NARW may help characterize site fidelity and transmission of migratory patterns, e.g., Fundy vs. non-Fundy females in NARW (Schaeff et al., 1993; Malik et al., 1999), and the segregation of mature males to, e.g., Browns Bank and Roseway Basin prior to 1993 (Clapham et al., 1999).

Contemporary Distribution

SRW

The SRW are circumpolar in the Southern Hemisphere between about 12°S and 65°S, albeit with a large historical and contemporary discontinuation between New Zealand and Chile. The austral winter distribution of SRW (**Figure 1**) includes the New Zealand sub-Antarctic Auckland and Campbell Islands (Carroll et al., 2013; Torres et al., 2017), with far fewer whales reported around mainland New Zealand (Carroll et al., 2014). In Australian coastal waters, SRW occur along the southern coastline including Tasmania, generally as far north as Sydney on the east coast and Perth on the west coast (Carroll et al., 2011). Similarly, SRW migrate up the east coast of South America to Brazil to breed in coastal shallows (De Oliveira et al., 2009), and along the west coast through Chile into Peru as far as 12°S (and possibly 4°S) (Aguayo-Lobo et al., 2008; Van Waerebeek et al., 2009), and on both the east and west coasts of southern Africa (Best et al., 1993; Mate et al., 2011, **Figure 1**). When in coastal habitat, SRW are usually within 2 km of shore and distinctly clumped in aggregation areas (**Figure 1**). SRWs tend to group into different demographic class along the coast, with cow-calf pairs and single adults or socializing groups using different sections of the coast or region, e.g., cow-calf pairs concentrate in Port Ross, Auckland Islands, while Campbell Island seems to contain more single whales (Torres et al., 2017).

In summer SRW probably forage between about 40°S and 65°S, including Magellan Strait and along the Antarctic Peninsula (Aguayo-Lobo et al., 2008; **Table 1**). Foraging and summer distribution have been determined from multiple sightings (**Table 1**); stable isotope studies (e.g., Rowntree et al., 2001; Valenzuela et al., 2009) and a small number of satellite tracking studies (Mate et al., 2011, see section “Migratory Culture, Extirpation and Recovery”). Direct movement between wintering

and feeding grounds is known from photo-identification with movement from southwest Australia to south of 60° (Bannister et al., 1999), and between Península Valdés and South Georgia (Best et al., 1993). Illegal Soviet whaling in the 1960s and 1970s supports these inferences, as SRWs were killed during the austral summer around South Georgia and other high latitude areas (Tormosov et al., 1998). Stomach content data from these whales showed that SRW were feeding on copepods north of 40°S and euphausiids south of 50°S and a mixture in between (Tormosov et al., 1998). The summer distribution of contemporary SRW is one of the least well understood aspects of the species’ biology.

NARW

In the western North Atlantic, individual right whales routinely range from Florida to the Gulf of St. Lawrence (Kraus and Rolland, 2007); however, they can be considered “condition-dependent partial migrators” (Krzystan et al., 2018). Recent sightings of “western” NARW have been reported from Iceland, Norway, Portugal and the Azores. The calving ground is in the coastal waters of the southeastern United States during the winter months, although there are at least two records of calves being born around Cape Cod in the spring. Non-calving females, and adult and juvenile males are also observed on the calving grounds (Schick et al., 2013). Winter aggregations also have been observed in the middle of the Gulf of Maine (Cole et al., 2013) and south of Cape Cod (Leiter et al., 2017), but the location of most of the non-calving whales is unknown. Historical whaling records suggest a winter-spring presence along the United States Mid-Atlantic coast (NY – DE; Reeves et al., 1999). In the spring, aggregations of right whales occur in Massachusetts Bay, and sometimes in the great South Channel east of Cape Cod. In the summer and fall, right whales are observed in the Bay of Fundy (between Maine and Nova Scotia), in Roseway Basin (50 km south of Nova Scotia), and recently in the southern Gulf of St. Lawrence. Photo-identification and some limited satellite tagging data show that seasonal movements into, out of, between, and around the so-called critical habitats are frequent and extensive (Baumgartner and Mate, 2005; Brillant et al., 2015). There is significant substructuring within the NARW population. Schaeff et al. (1993) inferred from genetic and photo-identification data that about one-third of the cows in the population do not bring their calves to the Bay of Fundy nursery area. This suggests that another summer and fall nursery area may exist, although its location is unknown.

