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POPULATION BIOLOGY OF FIN WHALES

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Population Biology of Fin Whales

Applying Demographic and Evolutionary Approaches to Studying
Populations

PhD thesis

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CHAPTER

01

1

Introduction

1. POPULATION BIOLOGY

The fields of population ecology, evolutionary biology, and conservation biology are tightly interconnected through their focus on population-level phenomena (Lewontin, 2004; Soulé, 1985). Despite the complementary nature of these population studies, the approaches employed to study different aspects of demography have evolved largely independently of each other for a long time. In the late 1950s, population biology arose as a new field from a movement among population ecologists and geneticists to bridge the gap between their respective disciplines (L. C. Cole, 1957; Lewontin, 2004). With the advent of new statistical models and molecular markers, a versatile toolkit is at the disposal of today's population biologists. This thesis aims to showcase the application of a multi-faceted approach to study the population biology of fin whales (*Balaenoptera physalus*).

1.1 What is a population?

It appears that several concepts of population coexist in biology. The term 'population' is used for all these concepts, so it is not amazing that confusion has arisen. This confusion is the more dangerous, since 'population' (in the meaning of local breeding population) plays an important part in the theory of (micro-) evolution.

Jonckers (1973)

The concept of 'population' is commonly used as unit of study in the fields of ecology, evolutionary biology, and conservation biology (L. C. Cole, 1957; Krebs, 1972). Yet, analogous to the debate surrounding the 'species' concept, there is no scientific consensus on the definition of a 'population' (Jonckers, 1973; Waples & Gaggiotti, 2006). Cole (1957) proposed to use the term 'population' to refer to "a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio, and an age structure in describing the properties of the unit". After reviewing the population biology literature, Waples and Gaggiotti (2006) concluded that the definition is largely dependent on the context and objective of a given study. Evolutionary biologists typically define populations in terms of reproductive cohesion (e.g. Hartl & Clark, 1988), as determined by the extent of gene flow, $N_e m$, where N_e denotes the effective population size and m represents the probability that an individual is an immigrant. In ecology, population is frequently used to refer to 'a group of organisms of the same species occupying a particular space at a particular time' (e.g. Krebs, 1972), generally implying a certain level of

spatial or demographic cohesion. However, Krebs (1972) added that ‘the boundaries of a population both in space and in time are vague and in practice are usually fixed by the investigator arbitrarily’. These differential paradigms have led to some confusion when genetic connectivity is used to infer levels of demographic cohesion (Lowe & Allendorf, 2010; Waples & Gaggiotti, 2006). Demographic connectivity implies that demographic population parameters, e.g. growth, survival, or birth rates, vary with the amount of immigration or emigration (Hanski, 1998). Demographic connectivity therefore depends on the relative contribution of m to population demography and not on the absolute number of dispersers $N_e m$ as inferred from levels of gene flow (Lowe & Allendorf, 2010; Waples & Gaggiotti, 2006).

The source of these nuanced concepts could be the largely independent development of the fields of population ecology and population genetics for most of their history (Lewontin, 2004). Population ecology is concerned with changes in population size and age distribution as a result of interactions with the physical environment, conspecifics, or individuals of a different species. Population genetics focuses on changes in genetic variation, e.g. allele frequencies, as a consequence of micro-evolutionary forces (i.e. gene drift, gene flow, mutation, selection). Evidently, there is considerable overlap among the ecological and evolutionary forces shaping populations. Population size expansions or contractions, as a result of extrinsic ecological factors, affect the genetic variation of the population (Hewitt, 2000); genetic drift has a stronger effect in small populations than in large populations, resulting in a reduction of genetic variability in declining populations and the persistence of rare alleles in expanding populations. While generally working towards a common goal of understanding the natural history of organisms, the different fields address different aspects of population biology.

