



The migratory whale herd concept: A novel unit to conserve under the ecological paradigm

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Abstract

Photographic and genetic studies have revealed the complex population structure of migratory large whales. Most research and management are geographically based, focusing on either wintering or summering areas, which in most cases fails to capture this complexity. We use examples from humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) to illustrate the concept of migratory herds, defined here as conspecific whales that migrate between the same wintering and feeding ground. In cases where individuals show strong fidelity to both feeding and wintering grounds, and therefore to a herd, dispersal between herds can be low enough to render them as demographically independent populations, where population dynamics are determined more by net internal recruitment (births minus deaths) than by immigration from outside sources. In these cases, the migratory whale herd is the appropriate unit to conserve under the ecological paradigm that focuses on groups united by demographic forces. We suggest that when addressing questions focused on ecological timescales for whale species with strong fidelity to migratory destinations, the migratory whale herd is a better initial working hypothesis rather than one based on geographically defined strata.

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KEYWORDS

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1 | INTRODUCTION

The term “population” has no single definition, yet populations are fundamental to most studies in ecology, demography, and evolution, and are the foundation of conservation management. In recent decades there has been a growing recognition that the definition of a population should depend on the type of question being asked (Palsbøll et al., 2007; Taylor & Dizon, 1999; Waples & Gaggiotti, 2006). For example, the population that is relevant to a study of dietary patterns of California sea lions, *Zalophus californianus* (DeLong et al., 1991) is very different from the population that is relevant to understanding the evolutionary history of that species (Schramm et al., 2009). Waples and Gaggiotti (2006) review different population concepts and classify them into two broad categories, the “Ecological Paradigm” and the “Evolutionary Paradigm.” Those that focus on groups that are united by demographic forces (e.g., dispersal of animals between groups, birth and death rates within groups, and other forces that operate on an annual timescale) fall under the Ecological Paradigm; those that focus on groups united by evolutionary forces (e.g., gene flow, selective pressure, and other forces that operate on the timescale of generations or longer) fall under the Evolutionary Paradigm.

The laws and frameworks that guide conservation and management can also be classified as falling under the Ecological or Evolutionary Paradigms, depending on their management objectives (Martien et al., 2013; Palsbøll et al., 2007; Taylor et al., 2010). Frameworks that focus on preventing extinction, such as the IUCN Red List, the U.S. Endangered Species Act (ESA), and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), clearly fall under the Evolutionary Paradigm. The units-to-protect under these management schemes are species, subspecies, and groups between which gene flow is sufficiently low to allow adaptations potentially significant to the resilience of the species (Taylor et al., 2010).

In contrast, many management frameworks focus on preventing the depletion of populations within species. These include the U.S. Marine Mammal Protection Act (MMPA), the International Whaling Commission's Revised Management Procedure (RMP), and Australia's Environment Protection and Biodiversity Conservation (EPBC) Act. The focus of these frameworks on ecological and demographic features of populations places them firmly under the Ecological Paradigm. The appropriate unit-to-protect for conservation and management efforts on ecological timescales is the Demographically Independent Population (DIP), which is defined as a group whose population dynamics is more a consequence of internal dynamics (births and deaths) than external dynamics (immigration and emigration; Brakes et al., 2021; Martien et al., 2012, 2013; Palsbøll et al., 2007; Taylor et al., 2010). The DIP is also the population concept relevant to basic research questions focused at ecological scales, such as estimating vital rates, trends in abundance, and metrics of population health.

Evaluating whether groups constitute DIPs requires determining whether the rate of dispersal between them is low enough to render them demographically independent (Hastings, 1993; Palsbøll et al., 2007; Taylor, 1997; Taylor & Dizon, 1999; Waples & Gaggiotti, 2006). The threshold level of dispersal below which two populations are demographically independent is 1%–10% per year, depending on several factors (Hastings, 1993; Taylor, 1997). Furthermore, if females exhibit strong site fidelity, demographic independence can be maintained despite substantial male-biased dispersal since male immigrants have little to no impact on birth rates within a population and therefore cannot compensate for reduced internal recruiting resulting from an increased mortality rate (Martien et al., 2012, 2019; Mesnick et al., 2011; Rosel et al., 1999). Thus, though even a low level of male-biased dispersal can prevent the evolutionary divergence of two populations, it will have negligible demographic impact.

The *DIP Delineation Handbook* (Martien et al., 2019) provides an extensive review of the various methods and data types that can inform such a determination once putative DIPs have been identified. However, in some cases,

deciding how to stratify individuals into putative DIPs can be challenging. This is particularly true for whale species that undertake annual migrations between high-latitude feeding grounds, where they spend most of the year, and low-latitude wintering grounds, where most breeding has been assumed to occur. The complicated annual movement patterns exhibited by these species can result in wintering grounds that are comprised of groups of individuals from multiple feeding grounds, and feeding grounds that are shared by groups of individuals from different wintering grounds (e.g., Calambokidis et al., 2000, 2001; Clapham et al., 1993b).

Most research on migratory whales has focused on either wintering grounds (e.g., Carroll et al., 2011; Darling et al., 2019a; Kershaw et al., 2017) or feeding grounds (e.g., Clapham et al., 2008; Frasier et al., 2011; Lang et al., 2014; LeDuc et al., 2007). While these are valid stratifications that are relevant to many questions, in many cases neither feeding nor wintering grounds represent demographically cohesive or independent units. This is particularly true in species where calves accompany their mothers during their first migration and subsequently exhibit strong fidelity to both feeding and wintering grounds throughout their lives, and where such grounds are used by animals from multiple geographic regions at the other end of the migration. There has been a growing recognition of the importance of considering both ends of the migratory route when studying population structure. Much of this focus has come from the animal culture literature, in which fidelity to natal wintering grounds and maternal feeding grounds is assumed to be an example of vertical social learning between mother and offspring (Carroll et al., 2015; Hoelzel, 1998; Valenzuela et al., 2009; Whiten, 2017). The entire system of migratory destinations and the connections between them are referred to as “migratory networks,” and fidelity to a particular wintering and feeding ground is termed a “migratory tradition” (Carroll et al., 2015) or “cultural variant” (Brakes et al., 2021). Many researchers have advocated accounting for these cultural variants when assessing both the long-term viability of the network and potential responses of species to changing environmental conditions (Brakes et al., 2019, 2021; Carroll et al., 2015; Keith & Bull, 2017; Taylor & Hall, 2012; Valenzuela et al., 2009).

Here we present a new concept called the “migratory whale herd,” which we define as, “conspecific whales that migrate between the same wintering and feeding grounds.” Entire migratory whale herds do not move together as a single cohesive group, as is seen in some ungulates, but simply utilize the same migratory destinations. Because recruitment into migratory whale herds is matrilineal, and all members of the group utilize the same habitats throughout the year, they represent the natural demographic unit for migratory whales and are therefore a special case of a DIP. A migratory whale herd can be thought of as the group of animals that share a particular migratory tradition. However, the migratory whale herd concept differs from previously published concepts in several important ways: (1) it applies to the group of animals rather than their behavior; (2) it is focused on demographic independence rather than cultural significance; and (3) it applies to any whale species with fidelity to natal wintering and feeding grounds, regardless whether that fidelity is acquired through social learning, genetic inheritance, geophysical imprinting, or some other mechanism. We recommend that research and management that falls under the Ecological Paradigm (Waples & Gaggiotti, 2006) should be focused on migratory herds for at least some species of large whales.