NPRW

The seasonal distribution of NPRW is largely understood through analysis of historical catch records and sightings data (Miyashita and Kato, 1998; Clapham et al., 2004), along with more recent visual and acoustic survey effort since the early 2000s. Critical Habitat for the eastern NPRW has been established in the southeast Bering Sea and in a small portion of the Gulf of Alaska based on consistent sightings in these areas (NOAA, 2008). Aerial and shipboard surveys, satellite tracking and acoustic monitoring efforts are largely focused in the southeast Bering Sea and confirm it is an important summer foraging area (Wade et al., 2006, 2011a; Zerbini et al., 2015). There is considerably less survey effort in

the northern Gulf of Alaska compared to the southeast Bering Sea, but individual sightings and acoustic detections (Waite et al., 2003; Mellinger et al., 2004; Allen and Angliss, 2012; Širović et al., 2015) including further south (Ford et al., 2016) suggest that alternative foraging grounds may exist. Eastern NPRW arrive in the southeast Bering Sea as early as May, move into mid-shelf waters throughout the summer, and are detected through December (Munger et al., 2008). Visual sightings and year-round acoustic detections of NPRW in Unimak Pass suggest this region may be used as a corridor between summer foraging and unknown winter grounds (Wright, 2015, 2016; Wright et al., 2017).

In fall and spring, NPRW sightings and detections are much more diffuse across the species' range from South Korea, Japan, and the Okhotsk Sea through British Columbia and California (Brownell et al., 2001; Clapham et al., 2004; Ford et al., 2016), and acoustic detections are less common (Munger et al., 2008; Wright, 2015, 2016).

Few historical sightings suggest that in winter, eastern NPRW ranged from between the Hawaiian Islands to the west coast of North America (Klumov, 1962) and for western NPRW, from offshore Kamchatka south to the Yellow Sea (Omura et al., 1969; Scarff, 1986; Brownell et al., 2001). Contemporary sightings remain within these ranges, and acoustic detections indicate winter residence in Alaskan waters (Wright, 2015, 2016). Mitochondrial DNA comparisons suggest that the populations in the eastern and western North Pacific are genetically distinct (Pastene et al., 2018). Calving areas remain unknown, and have never been reported by whalers; modeling studies have identified coastal areas in California, Hawaii, southern China and northern Vietnam as potential calving regions of based on habitat features (Good and Johnston, 2010). There is a single photo-identification match between Hawaii and the Bering Sea (Kennedy et al., 2012).

Investigating the Distribution of Species and Movement of Individuals Within and Between Populations

Many methods have been implemented to study the distribution of species and movement of individuals within and between populations (Table 1). These methods provide insight at different spatial and temporal scales and rely on different types of observations or samples. For example, biopsy, necropsy or sloughed skin can provide material for genetic analysis to determine identity, sex, parentage and population membership and stable isotope analysis to ascertain foraging location and trophic level. Baleen can also provide material for stable isotope analysis, providing more detailed histories of individual foraging locations (Best and Schell, 1996; Rowntree, 2001; Valenzuela et al., 2009).

Acoustic detections provide the approximate location of a whale, but only when it is calling and within the detection range of the hydrophone, but then will provide evidence of presence of one or more whales (Mellinger et al., 2004, 2007, 2011; Wade et al., 2006; Van Parijs et al., 2009; Širović et al., 2015) and seasonal distribution in space and in time (Morano et al., 2012; Davis et al., 2017). Behavior is the primary determinant of right whale calling

rates, and sound production varies between habitats (Matthews et al., 2001; Parks et al., 2011).

Photo identification of individuals has been used to demonstrate longer-range movements of all three right whale species (e.g., Knowlton et al., 1992; Best et al., 1993; Pirzl et al., 2009; Kennedy et al., 2012), as have genetic data in SRW (Carroll et al., 2014), but these paired observations essentially only provide information on the presence of the individual at both places at both times, usually lacking information on residence time, and how the animal moved from A to B (e.g., Whitehead, 2001). The different right whale catalogs contain individual sightings at scales from <1 day to 17 years (Hamilton et al., 2007). Eighty percent of sightings in the NARW catalog occur in consecutive years (Hamilton et al., 2007), compared to 3 years in SRW (Bannister, 2017; Charlton, 2017).

Various satellite telemetry systems have been developed for large whales and have been deployed on right whales since the mid 1980s (Mate et al., 1992, 1997; Goodyear, 1996; Andrews et al., 2008). The technology provides information at a higher temporal resolution compared to visual sightings and has been useful in confirming that right whales can travel long distances over short periods of time between subsequent sightings in the same habitat (e.g., Mate et al., 1992), as well as tracking movements between known summer and winter habitat areas (Mate et al., 1997, 2011; Childerhouse et al., 2010; Zerbini et al., 2016). All three right whale species have been satellite tagged (Table 1). Tag systems have evolved over decades (Mate et al., 2007; Andrews et al., 2008) improving attachment mechanisms and increasing deployment duration, which can now last >200 days (Zerbini et al., 2016). However, tag impacts must be evaluated in the context of the value of the information, and continued improvement of attachment mechanisms is necessary to address health and welfare concerns (Moore et al., 2012; Best et al., 2015; Moore and Zerbini, 2017; Norman et al., 2018).