1.2 Population genetics

Populations constitute the smallest unit of evolution. While genetic drift acts at the individual level (i.e. some individuals by chance produce more offspring than others), the evolutionary impact of genetic drift is only apparent in the changes in allele frequencies occurring over time at the population level. From an evolutionary perspective, divergence among populations could represent a stepping stone towards speciation (Templeton, 1981). Population genetics provide a theoretical framework for understanding the origin of reproductive isolation and adaptive divergence (Charlesworth & Charlesworth, 2017; Templeton, 1981). Given this central importance of populations, a large body of literature is dedicated to studying the spatio-temporal distribution of genetic variation in natural populations, building on the seminal work by Fisher, Haldane, and Wright.

Population genetic structure is shaped by the interplay of various ecological and evolutionary forces (Wright, 1943). Barriers to gene flow among populations, e.g. as imposed by insurmountable mountain chains, impassable rivers, or inaccessible islands, prevent random mating and allow changes in allele frequencies to accumulate in each population largely independently as a result of genetic drift, mutations, and natural selection (Wright, 1931, 1943). In the marine environment, there are seemingly few physical barriers to dispersal compared to the terrestrial environment. A comparative study on the levels of genetic differentiation among populations of marine, freshwater and anadromous fishes found generally higher levels of $N_e m$, and consequently lower genetic differentiation, among populations in marine species than in freshwater species (R. D. Ward et al., 1994). Large marine vertebrates have geographical ranges that can span entire ocean basins and even the majority of sedentary marine species have larval dispersal stages with neighbourhood sizes ranging between approximately 10 and 100 km (Palumbi, 2004). Nonetheless, oceanographic features, e.g. circulation patterns, temperature regimes or salinity gradients, can create effective barriers that limit dispersal in the marine environment (Galindo et al., 2006; Selkoe et al., 2008). Not all forms of population genetic structuring result in the formation of distinct clusters. When an individual's dispersal range is smaller than the species' entire range, there is the potential for isolation by distance (IBD; Slatkin, 1993; Wright, 1943). Similar to the concept of spatial autocorrelation, IBD arises when nearby individuals are more likely to mate than distant individuals (Hardy & Vekemans, 1999; Meirmans, 2012).

The study of the distribution of genetic variation among populations rests on a wealth of theoretical models (e.g. the Wright-Fisher model, the island model, or the stepping-stone model) that are employed to predict changes in allele frequencies under various conditions. With the advent of the coalescent theory (Kingman, 1982), population genetics also serves as a retrospective approach to infer the ancestral state of a population from contemporary samples. The theoretical framework of population genetics has provided, and continues to provide, valuable insights into the mechanisms of evolution by allowing theoretical models to be tested against empirical data (Charlesworth, 2015).

1.3 Population ecology

Population ecology is a diverse field, concerned with changes in population characteristics (e.g. population size, dispersion, or age-structure) and processes (e.g. growth, reproduction, or death) over time, often in relation to extrinsic factors (May & McLean, 2007; Vandermeer & Goldberg, 2013). The list of ecological factors exerting pressures on populations is long,

including environmental variables, predation, competition, disease, or parasitism. The classic Lotka-Volterra predator-prey model predicts, for example, that the population sizes of predators and prey have a tendency to oscillate with respect to one another (Wangersky, 1978). Naturally, these simplistic models do not capture the complexity of real population dynamics, but they form a useful starting hypothesis to develop more complex models (e.g. Bakun, 2006). In the absence of predators and competitors, population growth is predicted to follow a logarithmic growth model until reaching carrying capacity, i.e. the maximum population size that the environment can sustain (May & McLean, 2007; Wangersky, 1978). Density-dependent population regulation acts as a negative feedback loop to reduce birth rates or increase mortality rates as population density increases. The predation rate, in turn, is a function of the population density of the prey, for which different models of functional responses exist (May & McLean, 2007).

In natural populations, it can be challenging to determine density dependence and functional responses. Using controlled field experiments on a coral reef, Hixon and Jones (2005) found that an interplay of predation and intra-specific competition caused density dependent mortality in demersal marine fishes. Laboratory aquaria experiments have revealed that the functional response of blue crabs (*Callinectes sapidus*) predating on soft-shelled clams (*Mya arenaria*) differed depending on sediment type from a type III response in sand to a type II response in mud (Lipcius & Hines, 1986). However, such controlled settings are difficult to achieve in free-ranging marine species, which makes it more difficult to determine the direct underlying causes of changes in population growth. High adult mortality and low calving rates in gray whales (*Eschrichtius robustus*) in 1999 and 2000 were attributed to environmental changes related to shorter ice-free conditions on the feeding grounds, El Niño events and the population reaching carrying capacity (S. E. Moore et al., 2001; Perryman et al., 2002). Williams et al. (2013) suggested that fin whale (*Balaenoptera physalus*) populations show a density-dependent response of pregnancy rates to prey availability, mediated by body condition.