We illustrate the migratory whale herd concept by focusing on the humpback whale (*Megaptera novaeangliae*), for which the available data suggested this new way of thinking about DIPs for migratory animals. We then discuss gray whales (*Eschrichtius robustus*), which also exhibit migratory patterns consistent with the migratory whale herd concept. Drawing upon life history and behavioral traits of these two species, we conclude that, for some migratory baleen whales, the “herd” concept might prove to be a better initial working hypothesis than more traditional geographically based approaches when considering the unit to conserve within the Ecological Paradigm.

2 | HUMPBACK WHALE EXAMPLES

Much is known about humpback whales because of the ease of identifying individuals using photographs of the unique markings on the ventral surface of their flukes (Katona & Whitehead, 1981), and because many of their feeding and wintering areas are within easy reach of small research vessels. Humpback whales are also easily biopsied,

which has allowed thousands of tissue samples to be obtained for genetic analyses in the North Atlantic (Palsbøll et al., 1995), the North Pacific (Baker et al., 2013), the South Pacific (Constantine et al., 2012), and elsewhere. In these analyses, mitochondrial DNA (mtDNA) is the most commonly used marker, specifically the mtDNA control region, due to its ease of sequencing, high mutation rate, and haploid nature. Most importantly, because mtDNA is inherited only from the mother, and recruitment in humpback whales is matrilineal, this genetic marker not only provides an independent line of evidence for assessing demographic independence and site fidelity, but also gives insight over a longer time-frame than photographic identification, and will thus be referenced in all of the examples below.

Early studies revealed that calves exhibit strong, lifelong fidelity to the same feeding and wintering grounds as their mothers (Clapham et al., 1993a). Humpback whales are found on feeding grounds in summer, fall, and into early winter. Most animals migrate to warmer waters for a few months in winter, when calving occurs, though some whales may occasionally reside year-round in some feeding areas (Brown et al., 1995; Davis et al., 2020; Straley, 1990) or only migrate partway to the wintering ground (Best et al., 1995; Eisenmann et al., 2016); there is one well-documented nonmigratory population in the Arabian Sea (Pomilla et al., 2014). Studies that have accumulated around the globe for this species reveal complex migratory patterns that vary among ocean basins and are influenced by the different sizes of ocean basins and the currents within them (Kershaw et al., 2017; Rosenbaum et al., 2017). Here we focus on a few well-studied cases to argue that matrilineal recruitment driven by natal fidelity to migratory destinations results in all such humpback whale DIPs being migratory whale herds.

2.1 | West Indies to the Gulf of Maine migratory herd—an example of a shared wintering ground and a “private” feeding ground

The western North Atlantic has several discrete humpback feeding grounds: the Gulf of Maine, eastern Canada, and western Greenland (Figure 1; Katona & Beard, 1990; Stevick et al., 2006); additional feeding areas are located off Iceland and Norway in the central/eastern North Atlantic. The discreteness of the whales summering in these various areas is supported by photographic identification, with individually identified animals returning to the same feeding area for years or decades (Clapham et al., 1993a). It is also evident in analysis of mtDNA (Palsbøll et al., 1995).

During the winter, whales from all of the western North Atlantic feeding areas (including the Gulf of Maine) mate, calve, and mix spatially and socially on shared wintering grounds in the West Indies, with the largest concentrations occurring on platform reef systems north of Hispaniola (Clapham et al., 1993b; Katona & Beard, 1990; Kennedy et al., 2014; Palsbøll et al., 1997; Stevick et al., 1998, 2006). They share this breeding habitat with some of the animals that feed in the eastern North Atlantic (off Iceland and Norway), although the latter appear to arrive on average later in the winter, and are disproportionately represented farther east in the Leeward and Windward Islands (Stevick et al., 2018).

Furthermore, it is apparent that some of the eastern North Atlantic whales migrate elsewhere. This includes to the Azores (dos Santos et al., 2022) and the Cape Verde Islands (Wenzel et al., 2020), which were once the site of whaling in the 19th century (Reeves et al., 2002), although the small number of sightings in that archipelago today, relative to the abundance of whales off Iceland and Norway, suggests that many eastern whales are wintering in unknown areas.

An ocean-basin scale study was conducted in 1992–1993 that provided abundance estimates of 10,600, 95% CI [9,300, 12,100] humpback whales in the North Atlantic (Smith et al., 1999). The estimate from the same effort for the Gulf of Maine feeding aggregation was 889 (CV = 0.32; Smith et al., 1999). Between 1999 and 2003 the average annual human-caused mortality for the Gulf of Maine was estimated to be about four whales (Waring et al., 2006).

Gulf of Maine humpback whales are managed under the U.S. MMPA, which falls under the Ecological Paradigm. Until 2001, human-caused mortalities in the Gulf of Maine (notably fishing gear entanglements and ship strikes) were assessed against the North Atlantic abundance estimate of approximately 10,000 whales, despite the fact that

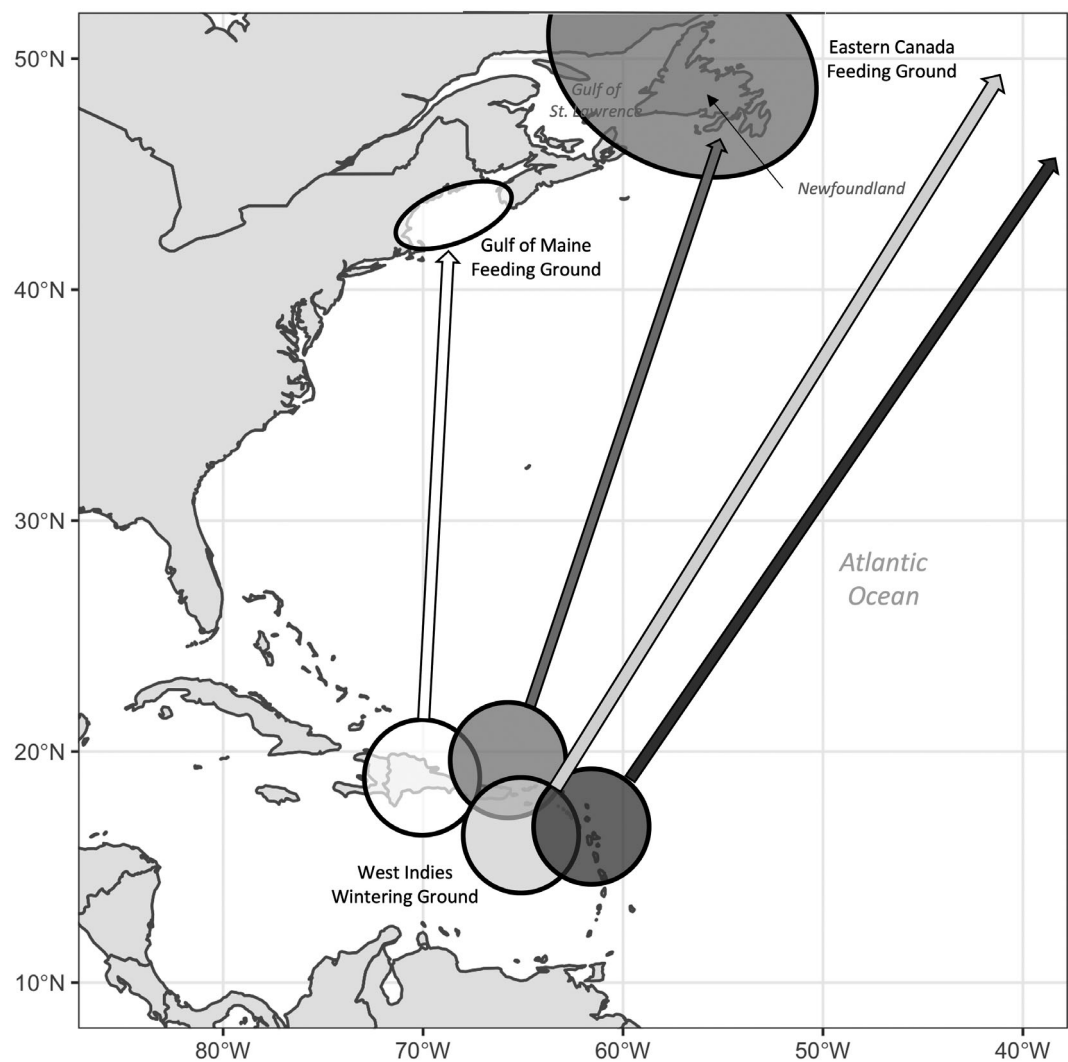


FIGURE 1 Conceptual map of West Indies humpback whale herds. Circles and ellipses represent herd wintering and summering areas and are not intended to indicate exact ranges. Arrows indicate migratory connections, including to feeding areas off the map, but do not represent precise migratory routes.