Going From Sightings and Distributions to Individual Movements

The ability to identify individuals (see section "Catalogs" above) and follow the change in location of subsequent sightings allows for the transition from describing general population movement, habitat use, and arrival times down to the resolution of specific individuals. Tracking individual movements provides a greater understanding of behaviors (Mayo and Marx, 1990), decisions, and corridors (Schick et al., 2009; Zerbini et al., 2016), and allows for movements to be predicted across a range of scales (Pendleton et al., 2012; Brillant et al., 2015, 2017). For example, Schick et al. (2013) characterized transition probabilities between broad geographic regions (i.e., feeding and breeding habitats) that differed between male and female NARW. Do similar differences in movement exist based on health or entanglement status (van der Hoop et al., 2016a)? Predicting how and when individuals, especially of different age, sex or life stage, distribute throughout the species' range has implications for marine spatial planning (Vanderlaan, 2010; van der Hoop et al., 2014). How individual movements scale to reflect the overall distribution of populations and species are open questions in movement

TABLE 2 | Global right whale research priorities.

Action	Information gained	Threats addressed	Technology	Population/species
Global catalog – total population assessment	Demography, Calving interval, Philopatry, Population mixing, Population trends, Movements, Distribution, Body condition/health status	Entanglement, Vessel strike, Resource availability, Loss of habitat (climate change, coastal development)	Photo-ID, Machine learning, Genomics	Existing for NARW, NPRW. Priority to coordinate SRW across ocean basins
Global catalog-genomic	Philopatry, Population mixing, Population trends, Pedigree, Genetic/genomic diversity (functional and neutral), Reproductive skew	Emerging diseases, Climate change effects, Cumulative threats	Genetic/genomic profile matching, Metagenomics, Epigenomics (aging)	Existing for NARW, NPRW. Priority to improve coordination SRW across ocean basins
Global catalog-health	Compromised recovery, Catalog diseases, Identify vectors, Morbidity/mortality causality, Genomic assessment of susceptibility	Entanglement, Emerging diseases, Climate change effects	Drones, Metagenomics, Microbes, Hormones, Biopsies, Post-mortems, Genomics	Existing for NARW. Priority for NPRW, improve coordination SRW across ocean basins
Coordinate acoustic monitoring repositories	Population monitoring, distribution	Acoustic exposure	PAM, Gliders, Detection and classification algorithms, Accessible repositories	All ocean basins
Develop universal population models	Population recovery, prioritize threats	Individual threats, Cumulative threats	Cumulative, individual-based and population matrix models, stable isotopes	All
Develop models of individual drivers	Individual movements, habitat requirements, foraging needs, energy acquisition and expenditure	Resource availability, Climate change, Industry impacts	Individual-based models, Sighting surveys, Biologging to improve empirical measurements of specific activities	All
Monitor low-recovery regions	Individual movements, Habitat requirements, Patterns of recovery	Resource availability, Climate change, Industry impacts	Sightings surveys, Remote sensing, eDNA, PAM, Photo ID/genomic profiles	All

ecology. For example, our understanding of SRW connectivity, and transition probabilities, would be highly informed by cross-catalog matching. Measuring large-scale and mesoscale movements with the approaches described above will help reveal individual residency and movement patterns and clarify how these scale to observed population distributions (Table 2).

Fine-Scale Movement and Orientation

Detailed measurements of how right whales orient and behave, especially in relation to prey patches and anthropogenic threats, e.g., fishing gear or near the surface, can be difficult to obtain. Detailed field observations (Mayo and Marx, 1990) have provided careful measurements of swimming paths and turning angles in traveling vs. foraging modes, and at a finer scale than offered by satellite telemetry. Similar measurements in other environments, populations or species are rare, yet these values are critical in informing modeling approaches for, e.g., spatio-temporal risk assessment (van der Hoop et al., 2012). We know that obstacle avoidance (Kraus et al., 2014), prey patch exploitation and decision making occur at these fine scales.

Bio-logging and bio-telemetry tags have been used to assess NARW diving behavior, specifically comparing different diving modes that may be associated with foraging, as well as the tracking of diel vertically migrating prey layers (Winn et al., 1995; Goodyear, 1996, Table 1; see section “Biologgers”). Simultaneous use of echosounders and tags can record the depth to which animals dive with respect to the vertical distribution of their

prey (Baumgartner and Mate, 2003). Depth-related time budgets have been effective in assessing the risk of entanglement in fishing gear or vessel strike (Parks et al., 2012; Baumgartner et al., 2017) as well as assessing potential avenues to reduce those risks (Nowacek et al., 2004). Diving behavior and fine-scale body orientation have been linked to differences in total buoyancy and changes in body condition (Nowacek et al., 2001; Nousek-McGregor et al., 2013), while tags have also been used to resolve changes in diving behavior, biomechanics and thrust production with entanglement in fishing gear (van der Hoop et al., 2013b, 2017b; Table 1). The fine-scale 3D movement, orientation, and behavior of right whales in the context of variable prey densities, conspecifics, or anthropogenic disturbances or threats is poorly known, especially for SRW and NPRW. For SRW, this is linked to poorly described and typically offshore and somewhat inaccessible location of foraging grounds.

Detecting Changes: What Do We Need to Know?

“Any effective study of the ecology, behavior, or patterns of distribution of western North Atlantic right whales must include studies of C. finmarchicus.” – Winn et al. (1995).