Population distribution and size are shaped by the interplay of competition, predator-prey interactions and dispersal patterns. The relationship between population distribution and environmental variables has been used to forecast shifts in population ranges in response to changing environmental conditions, e.g. due to climate change (Becker et al., 2012; Guisan & Thuiller, 2005; Redfern et al., 2006). Davis et al. (1998) cautioned against ignoring the effects of dispersal and intra-specific interactions when predicting population ranges based on the distribution-environment relationship alone. Overall frameworks are required for a better integration of species distribution models with ecological theory (Guisan & Thuiller,

2005). Tulloch et al. (2019) aimed to quantify the effect of climate change on the recovery of baleen whale populations. Their ecosystem-modelling approach accounted for predator-prey interactions, projected changes in sea surface temperature, changing prey availability, changing distribution of whales, shifts in migration patterns, and inter-specific competition. Baleen whale populations in the Southern Hemisphere were predicted to decline in response to reduced prey availability from increased sea surface temperature and increasing inter-specific competition (Tulloch et al., 2019). The study serves as an example of the complex dynamics between predator and prey populations and their physical environment. Statistical models may not succeed in the exact representation of natural systems, but they can offer useful approximations of the real world or in the words of George Box (1979) “all models are wrong but some are useful”.

1.4 Conservation biology

Conservation biology integrates conservation policy with theories developed in population ecology and evolutionary biology to mitigate anthropogenic impacts on biological diversity and to prevent the extinction of species (Soulé, 1985). Populations are the primary target of management and policy directives that aim to provide effective protection to small or declining populations (Shaffer, 1981). In this context, the terms ‘management unit’ or ‘stock’ are frequently used to refer to “geographical areas with restricted interchange of the individuals of interest with adjacent areas” (Taylor & Dizon, 1999). How this definition translates to delineating management units in natural populations is a matter of debate (Palsbøll et al., 2007; Taylor & Dizon, 1999). While population genetics provide a means of quantifying population differentiation, the decision on the threshold level of interchange, in this case gene flow, mainly depends on the demographic context and management objectives (Palsbøll et al., 2007; Taylor & Dizon, 1999). A statistical test on whether the null hypothesis of panmixia can be rejected at an arbitrary level is rarely sufficient to delineate meaningful management units (Palsbøll et al., 2007; Taylor & Dizon, 1999). Weakly structured populations or those following a stepping-stone model pose a particular challenge as to where to draw the line (Spies et al., 2015).

Once a management unit has been defined, population viability analysis (PVA) can be employed to estimate the likelihood of reaching a threshold level, e.g. extinction, under current or managed conditions (Boyce, 1992). PVAs are generally quantitative model-based assessments of extinction/persistence that can incorporate elements of spatially-explicit and/or individual-based models, sensitivity analysis, or genetic effects (Boyce, 1992; Reed et al., 2002). An ideal PVA is an integration of population models, allowing the interaction

between population structure and environmental conditions to affect demographic parameters, population growth rates, and ultimately the probability of extinction (Zabel et al., 2006). Elasticity and sensitivity analyses constitute another valuable complementary analysis to PVA, because they determine the model parameters with the largest proportional or absolute influence on the model outcome (Benton & Grant, 1999). Evaluation of parameter sensitivity can therefore be used to direct future research and management efforts, e.g. to target the life-history stage contributing most to population growth (Benton & Grant, 1999; Crowder & Crouse, 1994; Zabel et al., 2006).