recruitment into the Gulf of Maine feeding aggregation is driven primarily by the reproductive output of the roughly 900 whales that make up the aggregation. This ten-fold overestimate in the abundance of the affected group resulted in a dramatic underestimate of the impact of the human-caused mortality. In 2002, the assessment protocol changed such that only the estimated abundance in the Gulf of Maine was used in the assessment, which revealed that the human-caused mortality exceeded what was allowed under the MMPA. If human-caused mortality can be reduced to the levels allowed under the post-2001 management, the population should be able to recover more quickly, as intended. Correctly identifying the Gulf of Maine migratory herd as the management unit under the MMPA rather than combining it with the other West Indies herds became even more important when the West Indies wintering aggregation was removed from the U.S. Endangered Species list in 2016 (Bettridge et al., 2015), resulting in a five-fold increase in the allowed human-caused mortality for its constituent stocks (Hayes et al., 2017).

The Gulf of Maine feeding aggregation fits the definition of a migratory whale “herd” and is thus the appropriate “population” to manage under the Ecological Paradigm. It is important to note that the Gulf of Maine herd is not a closed population. Rather, it experiences occasional dispersal through the immigration of individuals from other herds. Stevick et al. (2006) estimated an exchange rate of 0.98% between feeding areas in the western North Atlantic between 1992 and 1993, though they noted that examination of photo-identification records that span 13 years revealed that most feeding area exchanges are temporary rather than reflecting permanent dispersal. Similarly, Stevick et al. (2016) found rare cases of exchange between the West Indies wintering area and the Cape Verde wintering area, which is used by animals that feed in the eastern North Atlantic (Wenzel et al., 2020). Stevick et al. identified four instances of exchange between the two wintering areas over the course of more than a decade, though again in the two cases where the animal was identified more than twice, it was observed to return to its original wintering ground after a single year. These levels of exchange between migratory destinations, most of which is likely to be temporary, are low enough to render the Gulf of Maine herd demographically independent.

Because there is substantial gene flow among the North Atlantic herds that winter in the West Indies, no significant differences in nuclear DNA were found among the western North Atlantic feeding grounds (Palsbøll et al., 1997). Using these nuclear DNA results as a basis to delineate populations of humpback whales in the North Atlantic would lead to erroneous pooling of migratory whale herds and potential mismanagement under the Ecological Paradigm. To delineate populations under the Ecological Paradigm, it is critical to evaluate the means of recruitment into the herd, which in this case does not depend on how the whales mate.

2.2 | Central America to California/Oregon/Washington herd—an example of a “private” wintering ground and shared feeding ground

A basin-wide study of humpback whales in the North Pacific, known as SPLASH (Structure, Population Levels, And Status of Humpbacks), took place between 2004 and 2006. The study found that whales that wintered in Central America were discrete based on both photographic identification (Barlow et al., 2011; Calambokidis et al., 2008) and mtDNA data (Baker et al., 2013) when compared with other North Pacific whales, including those that wintered in adjacent areas in Mexico. Because the Central America animals all migrate to the same summer feeding area off the coasts of California, Oregon, and Washington (Figure 2), they meet the migratory whale herd definition.

Like the Gulf of Maine herd, the Central America herd was not found to differ in nuclear DNA from the primary humpback whale wintering areas in Mexican waters, but did differ strongly in mtDNA (Baker et al., 2013). Photo-identification data from SPLASH also supported the discreteness of the Central America herd, with few to no photographic matches of the 105 unique individuals identified in Central America to either northern coastal Mexico (with 690 unique individuals identified) or the Revillagigedo Archipelago (562 unique individuals identified) (Calambokidis et al., 2008). This evidence is consistent with recruitment through natal fidelity to maternal migratory destinations.

Unlike the Gulf of Maine whales, the Central America whales share their feeding grounds with whales that winter farther north along the Mexico mainland. Within California and Oregon, the proportion of whales from these two different wintering grounds differs latitudinally, with Central America whales predominating in southern and central California, and mainland Mexico whales predominating in northern California and Oregon (Calambokidis et al., 2017). Human-caused mortality (from ship strikes and entanglements) also appears to be higher in Southern and Central California (Carretta et al., 2018; Rockwood et al., 2017), which is an area with a large proportion of the whales that winter off Central America. The assessment of the level of risk posed by the mortality in southern and central California to the Central America herd should be based upon the abundance of that herd, and the probability that a death was from that herd and not from other herds that feed in the same area (see Taylor et al., 2021 for further details in describing this herd).