Predicting how movements at any scale will change with environmental change requires a mechanistic understanding of the processes that drive movement and distribution. It also requires sufficient sightings or detections to quantify change;

shifts in distribution are difficult to detect when annual sightings are incredibly low. For example, Tynan et al. (2001) reported changes in eastern NPRW distribution and prey selection with climate forcing; however, the prey species were no different than those observed in the historical record of NPRW (Shelden et al., 2005), and the observed distribution of whales was likely the result of inadequate survey coverage (Wade et al., 2006, 2011b; Zerbini et al., 2015). Sightings presence is a poor indicator when annual sightings are fewer than ten individuals.

Only recently have we begun to understand and quantify the plasticity of migration in NARW. In recent years, fewer individuals have been sighted on the calving grounds (Krzystan et al., 2018), whereas more individuals are overwintering in northern habitats, e.g., Cape Cod Bay and the Gulf of Maine (Bort et al., 2015; Davis et al., 2017; Mayo et al., 2018). Other causal factors have been identified and described across a range of scales. For example, NARW were almost completely absent from their Roseway Basin feeding habitat in the mid-to-late 1990s (Brownell et al., 2001; Kenney et al., 2001; **Figure 3** in van der Hoop et al., 2012), whereas over 100 individuals have been sighted in that habitat in other years. This multi-year abandonment has been linked to interannual variation in copepod abundance (Patrician and Kenney, 2010), attributed to the volume, strength, and density of water masses transported to the basin (Davies et al., 2013, 2014). Studies emphasize the importance of prey mapping, modeling, and *in situ* and satellite-derived oceanographic conditions (Baumgartner et al., 2003; Jiang et al., 2007; Hlista et al., 2009; Krumhansl et al., 2018) at resolutions that match effort-corrected whale detections, as well as coordination between researchers in these disciplines.

Large scale changes in the overall distribution of NARW from 2004 to 2014 have also been resolved *via* acoustic monitoring. Davis et al. (2017) compiled acoustic records from Florida, United States to Greenland, and documented an increased presence of NARW in the mid-Atlantic and simultaneous decrease in the Gulf of Maine; these changes coincided with seasonal sightings data for the regions. From acoustic data, it is difficult to assess how movements of individuals within the population have led to these measured changes, or the strength of various drivers; however, such studies emphasize how the combination of many smaller-scale acoustic projects or programs can provide a larger-scale assessment of seasonality and habitat use, and changes therein.

Small-scale vertical and horizontal distributions of diving right whales correspond to the vertical and horizontal distributions of their prey. Collocated measurements of diving behavior (see sections “Automated Image Analysis” and “Biologgers”) and oceanographic and prey-field measurements have been useful in characterizing inter- and intra-annual changes in foraging activity in NARW (Winn et al., 1995; Baumgartner et al., 2017), but little similar work has been carried out in SRW or NPRW.

Technological Advances

Application of new and developing methodologies will help answer questions regarding how right whales adapt to their changing environment. Here we discuss several of these.

Passive Acoustic Monitoring

The development and improvement of tools to collect, store, and analyze underwater acoustic recordings have expanded their scope and application. Archival and real-time systems can be low-cost solutions to monitor cetacean presence at the mesoscale (Van Parijs et al., 2009, **Figure 3**). Fixed, autonomous acoustic recorders can operate continuously for months to years, through poor weather and darkness, and have proven useful in detecting eastern NPRW in known and new habitats (Mellinger et al., 2004; Širović et al., 2015; Wright et al., 2018). This greatly enhances aerial and vessel surveys (Rone et al., 2012; Baumgartner, 2014), helps identify changes in overall distribution, and arrival to and departure from specific habitats (Van Parijs et al., 2009; Davis et al., 2017). The coordination of many smaller-scale acoustic programs into larger-scale networks (Van Parijs et al., 2015) and *post hoc* analyses can describe changes at large scales, despite technical challenges in unifying datasets with varying duty cycles or deployment durations (Davis et al., 2017). However, it remains a challenge to estimate the number of individuals (and which individuals) or animal density from acoustic detections that reflect only pseudo-presence at variable detection ranges (but see Marques et al., 2011).

The development and implementation of detection and classification algorithms has helped automate species identification and ease data burden (Gillespie and Caillat, 2008; Baumgartner and Mussoline, 2011) and can be used for real-time monitoring for risk management and mitigation. For example, the Right Whale Listening Network created following the proposed building of deep-water ports for liquefied natural gas offloading near right whale critical habitat is comprised of 10 right whale automatic detection buoys, provided near-real time notifications to LNG vessels (Wiley et al., 2013). Other similar real- or near-real-time transmission systems have been deployed (e.g., in the New York Bight), and communicate by, e.g., twitter (@robots4whales) and the Whale Alert App. Real-time moored systems are being considered for other high-density areas in the NARW range with high vessel density (e.g., the Gulf of St. Lawrence, Canada) and could be implemented in similar habitat for SRW such as west of Melbourne, Victoria, Australia near the only known SRW calving habitat for the at-risk remnant south eastern population.