It can be challenging to convey parameter and prediction uncertainty to managers, who might be unwilling to act unless there is proof of population status deterioration (Gerrodette, 1987; Taylor & Gerrodette, 1993; P. M. Thompson et al., 2000). However, the precautionary principle, nowadays ingrained in much conservation and management legislation, upholds that preventive measures should be taken to minimise potential irreversible environmental damage even if cause and effect relationships are not fully established scientifically (Kriebel et al., 2001; Myers, 1993).

2. POPULATION BIOLOGY OF FIN WHALES

This thesis aims to provide a comprehensive view on the population biology of fin whales, including assessments of local population trends and genetic connectivity at different spatio-temporal scales. The focus on fin whales arose from the need for an updated abundance estimate in the Gulf of St. Lawrence, given previous indications of a decline in survival rates (Ramp et al., 2014). An extensive collection of fin whale DNA samples, resulting from a multinational effort to carry out an ocean-basin wide assessment of population genetic structuring, further lent itself to expand on previous work on this topic by Bérubé et al. (1998). Before giving an outline of the thesis, I will briefly summarise our current understanding on the population biology of fin whales.

2.1 Distribution and movement patterns

The fin whale is a cosmopolitan mysticete occurring in all major oceans from temperate to polar latitudes in both hemispheres (Edwards et al., 2015). Fin whales are generally rare to absent in equatorial latitudes between 20°N and 20°S (Edwards et al., 2015, although see M. Moore, Steiner, & Jann (2003) for Cape Verde Islands sightings and Weir (2019) for whaling catches off Angola). Their preferred habitat generally appears to be deep, offshore waters, with higher fin whale densities occurring over the continental shelf edge (Muirhead et al.,

2018; Víkingsson et al., 2015). Occasionally, fin whales can also be found in shallow (<150 m), coastal waters in areas characterised by high levels of productivity (Doniol-Valcroze et al., 2007; Ingram et al., 2007; Whooley et al., 2011).

The seasonal distribution of fin whales does not conform with the traditional baleen whale migration model, as described in humpback whales (*Megaptera novaeangliae*), North Atlantic right whales (*Eubalaena glacialis*), or gray whales. While data from multiple sources (e.g. line-transect surveys, whaling records, satellite tagging) have found fin whales to be more abundant at higher latitudes during warmer months and more abundant at lower latitudes during colder months, the traditional mysticete migration model does not account for the numerous alternative (non) migratory strategies (Edwards et al., 2015; Geijer et al., 2016). A comprehensive review on alternative migratory behaviours in fin whales is given by Edwards et al. (2015) and Geijer et al. (2016). In short, despite seasonal latitudinal movement in most individuals, year-round presence of fin whales at both high and low latitudes has been recorded (e.g. Kellogg, 1928; Lydersen et al., 2020; Mizroch et al., 2009; Simon et al., 2010). Fin whales in the Mediterranean Sea (Notarbartolo di Sciara et al., 2003) and Gulf of California (Bérubé et al., 2002; López et al., 2019; Tershy et al., 1993) appear largely resident.

Uncertainty in the full range of movement patterns remains due to a paucity of data and observation of fin whales during winter. Breeding grounds have thus far not been identified and mating related behaviours and newborn calves at high latitudes suggest that mating and calving may not be restricted to lower latitude, as is generally observed in humpback whales (Baines et al., 2017; Ingebrigsten, 1929; Kellogg, 1928; Simon et al., 2010). Given the scarcity of sightings during winter, it has been hypothesised that fin whales disperse to unobserved, offshore areas during winter (Cotté et al., 2009; Simon et al., 2010). Acoustic presence of fin whales was confirmed in the mid North Atlantic Ocean during winter months (Romagosa et al., 2020). Baines et al. (2017) suggested that fin whales may track highly productive habitats along the eastern margin of the North Atlantic, characterised by the eastern boundary upwelling system (e.g. Canary current), on their south-bound migration route in autumn and winter. Stable isotope signatures from fin whales observed on their north-bound trajectory in the Azores during spring were consistent with winter feeding off Iberia (Silva et al., 2019). Fin whales were found to suspend their spring and summer north-bound migration to feed in Azorean waters before some animals continued their movement towards Iceland and east Greenland (Silva et al., 2013).