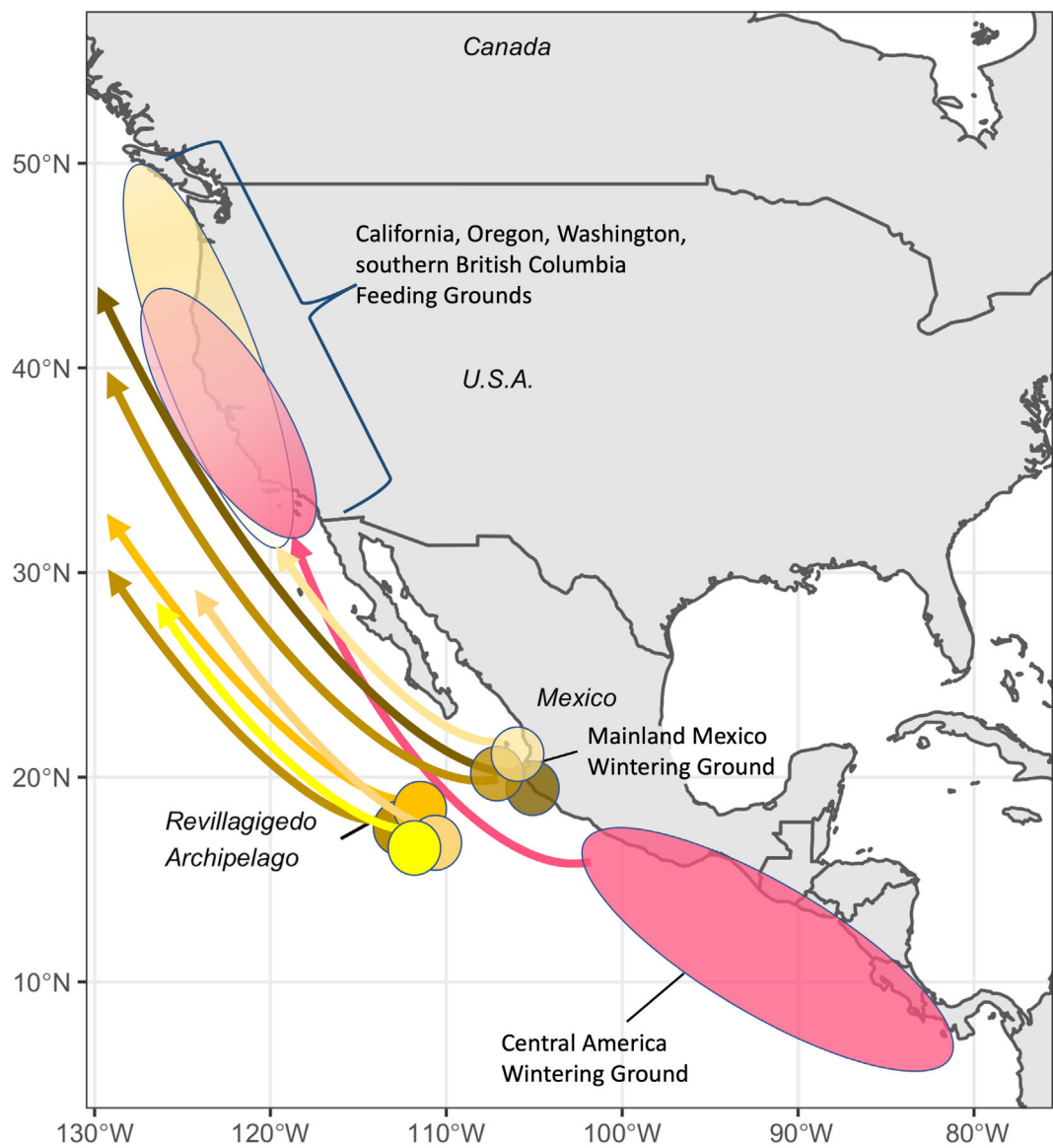


FIGURE 2 Conceptual map of humpback whale herds that migrate from mainland Mexico and Central America to the U.S. west coast. Circles and ellipses represent herd wintering and summering areas and are not intended to indicate exact ranges. All herds that winter in Mexico are shown in shades of yellow/brown, while the Central America herd is shown in pink. Arrows indicate migratory connections, including to feeding areas off the map, but do not represent precise migratory routes.

2.3 | Mainland Mexico to California/Oregon/Washington herd—an example of shared wintering and feeding grounds

Based on SPLASH data, most whales from the mainland Mexico wintering aggregation migrate to feeding grounds along the contiguous U.S. west coast (California, Oregon, and Washington; Figure 2). However, some migrate to more northerly feeding grounds in British Columbia and Alaska, with a concentration in the Aleutian Islands and

Bering Sea areas. Because of ease of access by small boats, nearly continuous research along the contiguous U.S. west coast has provided good data to document the same pattern of maternally driven recruitment and site fidelity seen in the last two examples. The mainland Mexico whales that migrate to the U.S. west coast are exposed to different feeding conditions and different risks from human-caused mortality and predation compared to those who migrate to other feeding areas. They also likely expend different proportions of their energy budgets on migration (Villegas-Amtmann et al., 2017). Martien et al. (2020) found that whales that migrate between mainland Mexico and the U.S. west coast have different mtDNA haplotype frequencies from the Central America herd, with which they share most of their feeding ground. In addition, Martien et al. found that this group of whales differs significantly in mtDNA haplotype frequencies from the overall mainland Mexico wintering aggregation analyzed in Baker et al. (2013), which contains whales with multiple feeding destinations. Thus, the whales that migrate between mainland Mexico and the U.S. west coast fit the migratory whale herd definition, with maternally-driven recruitment and strong fidelity to both feeding and wintering grounds.

This herd shares their wintering grounds with whales that feed on more northerly feeding grounds, and shares their feeding grounds with Central America whales. Human-caused mortalities off Central California of whales that winter in mainland Mexico should not be assessed against all mainland Mexico whales, nor against all U.S. west coast whales, as both approaches would overestimate the abundance of the demographic unit impacted by the mortalities (see Martien et al., 2021 for further details describing this herd). Appropriate assessment of the death of a whale of unknown population origin killed off California should be prorated across two migratory whale herds: Central America, and the herd from mainland Mexico that feeds along the contiguous U.S. west coast.

2.4 | Hawai'i to Southeast Alaska migratory whale herd—an example of a shared wintering ground and nearly private feeding ground

Whales that winter in the Hawaiian Archipelago migrate, in various proportions, to feeding grounds that span the North Pacific Basin (Figure 3). Nearly all these feeding grounds are to a greater or lesser extent shared with whales from other wintering grounds. The exception is the Southeast Alaska feeding ground, which during the SPLASH years (2004–2006) was occupied almost entirely by animals from Hawai'i, with a small number migrating from Mexico (Barlow et al., 2011; Urbán R. et al., 2000). The Hawai'i–Southeast Alaska migratory herd is of interest for two reasons: (1) the overall nuclear DNA profile of Southeast Alaska differs from that found in the Hawai'i wintering ground, where the herd is mixed with herds from multiple feeding grounds (Baker et al. 2013), and (2) only five mtDNA haplotypes have been found in Southeast Alaska whales, with over 96% of individuals possessing the two most common haplotypes. In comparison, Baker et al. (2013) detected 11 haplotypes in Hawai'i, with the two most common comprising only 71% of the population. The first point is of interest because it suggests that Southeast Alaska whales are more likely to breed with each other than with other whales that migrate to Hawai'i, either due to mating on the migratory route or temporal or spatial segregation on the wintering ground (Lammers et al., 2023). If nearly all Southeast Alaska whales migrate to Hawai'i and were equally likely to mate with any other Hawai'i whale, then nuclear DNA differences would not be expected. Until there is a better understanding of when and where mating occurs, the wintering area cannot be assumed to be the only place where breeding occurs. This is consistent with the occurrence of humpback whale song (widely assumed to be related to reproduction) both on migratory routes and feeding grounds (Charif et al., 2001; Clark & Clapham, 2004; Garland et al., 2013; Noad & Cato, 2007; Schall et al., 2021b, 2022; Vu et al. 2012).

From the perspective of the migratory whale herd concept, the second finding—that 96% of the Southeast Alaska herd has only two haplotypes—is of great interest because it yields insight into the long-term stability of the herds. Shore-based whaling killed humpback whales in Southeast Alaska in the early 1900s (Andrews, 1909) but ceased by 1922 (Rice & Wolman, 1975). By 1986, Baker et al. (1992) estimated 547 whales in Southeast Alaska. By 2008, estimated abundance had increased to 1,585 (Hendrix et al., 2012). Haplotypic diversity (h) is the probability