Autonomous Platforms

Incorporation of these types of acoustic monitoring devices and detection and classification algorithms into autonomous ocean platforms (i.e., gliders **Figure 3**) has extended the duration, season, and track-line distance of sampling and surveying ability through poor weather (vs. shipboard surveys), while sampling simultaneous relevant *in situ* oceanographic information. Gliders have successfully detected fin, sei, humpback, and NARW in habitats ranging from the Gulf of Maine to the Gulf of St. Lawrence¹ (Baumgartner et al., 2013a; Davis et al., 2016). Gliders have also been deployed in the Chukchi sea area, primarily to detect bowhead, beluga, and fin whales (Baumgartner et al., 2014b); however, this region is further north than the most

¹<http://dcs.whoi.edu>

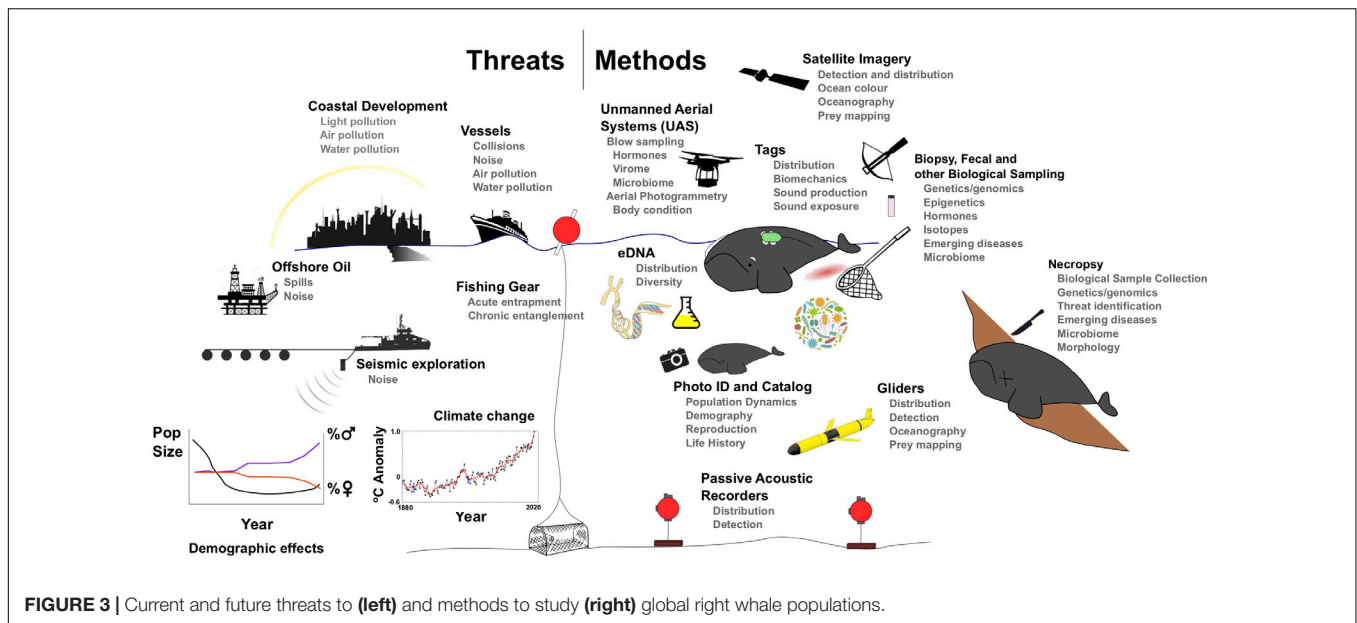


FIGURE 3 | Current and future threats to (left) and methods to study (right) global right whale populations.

frequented eastern NPRW habitats. Autonomous gliders could prove useful in surveying contemporary and historical right whale habitats around the world, especially in the context of oceanographic features.

Satellite Imagery

It is possible to detect and count individual animals in Very High Resolution (VHR) satellite imagery available either from open source platforms (e.g., Google Earth Imagery) or private companies (e.g., Digital globe; Cubaynes et al., 2018) (Figure 3). Fretwell et al. (2014) identified at least 55 SRW in a single image of the calving grounds of Golfo Nuevo, Península Valdéz, Argentina. This method can detect right whales where real-time sightings are available to validate detections, where weather conditions are favorable for cloud-free imagery, and where whales are frequently observed at or just below the surface. Satellite imagery suffers from availability biases in deeper waters, as dive times and surface detectability may differ across locations, seasons, activity patterns and demographic groups. This method might also prove useful for detecting beach-cast mortalities in remote environments.