The range of movement patterns was perhaps best summarised by Kellogg (1928), who stated that “Climate seemingly has little influence in curtailing their wanderings, for

finbacks appear to be indifferent alike to Tropic and Arctic temperatures, and travel where they will.”

2.2 Ecological interactions

Fin whales feed primarily on species of euphausiids, notably *Euphausia superba* in the Southern Hemisphere or *Meganyctiphanes norvegica* (Atlantic), *E. pacifica* (Pacific), and *Thysanoessa inermis* in the Northern Hemisphere (Mizroch et al., 1984; Víkingsson, 1997). In the Northern Hemisphere, fin whales show a greater feeding plasticity and are known to switch to small fish prey, like capelin (*Mallotus villosus*), herring (*Clupea harengus*), or sandlance (*Ammodytes americanus*), when the opportunity arises (Coakes et al., 2005; Gavrilchuk et al., 2014; Mizroch et al., 1984; Stefánsson et al., 1997). This broader trophic niche allows fin whales to exploit a wider range of environmental conditions when making foraging decisions compared to specialist species, like the blue whale (*B. musculus*), that only feed on krill (Mizroch et al., 1984; Scales et al., 2017). Feeding plasticity was also suggested to reduce inter-specific competition between fin and blue whales on a feeding ground in the Gulf of St. Lawrence (Gavrilchuk et al., 2014). In that study, the isotopic niche of fin whales also overlapped considerably with that of minke whales (*B. acutorostrata*), but they may be feeding on the same prey in different proportions (Gavrilchuk et al., 2014). Temporal or spatial segregation of feeding could further reduce inter-specific competition (Doniol-Valcroze et al., 2007; Santora et al., 2010). Santora *et al.* (2010) found a significant spatial segregation among baleen whales off the Antarctic Peninsula in relation to krill “hotspots” that differed in size structure. A combination of feeding plasticity and feeding habitat segregation may therefore reduce direct competition with other baleen whales.

The feeding ecology of fin whales also affects their habitat use (Laidre et al., 2010; Santora et al., 2010). While fin whales were found to display high seasonal site fidelity to feeding grounds in the Gulf of Maine (Agler et al., 1993), the Gulf of St Lawrence (Ramp et al., 2014) and Ireland (Whooley et al., 2011), they have also been reported to take advantage of prey hotspots outside their usual feeding grounds (Baines et al., 2017; Coakes et al., 2005; Silva et al., 2013). Satellite tracking data revealed year-round residency of fin whales in the Southern California Bight as a result of highly productive foraging areas that could support the fin whale population year-round (Scales et al., 2017). An increase in fin whale abundance and expansion to deeper waters in the Irminger Sea, located between Greenland and Iceland, was linked to changes in the physical and biological features of the feeding habitat (Víkingsson et al., 2015).

Prey availability was also suggested to play a key role in the timing of spring migration of baleen whales in the North Atlantic (Visser et al., 2011). Peak abundances of fin whales in the Azores were linked to the onset of the phytoplankton bloom, with an average temporal lag of 15 weeks (Visser et al., 2011). A recent investigation of the environmental drivers of north-bound movements of fin whales in the mid North Atlantic did not find a clear environmental correlation; movements were linked both to cold waters with high low trophic level plankton biomass and to warm waters (Pérez-Jorge et al., 2020). In the western North Atlantic (Gulf of St. Lawrence), fin whales were found to have shifted their arrival date to the feeding ground at a rate of 1 day earlier per year over three decades, linked to earlier winter sea ice break up and higher sea surface temperatures (Ramp et al., 2015).

Fin whales have thus shown a remarkable plasticity in movement patterns and feeding ecology, which likely also influenced their persistence and recovery through past periods of large-scale climatic events and population depletions by whaling.