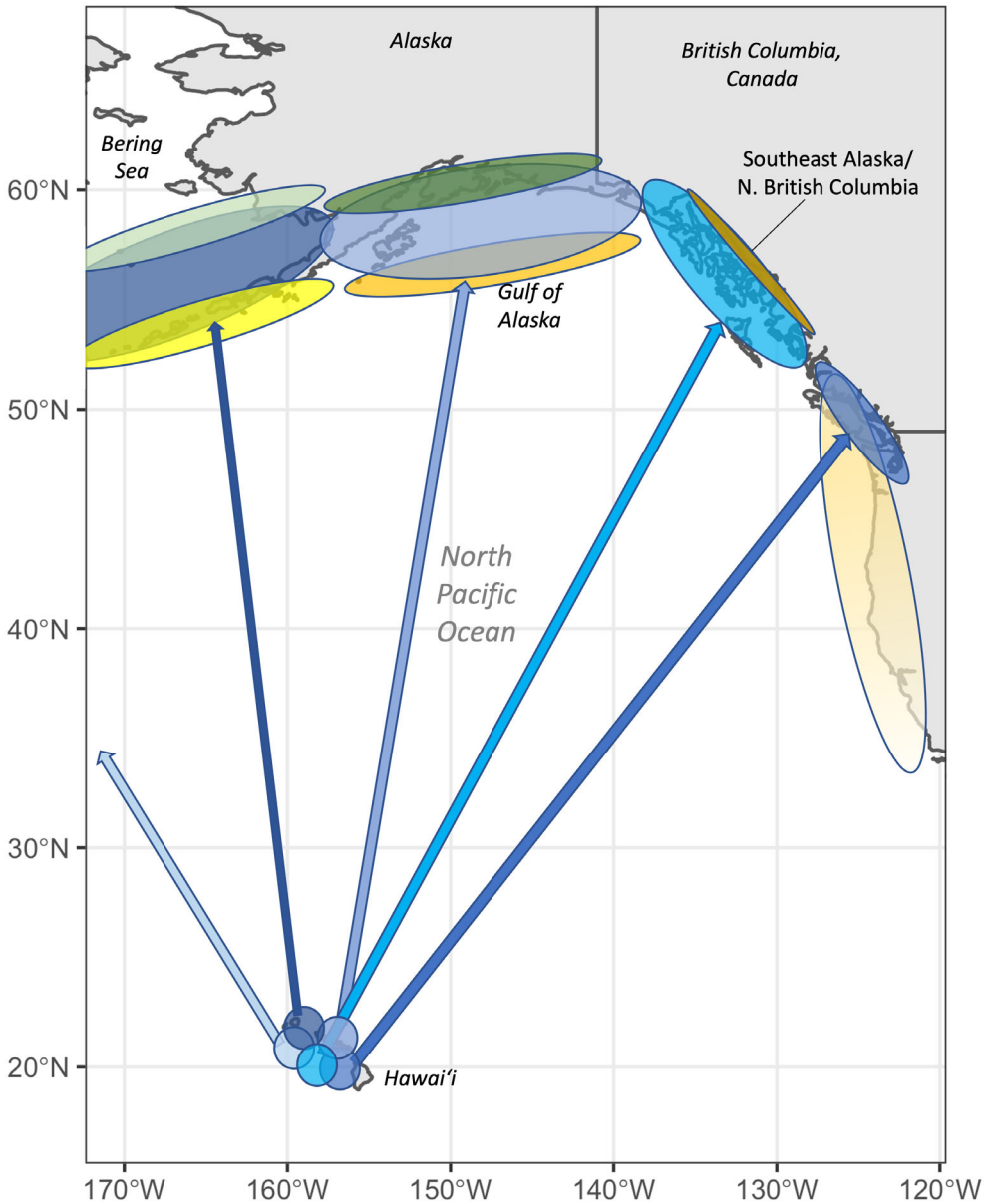


FIGURE 3 Conceptual map of the migratory connections of Hawai'i humpback whale herds. Circles and ellipses represent herd wintering and summering areas and are not intended to indicate exact ranges. All herds that winter in Hawai'i are shown in blue, those that winter in Mexico are shown in shades of yellow/brown, and those that winter in the western Pacific are shown in green. Arrows indicate migratory connections from Hawai'i, including to feeding areas off the map, but do not represent precise migratory routes. Migratory connections for Mexico and western Pacific herds are not shown.

that two individuals randomly sampled from the same population will have different haplotypes. Haplotypic diversity is relatively high for all feeding areas combined ($h = 0.81$) but is very low ($h = 0.47$) for Southeast Alaska (Baker et al., 2013). The five haplotypes found in Southeast Alaska compares with 11 in Hawai'i and 14 in the northern Gulf of Alaska. The most common haplotypes in Southeast Alaska (A– and A+; Baker et al., 2013) are uncommon in

California and Oregon, and the most common haplotype in California and Oregon (F2; Baker et al., 2013) is completely absent from Southeast Alaska. The most parsimonious explanation for most whales in Southeast Alaska sharing one of two common haplotypes is that recovery from the low numbers following whaling was completely through matrilineal recruitment, likely in conjunction with whaling-induced stochastic lineage extinction. Thus, this strong maternal fidelity and natal philopatry has lasted at least over several whale generations.

2.5 | Limitations and considerations

Despite the tremendous amount of data available for humpbacks in the North Pacific, delineating migratory herds remains challenging in many areas, particularly from the less-accessible feeding areas in Alaska and Russia. Even for the Central America wintering aggregation, which is composed of a single herd, stratifying by geography is problematic because data collected since the SPLASH study suggest that the Central America wintering aggregation extends into southern Mexico (Martínez-Loustalot et al., 2022), and may overlap in range with the herds that winter along the coast of northern Mexico (Ortega-Ortiz et al., 2022; Taylor et al., 2021). The situation is even more challenging in other wintering aggregations, where not only are there individuals from multiple feeding areas, but a growing body of data challenging our understanding of geographic structure within and possible connections between wintering grounds (Darling et al., 2019b; Derville et al., 2020; Garrigue et al., 2015; Lammers et al., 2023).

Nonetheless, there is reason to be optimistic that humpback herds can be delineated in the near future. The advent of highly accurate automated matching algorithms that use photographs from researchers and citizen scientists has dramatically increased the number of individuals for which both the wintering and feeding ground, and therefore the herd affiliation, are known (Cheeseman et al., 2021). The large number of biopsy samples available from photographed animals makes it likely that once the match of photographic data sets is complete, herd affiliations can be determined, enabling the assessment of genetic differentiation between and genetic assignment to herds. Geographic areas with higher human impacts are likely to be the areas with the most detailed data available.

While automated matching algorithms have dramatically increased the amount of data available to delineate herds, they have also produced data that challenge our understanding of humpback movement and population structure. There have long been rare, documented cases of interchange of animals between feeding areas and between wintering areas in both the Northern Hemisphere (Calambokidis et al., 2001; Darling et al., 2022; Stevick et al., 2006, 2016; Urbán R. et al., 2000), and Southern Hemisphere (Félix et al., 2020; Garrigue et al., 2011; Steel et al., 2018; Stevick et al., 2013). However, the advent of large, integrated databases enabled by automated matching has resulted in an increase in the number of documented movements between wintering areas. Though most researchers have interpreted these movements to be the results of vagrant animals, they have led some to hypothesize that North Pacific humpback wintering grounds may be fluid, temporary aggregations (Darling et al., 2019a), and that humpback whales may represent one panmictic or several highly overlapping populations in the northeastern Pacific (Darling et al., 2022). However, the number of matches between different wintering grounds still represents a minuscule proportion of the matches found within wintering areas, which have also dramatically increased as a result of automated matching. It is possible that as additional data are amassed, we will discover that the rate of movement between wintering areas is demographically significant. However, to date the documented movements are still consistent with the broader findings of a high level of fidelity to wintering grounds. Migratory whale herds need not represent closed populations, and are likely to experience some level of dispersal as the result of individuals changing their migratory fidelity. When viewed from the perspective of migratory whale herds, the movements between wintering grounds simply represent possible dispersal events (if the interchange is permanent) rather than counterexamples that potentially disprove a population structure paradigm, and are likely to have no demographic impact.

Advances in acoustic recording and analysis technology have also resulted in a dramatic increase in data in recent decades that has challenged previous understandings of humpback whale song and its transmission. Specifically, in the past decade humpback whale songs have been observed to be transmitted among wintering grounds

within an ocean basin (Darling et al., 2019a; Garland et al., 2011). Darling et al. (2019a, 2022) concluded that these observations are indicative of ocean basin-wide panmixia, on the assumption that they could only result from extensive exchange of singing males between wintering areas. However, though singing was once thought to be largely confined to wintering grounds (Charif et al., 2001; Clapham & Mattila, 1990), we now know that humpback whales sing both on their feeding grounds late in the season and on migration (Clark & Clapham, 2004; Magnúsdóttir et al., 2014; Mattila et al., 1987; Noad & Cato, 2007; Norris et al., 1999; Schall et al., 2022; Stimpert et al., 2012; Tyarks et al., 2021; Vu et al., 2012), providing a mechanism for transmission of songs among winter areas in the absence of direct exchange of individuals between wintering grounds (Garland et al., 2013; Owen et al., 2019). Rapid annual shifts in humpback whale song, called song “revolutions,” have been attributed to exposure to song from other populations, either on the feeding ground or migratory route (Garland et al., 2011, 2013; Owen et al., 2019; Tyarks et al., 2022) or due to the movement of a small number of males between wintering areas (Allen et al., 2018; Noad et al., 2000). Thus, though humpback song transmission is an active and intriguing area of research that may yet fundamentally alter our understanding of humpback whale behavior and learning, the data to date are consistent with the high site fidelity to migratory destinations implied by the migratory herd concept.