Environmental DNA (eDNA)

Ecological questions are now being addressed using environmental sampling of water in combination with high through-put sequencing. Work in marine mammals shows that the method can be used to identify species (Foote et al., 2012) and even genetically distinct killer whale ecotypes up to 2 h after the species was present in an area (Baker et al., 2018). Population-level data are also able to be obtained from aggregations of marine animals, as shown by work in whale sharks (Sigsgaard et al., 2016), which could be useful in the context of right whale wintering ground aggregations. In the future, eDNA could be used to detect the presence of right whales, in combination with other systematic survey methods, or

in regions where other survey types (e.g., aerial) may be difficult due to logistical considerations (Figure 3).

Unmanned Aerial Systems

Aerial photographs from manned aircraft have long been used to identify and measure NARW, SRW, and eastern NPRW (Best and Rütther, 1992; Miller et al., 2011; Clapham et al., 2012). The recent development of small unmanned aerial systems (UAS) with lightweight, high-resolution cameras, provides improved image resolution at lower cost and risk compared to manned flight (Figure 3; Durban et al., 2015; Koski et al., 2015). UAS photogrammetry and sampling has recently been applied to SRW (Apprill et al., 2017; Christiansen et al., 2018) and NARW (Moore et al., 2017) to address a variety of research questions. One direct benefit of UAS photography is obtaining high-resolution aerial images that can be used to identify individuals. UAS imagery represents a small but growing proportion of the NARW and SRW catalogs. This could be expanded in future if the technology is adapted to more challenging weather conditions seen in high latitudes.

Automated Image Analysis

Automated and semi-automated computer image analysis methods have been increasingly used to detect whales in images, and match whales to a catalog of known individuals (Hillman et al., 2008; Kniest et al., 2010) including SRW (Hiby and Lovell, 2001) and NARW (Bogucki et al., 2018). Bogucki et al. (2018) identified individual NARW with 87% accuracy using a series of convolutional neural networks in a fully automated pipeline with no need for user input. These computer vision identification methods may increase the efficiency of matching, and enable the processing of larger volumes of data, especially from different sources (still images and video taken from aircraft, UAS, and land and shipboard surveys). These methods could be especially helpful in coordinating catalogs from different populations

and right whale species to assess connectivity, ranging and movement.

Biologgers

Instrumenting animals with high-resolution inertial sensors (e.g., accelerometers, magnetometers, and gyroscopes; **Figure 3**) has provided detailed information on their fine-scale movements and biomechanics in foraging patches. Time-depth recorders have been deployed on NARW (Winn et al., 1995; Baumgartner and Mate, 2003; Baumgartner et al., 2017) and SRW (Argüelles et al., 2016), while tags with additional sensors (acoustic and/or inertial, e.g., DTAGs; Johnson and Tyack, 2003) have been deployed on NARW (Nowacek et al., 2001, 2004; Parks et al., 2011; Nousek-McGregor et al., 2013; van der Hoop et al., 2017b, **Table 1**). Efforts to bridge the gap toward high-resolution, medium-duration tags with minimally invasive attachment are underway (Baumgartner et al., 2014a; Johnson et al., 2014; Mate et al., 2017).

Synthesis

Despite our best efforts to sight, photograph, record, sample, and track individual right whales, and to synthesize these observations into general consensus on the species' ecology and distributions, individuals will continue to surprise us. NARW have given birth in Cape Cod, a generalized springtime foraging ground (Patrician et al., 2009), and NARW and SRW show out-of-season foraging (Mayo and Marx, 1990; Best and Schell, 1996; Kenney et al., 2001; Hoffmeyer et al., 2010). All species and populations show rare long-distance movements, and acoustic detections indicate that our understanding of all species' seasonal distributions and contemporary ranges is always changing. This highlights the continued need to survey, identify, and acoustically monitor right whale habitats year-round, and in all weather conditions, expanding survey efforts beyond current methods (**Table 2**).

Quantifying changes in movement patterns at any temporal or spatial scale requires data at sufficient resolution, a mechanistic understanding, and long-term measures of potential drivers. Whaling records and sightings provide a reasonable foundation for many basic questions on the populations and their movements. Combining these sightings with individual identification (by genetics or visible marking), isotopes, acoustics, and simultaneous oceanographic measurements or models will increase our understanding of where animals are, why they are there, and where they might go next. Synthesizing data from across different populations is particularly important in this context. There may be local (wintering or feeding ground) or global (climate change) drivers that can be inferred from such a comparative approach, particularly in SRW where there are multiple wintering grounds with long-term monitoring projects (**Table 2**).

METHODS FOR ASSESSING FACTORS AFFECTING RIGHT WHALE HEALTH

Marine mammals are vulnerable to a variety of intrinsic stressors, including infectious diseases, harmful algal blooms, prey

shortages, and climate change, particularly when subjected to extrinsic stressors such as fishing gear entanglements, pollution, and acoustic disturbance (**Figure 3**). Both independently and in synergy these stressors may have an effect on infectious disease transmission dynamics (Gulland and Hall, 2007), and they are also likely to affect reproduction and the potential for mortality. Although stress is beneficial in the short-term to respond to and recover from a stimulus or perceived threat, remaining in a stressed state in the long-term is maladaptive. Maintaining this unbalanced 'allostatic state' can impair future stress response and fecundity and result in immune and other physiological dysfunction (McEwen and Wingfield, 2003; McEwen and Wingfield, 2010; Houser et al., 2016).