2.3 Population trends

Balaenopterids were a difficult target for whalers until modern whaling techniques using explosive harpoons mounted on the bows of steam-powered catcher boats were introduced in Norway in the 1860s (Mizroch et al., 1984; Reeves & Smith, 2006). Fin whale catches peaked before the Second World War at around 30,000 animals, but an estimated 20,000-30,000 fin whales per year were harvested (mainly in the Southern Ocean) until the mid-1960s, by which time most stocks were depleted and whaling became economically unviable (Schneider & Pearce, 2004). However, estimations of total catches were found to be biased by underreporting and falsification of whaling logbook data, which make it difficult to compare current abundance estimates to presumed pre-exploitation levels (Mizroch et al., 1984; Palsbøll et al., 2013; Reeves & Smith, 2006; Roman & Palumbi, 2003). The International Whaling Commission (IWC) Scientific Committee has produced “best” and “high” estimates of harvested fin whales of 98,000 and 115,000, respectively, in the North Atlantic (IWC 2017). Since the moratorium on commercial whaling implemented in 1986, the IWC reported that 1,546 had been taken (including lost whales) up to 2018 (<https://iwc.int/total-catches>). Subsistence whaling in Greenland accounted for 25% of the total catches, whaling under Special Permit by Iceland and Japan accounted for 20%, and commercial whaling under objection by Iceland and Japan accounted for the remaining 55%.

Several series of large-scale surveys have been conducted in the North Atlantic since the 1980s to estimate the abundance of fin whales, including the North Atlantic Sighting

Surveys (NASS) in 1987, 1989, 1995, 2001, and 2015 (Pike et al., 2019; Víkingsson et al., 2009), the Trans North Atlantic Sighting Survey (T-NASS) in 2007 (Pike et al., 2008, 2020), and the cetacean surveys in European Atlantic waters, namely SCANS-II in 2005, CODA in 2007, and SCANS-III in 2016 (Hammond et al., 2011, 2017). Based on the latest NASS in 2015, covering the area between Greenland and the Faroe Islands, fin whale abundance was estimated at 31,953 (CV = 0.17, 95% CI 22,536 – 45,306; Pike et al., 2019). The highest density of fin whale sightings in NASS and T-NASS occurred in the Irminger Sea-Denmark Strait to the west of Iceland (Pike et al., 2019, 2020; Víkingsson et al., 2009, 2015). In European Atlantic waters the highest density of fin whale sightings was reported northeast of Galicia (Spain) and in the Bay of Biscay during CODA and SCANS-III surveys with an estimated abundance of 18,100 (CV = 0.38) (Hammond et al., 2017).

The current population trend has been classified as “increasing” in the most recent assessment of the IUCN Red List of Threatened Species, which lists the species as “vulnerable” to extinction (Cooke, 2018). There are some indications that the population in the North Atlantic may be reaching carrying capacity and that population growth is regulated by density-dependent effects on pregnancy rates, mediated through body condition (Víkingsson et al., 2015; Williams et al., 2013).

2.4 Population structure

The Committee on Taxonomy of the Society for Marine Mammalogy currently recognises four distinct subspecies of fin whales: the North Atlantic fin whale (*Balaenoptera physalus physalus*), the Southern fin whale (*B. p. quoyi*), the pygmy fin whale (*B. p. patachonica*; proposed by Clarke, 2004), and the North Pacific fin whale (*B. p. velifera*; proposed by Archer et al. (2019); Committee on Taxonomy, 2020).

A population structure analysis of North Pacific and North Atlantic fin whale samples found evidence of two to three population clusters in the eastern North Pacific (Hatch, 2004). Fin whales in the Gulf of California constitute a highly isolated population from the eastern North Pacific fin whales based on population genetic analyses of multi-locus microsatellite genotypes and mitochondrial control region DNA sequences (Bérubé et al., 2002; Rivera-León et al., 2019). Significant deviation from panmixia was also detected among fin whales from the North Atlantic and Mediterranean Sea (Bérubé et al., 1998; Palsbøll et al., 2004).

Sergeant (1977) described the stock structure of fin whales in the North Atlantic as ‘a patchy continuum, with relatively small movements necessitated mainly by the search for food’.