Like most migratory whales, humpback whales are still recovering from the impacts of commercial whaling (Clapham et al., 2009; Clapham & Baker, 2002). At the same time, they are now being impacted by global climate disruption (Cartwright et al., 2019; Fleming et al., 2016; Gabriele et al., 2022; Kershaw et al., 2021). As a result, their genetic, demographic, and population structure are likely out of equilibrium, and are unlikely to reach equilibrium any time soon. Numerous studies have documented distributional shifts on humpback feeding grounds and changes in migration timing in response to changing environmental conditions (Askin et al., 2017; Avila et al., 2020; Pelayo-González et al., 2022; Schall et al., 2021a,b; Szesciorka et al., 2022). Extreme environmental conditions may also play a role in some movements of animals between wintering grounds (Félix et al., 2020; Stevick et al., 2013). Similarly, population growth may be contributing to expansion of some feeding grounds and greater overlap on feeding grounds of whales from different wintering aggregations (Félix et al., 2020; Marcondes et al., 2021). As populations continue to recover from whaling and adapt to a changing climate, there could be changes in their movement patterns and population structure, including the composition of migratory herds.

2.6 | General conclusions from humpback whale examples

The four examples of humpback migratory herds presented above illustrate every combination of shared and private feeding grounds and wintering grounds, with the exception of one-to-one private wintering and feeding grounds. Having both mixed feeding grounds and wintering grounds makes any stratification based on geography problematic, and has contributed to debate regarding humpback population structure, particularly in the North Pacific (Baker et al., 1994, 2013; Barlow et al., 1997; Calambokidis et al., 2001; Darling et al., 2022; Darling & McSweeney, 1985; Donovan, 1991). Though the wintering grounds remain the presumptive breeding unit for humpback whales, the fact that animals spend the majority of the year on their feeding grounds has led many researchers to suggest that the feeding aggregations are the more appropriate choice for studies focused on ecological processes. Much of the debate concerning population structure in humpback whales hinges on this feeding vs. wintering ground dichotomy, while the herd concept recognizes that it is the combined fidelity to both feeding and wintering grounds that shapes population structure in humpback whales.

Assessing the impact of human-caused mortality should be based upon the migratory whale herd since it is the demographically independent population (DIP). Such an approach is being used in the International Whaling Commission's ongoing assessment of North Pacific humpbacks. Though the term “migratory herd” is not used in the assessment, the population structure scenarios being used in the assessment model categorize individuals based on the combination of their feeding and wintering ground affiliation (International Whaling Commission, 2022). The migratory whale herd concept should also change the way ecological and demographic analyses are conducted. For

example, whenever possible samples should be stratified by migratory herd when calculating allele frequencies of “pure stocks” in a mixed stock analysis (Utter & Ryman, 1993), estimating trends in abundance, or using stable isotopes to examine dietary preferences.

3 | GRAY WHALE EXAMPLES

Another species with population structure consistent with the migratory whale herd concept is the gray whale. Gray whales use three primary feeding areas within the North Pacific (Figure 4): (1) the northern feeding ground (NFG), which includes waters of the northern Bering, Chukchi, and Beaufort Seas and is used by the majority of whales (~21,000 in 2009/2010; Durban et al., 2015); (2) the Pacific Coast Feeding Group (PCFG) feeding ground, which includes waters from northern California through southeastern Alaska (Calambokidis et al., 2002; Darling, 1984; Gilmore, 1960; Hatler & Darling, 1974; Pike, 1962) and is regularly used by a small number of whales (~230; Calambokidis et al., 2019); and (3) the Sakhalin Island (SI) feeding ground, which is located off the northeastern coast of Sakhalin Island, Russia, in the Okhotsk Sea/western North Pacific (WNP; Meier et al., 2007; Weller et al., 1999, 2002) and is used by a small number of whales (102–144 mature whales, Cooke et al., 2018). Smaller concentrations of feeding whales can be found off the southern and southeastern coast of Kamchatka, Russia, which is used by at least some of the same whales that feed off SI (Tyurneva et al., 2010). The majority of whales, including all of those from the NFG and PCFG feeding grounds, winter in the lagoons and coastal waters off Baja California, Mexico, while a much smaller number of whales are thought to winter in the WNP wintering grounds (discussed below). Here we

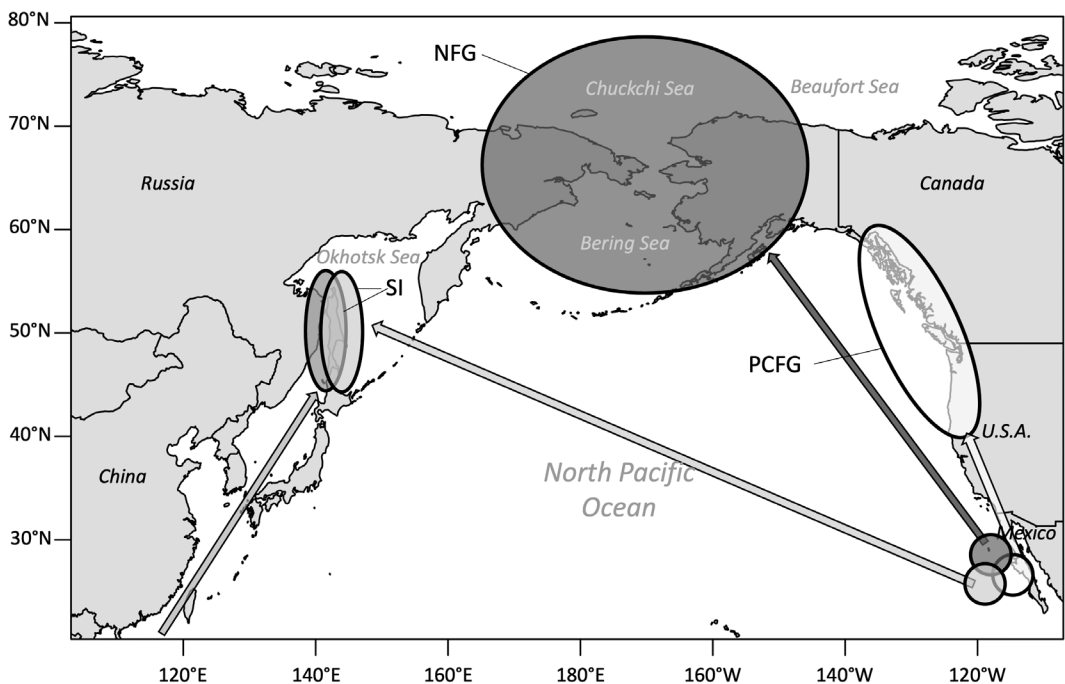


FIGURE 4 Conceptual map of the North Pacific gray whale herds. Circles and ellipses represent herd wintering and summering areas and are not intended to indicate exact ranges. Arrows indicate migratory connections, including to the WNP wintering area off the map, but do not represent precise migratory routes. SI = Sakhalin Island, NFG = Northern Feeding Ground, PCFG = Pacific Coast Feeding Ground.

restrict our evidence for the migratory herd concept in gray whales to those areas where photographic identification and genetic data are available to assess population structure patterns.