In aquatic mammals, contemporary assessments of marine mammal health are almost invariably biased toward animals whose health is already compromised, such as stranded animals (Gulland and Hall, 2007; Hunt et al., 2015), which in part reflects the difficulties in sampling aquatic environments. Yet identification of chronic changes requires monitoring of free-living animals. There are several tools available and more are emerging (**Figure 3**).

Dolphins and seals are vulnerable to viral infection, with serious pandemics of influenza virus (Cox and Subbarao, 2000; Groth et al., 2014), poxvirus (Fiorito et al., 2015) and morbillivirus (Sierra et al., 2014, 2016). Although no pandemics have been reported for large whales, as right whales undertake large scale migrations they could be the source of, and vectors for, potentially serious zoonoses (Bogomolni et al., 2008). Their inshore movements into urbanized coastal waters further increase their vulnerability. As Gulland and Hall (2007) point out, morbidity and mortality in marine mammals have resulted from terrestrial pathogens spreading to the ocean, from harmful algal blooms to epidemics of virulent viruses and bacteria (Geraci et al., 1999; Miller et al., 2002). Brucellosis, a pathogen that affects reproduction in mammals, has been reported in whales (Van Bressema et al., 2009), with potential for widespread population consequences. SRW adults and calves in Argentinian waters that suffer injuries from kelp gull attacks (Rowntree et al., 1998; Sironi et al., 2009), are exposed to pathogens such as *Klebsiella*, *Salmonella*, and *Shigella* confirmed in kelp gull feces (Fazio et al., 2012). Necropsies with pathology studies and metagenomic surveys of viral and bacterial diversity are therefore important for developing a greater understanding of the impact of oceanic pathogens (Geoghegan et al., 2018) on right whales' population biology.

In NARW, there has been a long-standing visual health assessment program that uses individual identification photographs to monitor individual whale health (Pettis et al., 2004). This tool has been applied to predictions of outcomes for animals that are entangled (Pettis et al., 2017), and has been used to model the health of the population and individual demographic groups (Rolland et al., 2016). These methods could easily be applied to other right whale populations where photo-identification catalogs are maintained (**Figure 3**).

Another approach is the use of various matrices to assess reproductive and stress hormones in feces of individual right whales (Hunt et al., 2015). Hormonal profiles can reveal

reproductive status (Rolland et al., 2005; Corkeron et al., 2017), increases in stress due to chronic entanglement (Rolland et al., 2017) and evidence of chronic stress due to shipping noise (NRC, 2005; Hunt et al., 2006; Rolland et al., 2012; Hunt et al., 2015). The findings of this program highlight the need to monitor free-ranging animals. Fecal collection is largely opportunistic and not viable for animals that are only available during fasting periods (e.g., most SRW). A potentially more accessible and repeatable method is to use whale respiratory vapor to assess hormone levels, disease organisms, and microbiome information. Burgess et al. (2018) demonstrated the feasibility of using pole-mounted collection of whale blow for hormone analyses with the caveat that sample concentrations must be normalized as an unknown amount of salt water is mixed with every exhalation (Burgess et al., 2018). UAS collection provides the opportunity to sample while keeping the boat further away from individual whales. Pirodda et al. (2017) used a drone to collect an extraordinary diversity and abundance of microbiota from the blow in migrating populations of humpback whales, clearly and unambiguously distinguishing microbial communities from surrounding control seawater and air samples (Pirodda et al., 2017). Drones such as these can sample whale blow and provide an assessment of respiratory bacteria, lipids, proteins, and even viruses (Apprill et al., 2017; Pirodda et al., 2017; Geoghegan et al., 2018). As with all new techniques, further refinement is needed to determine how consistently representative bacterial and viral samples may be for the animal, and therefore its health. Nevertheless, this area shows great promise and is evolving rapidly.

During whaling, body condition measurements included measures of girth and blubber thickness, with fine-scale measurements of percent lipid, protein, and ash contents in different parts of the body (Lockyer et al., 1985). More recently approximations to body condition have used indirect estimates of buoyancy (e.g., with bio-logging tags; Nowacek et al., 2001; Nousek-McGregor et al., 2013), direct measurements of blubber thickness with pole-mounted ultrasound (Miller et al., 2011) or body shape changes from photogrammetry, from aerial photographs (Best and R  ther, 1992; Miller et al., 2012) including from drones (Moore et al., 2017; Christiansen et al., 2018).

Harmful algal blooms and marine pollutants remain a concern. In NARW whales feeding close inshore are repeatedly exposed to multiple environmental neurotoxins produced by marine algae (Durbin et al., 2002; Doucette et al., 2012). Less well understood across the three species is the impact of marine pollutants: NARW are exposed to low but chronic levels. In this context, understanding the level of genomic diversity in populations and susceptibility of individuals to pathogens, harmful algal blooms and toxins will also help understand individual and population level impacts (Leroy et al., 2017).