Sergeant (1977) observed that some whaling stocks were more quickly depleted than others, despite equal catch effort. Rates of immigration from neighbouring stocks were insufficient to compensate the number of whales taken by whaling, suggesting some degree of population structuring. Based on population genetic analyses of multi-locus microsatellite genotypes and mitochondrial control region DNA sequences, Bérubé et al. (1998) found significant levels of heterogeneity among fin whales from more distant sampling areas, mainly among western and eastern North Atlantic fin whales. Overall the population genetic structure of North Atlantic fin whales was characterised by IBD (Wright 1943), supporting the notion of a ‘patchy continuum’ originally proposed by Sergeant (1977). The results also supported the hypothesis of recent population expansion in the western Atlantic, which was hypothesised to be the result of feeding habitat expansion following the last glacial maximum (Bérubé et al., 1998). A recent population expansion could have contributed to the overall low levels of population differentiation (Bérubé et al., 1998; Palsbøll et al., 2004). However, the results did not support the notion of fine-scale structure among neighbouring sampling areas, as originally proposed by Sergeant (1977). It also remains unclear to what degree fin whales from different feeding grounds are demographically or genetically independent from each other (Bérubé et al., 2006).

3. THESIS OUTLINE

This thesis aims to improve our understanding on the population biology of fin whales at different spatio-temporal scales. Chapters 2 and 3 focus on the population ecology of fin whales in the Gulf of St. Lawrence using mark-recapture and survey data collected by the Mingan Island Cetacean Study. The Mingan Island Cetacean Study has been conducting longitudinal studies in the Jacques Cartier Passages since the late 1970s, providing crucial data for the monitoring of demographic population trends. In chapters 4 and 5, the evolutionary biology of fin whales is investigated at a much broader spatio-temporal scale in terms of population genetic structure and demographic histories. This work is based on an extensive genetic database that resulted from a multinational, collaborative effort to collect tissue samples over the course of 40+ years.

In Chapter 2, “Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence”, mark-recapture modelling is employed to investigate changes in abundance and survivorship of fin whales in the Jacques Cartier Passage. Photo-identification data of the chevron and dorsal fin are used to create a catalogue of capture histories for each individual. Ongoing anthropogenic pressures and

changing environmental conditions are hypothesised to have affected the local population demography. To account for capture heterogeneity due to divergent patterns of site fidelity, agglomerative hierarchical cluster analysis is employed to categorise individuals based on their seasonal site fidelity patterns.

Chapter 3, “Spatio-temporal patterns in fin whale *Balaenoptera physalus* habitat use in the northern Gulf of St. Lawrence”, aims to test the hypothesis that the decline in abundance and apparent survival (as detected in chapter 2) is correlated to changing environmental conditions. Cetacean sighting data from 292 surveys in the Jacques Cartier Passage in 2007–2013 are used to fit two generalised additive models in terms of (1) bathymetric and oceanographic variables (the proxy model) and (2) modelled krill biomass (the prey model). The performance of the prey and proxy models are compared in terms of percentage deviance explained in the sightings data. Survey effort is quantified as time spent searching for fin whales in a given area, which was corrected for “handling time”, defined as the time spent collecting auxiliary data.

In Chapter 4, “Multi-faceted approach to studying the population genetic structure in a low divergence species: the case of the North Atlantic and Mediterranean Sea fin whales (*Balaenoptera physalus*)”, the population genetic structure of North Atlantic and Mediterranean Sea fin whales is investigated. The study is based on over 1,600 multi-locus microsatellite genotypes and 450 base-pair long mitochondrial control region DNA sequences, generated from fin whale samples collected in 15 sampling areas across the North Atlantic and Mediterranean Sea. Traditional population genetic methodology, i.e. fixation indices (F_{ST}) and STRUCTURE, is combined with coalescent- and kinship-based approaches to provide a multi-faceted insight into the population genetic structure of fin whales in the North Atlantic and Mediterranean Sea.

In Chapter 5, “Evaluating the global genomic diversification process of fin whales using demographic model selection”, genome-wide single nucleotide polymorphism data (i.e. ddRAD) in conjunction with a demographic model testing framework are used to test the hypothesis that past climate variability shaped the contemporary population structure of fin whales in a global setting. It is hypothesised that large-scale climate variability during the Pleistocene glaciations led to secondary contact among North Pacific and North Atlantic fin whales during periods of deglaciation and an increase in gene flow between Southern and Northern Hemisphere fin whales during periods of glaciation.