3.1 | Western North Pacific wintering ground to Sakhalin Island—an example of a private wintering and a shared feeding ground

All gray whales are individually identifiable from birth by natural and permanent pigmentation patterns (Darling, 1984), which has facilitated understanding of internal recruitment in this species (e.g., Bröker et al., 2020). The strongest evidence of matrilineal fidelity to feeding areas comes from long-term photo-identification studies of the whales using the SI feeding ground in the WNP (Bradford et al., 2006; Bröker et al., 2020; Weller et al., 1999, 2002). After the initial years of study, the majority of “new” (i.e., previously unidentified) whales photographed on the SI feeding ground have been calves brought to the area by known SI mothers. The mtDNA data provides further evidence that this pattern has persisted over multiple generations (Lang et al., 2021; LeDuc et al., 2002). Although a relatively large number of mtDNA control region haplotypes ($n = 22$) are found among whales sampled off SI, a high proportion (69%) of the SI whales, including most known reproductive females, carry one of two haplotypes. Of the four additional haplotypes that are found at moderate frequencies, three are carried by known mothers, and their frequencies have grown over time. Eleven of the remaining haplotypes are found only in a single individual, all of which are males. Correspondingly, the haplotype diversity found among the SI whales ($h = 0.760$) is markedly lower than that found among whales sampled on the feeding and wintering areas in the eastern North Pacific (ENP) ($h = 0.952$). The same is true when full mitogenomes are examined (Sakhalin $h = 0.723$, ENP $h = 0.975$; Brüniche-Olsen et al., 2021).

The exact location of the wintering ground(s) in the WNP remains unknown. Records from sightings, strandings, and historical whaling catches indicate that at least some gray whales occurred in the coastal waters off China in the South China Sea (see review in Weller et al., 2002), although only two records of gray whales in these waters have been reported in the last 25 years (Wang et al., 2015; Zhao, 1997; Zhu, 2012). While all of the whales feeding off SI were originally presumed to overwinter in the WNP (i.e., South China Sea region), recent evidence indicates that some of these whales migrate to the ENP, where they have been sighted in the lagoons and coastal waters off Baja California, Mexico (Mate et al., 2015; Weller et al., 2012). This separate migratory herd (WNP to ENP) is considered below. Other gray whales that feed off SI are presumed to remain in the WNP year-round, as supported by records of sightings, strandings, and entanglements of gray whales in Japanese and Chinese waters (Nakamura et al., 2017; Nambu et al., 2014; Wang et al., 2015; Weller et al., 2008; Zhao, 1997); most of these records, which include those from at least two whales that were first identified as calves with their mothers on the SI feeding ground (Weller et al., 2008, 2016), are from months when whales would likely be migrating. One of the two whales matched between SI and Japan was photographed in Japanese waters during winter and spring of multiple years (Weller et al., 2016), providing some evidence of fidelity to WNP migratory paths and wintering destination(s).

Unlike the whales that migrate between Mexico and SI, little is known about the identity of the SI whales that remain in the WNP year-round. Consequently, although a high proportion of the whales that feed off SI have been biopsied (Lang et al., 2021), it is not possible to make genetic comparisons of SI whales that overwinter in the WNP to other groups.

3.2 | Mexico lagoons to SI—a case of shared wintering and feeding areas

The case for site-fidelity to SI has been made above. Photo-identification and satellite tracking data have shown that some gray whales known to show fidelity to the SI feeding ground have also been recorded using the ENP wintering grounds off Baja California, Mexico (Mate et al., 2015; Weller et al., 2012). Some of these whales have been

photographed in the lagoons of Mexico in multiple years (Urbán R. et al., 2019), providing some evidence of fidelity to these wintering areas. Six SI whales have been photographed off southern Vancouver Island, British Columbia, during the northbound migration from Mexico to SI; all of these sightings occurred on only 2 days, with three whales sighted as part of a single group on one day and the other three whales sighted in two groups in close proximity to each other on a single day (Weller et al., 2012).

Significant nuclear genetic differences have been found when comparing the SI whales with the whales that feed on the NFG (Lang et al., 2021) as well as with whales sampled on the Mexico wintering grounds (Brüniche-Olsen et al., 2018), indicating a lack of random mating between these groups. These genetic differences remain apparent when only those SI whales known to overwinter in Mexico are compared to the NFG whales (Lang et al., 2021). The data available on gray whale reproduction, which are largely based on whales taken under scientific permit whaling off the coast of central California in the late 1950s and 1960s, suggest that most mating takes place during migration, with conception thought to primarily occur during a 3-week period from late November to early December (Rice & Wolman, 1971). For the whales migrating between SI and Mexico, this mating period may occur before the SI whales join the southbound migration of NFG whales, potentially providing a mechanism for SI whales to largely (but likely not exclusively; see Brüniche-Olsen et al., 2018; Lang et al., 2021) interbreed with each other and, in turn, create the signal of nuclear genetic differentiation that has been observed.

3.3 | Mexico lagoons to the Pacific Northwest Coast—a case of a shared wintering and semiprivate feeding areas

Patterns of fidelity to the PCFG feeding area in the ENP are more complex. This area is used by two categories of whales, one that is comprised of whales that return frequently to this feeding ground and account for the majority of sightings, and another that consists of individuals seen only in one year and generally for shorter time periods and in more limited areas (Calambokidis et al., 2019, 2002). Individuals in the first category are considered part of the Pacific Coast Feeding Group, while those in the second category appear to be individuals that have deviated, temporarily, from the northward migratory route and that otherwise feed on the NFG. The IWC considers whales that are seen in two or more years during the feeding season (June through November) within the region extending from northern California through northern British Columbia to be part of the PCFG (International Whaling Commission, 2011). These whales show a wide range of annual sighting patterns, with some being sighted in most years while others are sighted more sporadically. Photo-identification studies of the PCFG whales indicate matrilineal fidelity to the PCFG feeding ground, as supported by the subsequent return of individuals first identified as calves that were affiliated with a known PCFG female (Calambokidis et al., 2019, 2002). However, new noncalves are sighted each feeding season, many of which return to the area to feed in subsequent years and are thus considered to have been recruited into the PCFG. Some of these whales may be individuals born to PCFG mothers but not identified as calves prior to weaning, while others may represent dispersal from other herds.

The more complex pattern of matrilineal fidelity to the PCFG feeding ground can also be seen in the mtDNA genetic data. Comparisons of PCFG whales with NFG as well as with whales sampled on the migratory route have revealed significant mtDNA differences, consistent with the occurrence of matrilineal fidelity (Frasier et al., 2011; Lang et al., 2014). However, the magnitude of those differences is relatively low when compared to that seen between SI whales and NFG whales, and the haplotype diversity found among PCFG whales is slightly lower than, but similar to, that found in the NFG.