Finally, in the case of animals that have been entangled, the increased drag, altered behavior, and additional energy demand, leads to decreases in body condition (Cassoff et al., 2011; Moore et al., 2013; van der Hoop et al., 2013b; Barratclough et al., 2014; van der Hoop et al., 2016b), elevated stress hormones (Rolland et al., 2017), poor health condition (Rolland et al., 2016; Pettis et al., 2017) and reduced reproductive success (Knowlton et al.,

2012b). Future research along this cascade includes clarifying the interactions between stress, energetic demand, nutrition, and metabolism, and ultimately the population consequences of those stressors (Figure 3).

COMPARATIVE SYNTHESIS AND CUMULATIVE EFFECTS

The lack of a cumulative effects analytical approach impedes any understanding of multi-stressor conditions affecting marine mammals, especially those in more industrialized sections of ocean (Figure 3). It also hampers effective management, as it is impossible to know that managing stressor A is a better approach than managing stressor B, if stressor B is exacerbated by interactions with stressors C, D, and E. *“If cumulative effects cannot be accounted for, then unexpected adverse impacts from interactions between stressors pose a risk to marine mammal populations and the marine ecosystems on which people and marine mammals depend”* (National Academies of Sciences, and Engineering and Medicine, 2017). Without such a framework every stressor is managed in isolation, wasting resources, and reducing efficacy. There are many marine mammal examples. In harbor porpoise, Hall et al. (2006) showed that previous exposure to PCBs increased the risk of death from infectious diseases. In killer whales, Ford et al. (2010) suggest high POP concentrations may have acted synergistically with limited food resources, increasing mortality during times of low prey abundance. In baleen whales, the poster child for the cumulative effect problem is the NARW. As discussed earlier, the NARW is subject to multiple anthropogenic stressors that are well studied, and multiple environmental stressors that are known, although the effects are not fully understood (Figure 3).

Early work in this area was the development of a conceptual model of the Population Consequences of Acoustic Disturbance (PCAD), with subsequent models discussed by New et al. (2014); Fleishman et al. (2016), and Pirodda E. et al. (2018). Further developments in the field resulted in the National Academies of Sciences, and Engineering and Medicine (2017) report, and another conceptual model called Population Consequences of Multiple Stressors (PcoMS: National Academies of Sciences, and Engineering and Medicine, 2017). Both of these models are dependent upon a series of transfer functions that describe how exposure to stressors affects individual behavior or health, which is defined as all factors that comprise “fitness” or homeostasis. Variations in health can affect individual vital rates, and the variation in severity or level of exposure to a given stressor can be used to scale up to predictions of population level effects. National Academies of Sciences, and Engineering and Medicine (2017) provided a decision tree for thinking about cumulative effects analyses, and also recommended stepwise, hypothesis driven, adaptive management strategies to deal with the uncertainties inherent in most marine mammal/stressor interactions. The NAS Committee concluded that current scientific knowledge is not up to the task of predicting cumulative effects of different combinations of stressors on marine mammal populations.

Nevertheless, there are many things that we can do to enhance future PcoMS or other cumulative effects models. A comparative synthesis of biological parameters, known ecological parameters, and known anthropogenic threats, using data from many well-studied right whale populations, can inform ongoing and future cumulative effect analyses on this taxon and we outline research priorities to move toward this goal as we see them (Table 2).

The findings of such cumulative impact models, and its components, could be integrated into international legislation to ensure the continued survival of the right whales. Today, the hunting of whales is controlled by the International Whaling Commission (IWC), and the trade in whale products is governed by the Convention on the International Trade of Endangered Species of wild fauna and flora (CITES). In addition, the Convention on the Conservation of Migratory Species of Wild Animals (CMS), which operates under the auspices of the United Nations Environmental Programme, provides a cross-border mechanism for protecting right whales throughout their migratory networks. All three species are listed under Appendix I of the CMS convention, and could be subject to a special agreement under the treaty. Such agreements should promote co-ordinated conservation and management plans across the range of species, in addition to promoting conservation and restoration plans for important habitat areas². This would link together national

level legislation to provide a web of protection for the species around the world.

CONCLUSION

The name *right whale* was not a misnomer. The three right whale species were easy to exploit and all driven very close to extinction. Only a few populations of the SRW can be considered to have recovered well and the status of the eastern NPRW and NARW along with some populations of the SRW remain precarious. In this review we have outlined the manner in which the right whales were exploited and how we have monitored their recovery. The fragile status and in particular the recent reversal in recovery trajectory by NARW call for urgent action. Yet the close phylogenetic relationship and ecological equivalence between the three species may provide fruitful avenues for avoiding catastrophe. Insights from careful examination of the populations that have recovered, combined with approaches that draw on novel methods developed separately for different populations may provide guiding principles for future conservation research, to hopefully make these the right whales to survive.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

²<https://www.cms.int/en/cms-instruments/agreements>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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