3.4 | General conclusions from gray whale examples

Like the humpback whale examples, stratification of gray whale data based on geography alone is problematic. The two herds that feed in the WNP face shared risks during the summer feeding season off SI, including entrapment in

salmon fishing trap nets (Lowry et al., 2018) and potential disturbance or injury due to oil and gas extraction activities, including those associated with vessel traffic (Silber et al., 2021; Weller et al., 2002). Furthermore, they face unique risks while migrating, and presumably also while on their different wintering grounds; the whales migrating from SI to the WNP wintering ground must navigate past high-volume commercial seaports along the coast of Asia and through areas with extensive use of gill nets and set nets in the coastal waters of Japan (Lowry et al., 2018; Silber et al., 2021). The whales migrating from SI to wintering areas in the ENP (e.g., Mexico) also travel through regions with apparently high risk of vessel interactions and commercial fishing operations, and traverse through areas where killer whales (*Orcinus orca*) regularly attack gray whale calves (Barrett-Lennard et al., 2011; Goley & Straley, 1994; Silber et al., 2021). Whales that feed off SI and winter in Mexico undertake one of the longest migrations of any mammal (on the order of 22,000 km round trip; Mate et al., 2015), and are estimated to have higher mean energy requirements than whales migrating between Mexico and the NFG (Villegas-Amtmann et al., 2017). PCFG whales, which have a markedly shorter migration between the Pacific Northwest and Mexico, also face unique risks, including spending the summer and early fall feeding in an area where large commercial fishing and shipping ports are located and shipping traffic is pronounced (Lagerquist et al., 2019; Silber et al., 2021). Although we did not discuss the most abundant group of gray whales that summers in the Chukchi and Bering Seas, they are likely to experience the greatest changes to their habitat from global warming.

Recognizing the complex population structure of gray whales across their range, the conservation advice provided by the IWC's Scientific Committee is based on the assessment of units that, while not explicitly referred to as migratory herds, are delineated by their feeding ground affiliation and their breeding stock, which is in turn defined by the wintering area used. Under this framework, two gray whale stock structure hypotheses are recognized as high priority for evaluation; the units considered under one or both of these hypotheses include the three examples of migratory herds provided above as well as the herd that migrates between the NFG and the Mexican wintering grounds (International Whaling Commission, 2021).

4 | CONCLUSIONS

The coastal habits of humpback and gray whales has made possible the accumulation of photographic and genetic data that facilitated the development of the migratory whale herd concept. However, this model of population structure likely applies to other whale species as well. For instance, both North Atlantic right whales (*Eubalaena glacialis*) and southern right whales (*E. australis*) show evidence of maternally driven fidelity to natal wintering and feeding grounds (Bishop et al., 2022; Carroll et al., 2015, 2016; Crowe et al., 2021; Malik et al., 1999; Valenzuela et al., 2009). Many other large migratory whale species share the life history trait of substantial maternal investment, necessitating a nursing period that spans the mothers' return migration to their feeding grounds. The resulting maternally derived migratory route, together with strong fidelity to wintering and summering areas, are defining characteristics of the migratory whale herd. We suggest that if migratory whales have maternally derived migratory routes, the default assumption should be that the migratory whale herd is the demographically independent unit. We have demonstrated that management under the ecological paradigm is improved through treating these herds as the unit to conserve.

For species that are not as easily studied as northern hemisphere humpback whales and gray whales, including those with more offshore distributions and often unknown wintering areas, obtaining sufficient photographic identification or genetic data to delineate herds may be infeasible. In these cases, researchers may need to bring to bear alternative data types for herd delineation. For instance, stable isotope ratios may be useful in stratifying southern right whale samples collected on summer feeding grounds to wintering grounds (Carroll et al., 2015; Valenzuela et al., 2009). Similarly, acoustic data may be useful for identifying migratory herds (Archer et al., 2019; Oleson et al., 2014; Schall et al., 2021b, 2022; Širović et al., 2013). Martien et al. (2019) provide details regarding the utility

of multiple different data types for delineating DIPs and the value of bringing together scientists with a range of expertise to facilitate integration of the best available scientific data for the purpose of DIP delineation.

In cases where collecting sufficient data for herd delineation is difficult, priority should be placed on delineating herds with the greatest conservation and management needs. For example, fin whales (*Balaenoptera physalus*) are difficult to photograph and biopsy and often inhabit areas with few known anthropogenic threats (Edwards et al., 2015; Mizroch et al., 2009). However, those that spend time off the U.S. west coast face high ship-strike threat in some parts or all of the year (Rockwood et al., 2017), and thus should be prioritized for herd delineation. This could be accomplished by coupling genetic samples collected in winter with acoustic data (Archer et al., 2019; Oleson et al., 2014; Širović et al., 2013) or other data that may be indicative of feeding grounds (such as stable isotope ratios, scarring patterns, or pollutant data) for the purpose of stratifying by potential herds. Even before reliable delineation is possible, ship strikes in winter can potentially be allocated to putative herds according to the proportion of acoustic calls from each feeding group, assuming call rates are comparable (see Monnahan et al., 2014 for an example with blue whales). Monitoring of ship strikes and other human-caused mortality based on feeding group acoustic call representation could allow for immediate assessment of possible herd-specific threats.

There will likely be many situations in which a wintering or feeding ground is known to be comprised of multiple herds, but there are only sufficient data available to delineate one of the herds. Such was the case in recent reviews of potential DIPs within the Mexico and Hawai'i humpback whale DPSs (Martien et al., 2021; Wade et al., 2021). For each DPS, there were strong data supporting the delineation of one herd (the Mainland Mexico to California/Oregon/Washington herd and Hawai'i to Southeast Alaska migratory whale herd examples discussed above in sections 2.3 and 2.4, respectively). There were also strong data indicating the existence of multiple herds in the remainder of the DPS, but the data were not deemed sufficient to delineate the remaining herds. In these cases, herds can be managed individually where they can be delineated while the remainder of the animals from a geographic stratum are combined into a single management unit, as was done for the Mexico DPS (Martien et al. 2021). When managing a unit that is believed to include multiple herds, it is important to explicitly acknowledge that the unit does not represent a DIP and to report any DIP-level data that are available.

For many species and many parts of the world, the data necessary to delineate herds does not exist and is unlikely to be collected in the near future. Indeed, for many migratory whales we do not even know the locations of the wintering or feeding grounds. In these cases, management and conservation will likely have to continue to be based on geographic strata. Nonetheless, research and management can still benefit from considering the possibility of migratory herd structure and stratifying data by herd where possible.

The implications of migratory whale herd structure warrant particular consideration when predicting species' resilience to a changing climate (e.g., Gulland et al., 2022; Hazen et al., 2012; Peters et al., 2022). Population structure that is mediated by behavior learned during the natal migration might be expected to change more rapidly than population structure defined by geographical constraints, possibly conferring greater resiliency to the changes in habitat quality expected to result from climate change (Keith & Bull, 2017). For humpback whales, there are numerous studies documenting shifts in feeding ground distribution and migratory timing in response to environmental variation (Askin et al., 2017; Avila et al., 2020; Pelayo-González et al., 2022; Schall et al., 2021a,b; Szesciorka et al., 2022). However, the lack of recovery of some herds following cessation of industrial whaling suggests that strong intergenerational fidelity to wintering and feeding grounds may inhibit some migratory whale species' ability to adapt to a changing environment (Brakes et al., 2021; Carroll et al., 2015).

No population structure paradigm will ever fully capture the complexity of migratory whale behavior, nor will our knowledge of it ever be complete. Scientists and managers will sometimes delineate management units that do not correctly reflect the underlying biological units that they are intended to regardless of which population structure paradigm is used. For instance, we now understand that the previously identified humpback whale "Western North Pacific" wintering ground, a geographically defined stratum, is likely comprised of two different wintering grounds—one off of the Philippines and Okinawa (Bettridge et al., 2015) and a newly described wintering ground along the Mariana Archipelago (Hill et al., 2020). We will likely also make mistakes when delineating migratory herds, and those

mistakes will have to be corrected as new data are collected. Nonetheless, given the compelling evidence from genetic studies and overwhelming evidence from photo-identification matches showing fidelity to both winter and feeding areas, it is clear that failing to recognize demographic structure represented by migratory herds in management would result in a major loss in regional protections for humpback whales.

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AUTHOR CONTRIBUTIONS

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