Chapter 6 summarises the main findings of the thesis and discusses the results in the context of fin whale population biology and their implications for conservation biology.

CHAPTER

02

2

Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence¹

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ABSTRACT

Estimates of abundance and survivorship provide quantifiable measures to monitor populations and to define and understand their conservation status. This study investigated changes in abundance and survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence (GSL) in the context of anthropogenic pressures and changing environmental conditions. A long-term data set, consisting of 35 years of photo-identification surveys and comprising more than 5,000 identifications of 507 individuals, formed the basis of this mark-recapture study. Based on model selection using corrected Akaike Information Criterion, the most parsimonious Cormack-Jolly-Seber model included a linear temporal trend in non-calf apparent survival rates with a sharp decline in the last five years of the study and a median survival rate of 0.946 (95% confidence interval (CI) 0.910-0.967). To account for capture heterogeneity due to divergent patterns of site fidelity, agglomerative hierarchical cluster (AHC) analysis was employed to categorise individuals based on their annual and survey site fidelity indices. However, the negative trend in survivorship remained and was corroborated by a significant decline in the estimated super-population size from 335 (95% CI 321-348) individuals in 2004-2010 to 291 (95% CI 270-312) individuals in 2010-2016. Concurrently, a negative trend was estimated in recruitment to the population, supported by a sharp decrease in the number of observed calves. Ship strikes and changes in prey availability are potential drivers of the observed decline in fin whale abundance. The combination of clustering methods with mark-recapture represents a flexible way to investigate the effects of site fidelity on demographic variables and is broadly applicable to other individual-based studies.

1. INTRODUCTION

Detecting trends in population abundance and identifying the underlying factors driving any increase or decline in population size are important aspects of conservation biology and wildlife management (Lawton, 1993; Taylor & Gerrodette, 1993). Small populations that occur at low population densities and/or occupy restricted geographical ranges face an enhanced extinction risk and are especially in need of focussed monitoring (Purvis et al., 2000). In this context, abundance and survival rate estimation provide quantifiable measures to define the status of populations and to assess the efficiency of management actions (Cheney et al., 2014; Pace et al., 2017). While a time-series of abundance estimates can reveal population trends, reproductive and survival rates can provide insights into causes of observed changes in population abundance (Pace et al., 2017; Pendleton et al., 2006; Ramp et al., 2014). In marine vertebrates, robust estimation of reproductive (birth)

rates are available for several seabird, sea turtle and pinniped species, facilitated by the confinement to terrestrial birthing and breeding colonies (Cury et al., 2011; Pomeroy et al., 1999; Troëng & Rankin, 2005). In cetaceans, robust estimates of birth rates are more difficult to obtain and are limited to a few well studied populations (e.g. Arso Civil, Cheney, Quick, Thompson, & Hammond, 2017; Mann, Connor, Barre, & Heithaus, 2000; Rolland et al., 2016).

Well-established analytical frameworks are available to generate robust estimates of abundance and survival from suitable data to inform decision-making (Hammond, 2017; L. Thomas et al., 2010). However, the statistical power to detect population trends depends, amongst other factors, on the life history of the species under investigation (Taylor & Gerrodette, 1993; P. M. Thompson et al., 2000). In particular, population assessments in long-lived and wide-ranging species pose logistical challenges relating to monitoring regimes and spatial coverage (Taylor, Martinez, et al., 2007; Tyne et al., 2016). First, long-term monitoring programmes increase the power to detect trends in long-lived species. For instance, Wilson et al. (1999) calculated that research effort during more than eight years was required to detect changes in bottlenose dolphin population abundance with a statistical power at 90%. Second, as a result of limited resources, surveys often cover a small part of a population's distribution, although exceptions include large-scale surveys covering the North Atlantic (Lockyer & Pike, 2009), Antarctic waters (e.g. Branch, 2007), and the eastern tropical Pacific (Gerrodette & Forcada, 2005). In studies with restricted spatial coverage, it is difficult to interpret changes in estimated abundance as true changes in population size because of natural shifts in distribution or because of temporary emigration from the study area (Cheney et al., 2013; Forney, 2000; Víkingsson et al., 2015; Ben Wilson et al., 2004).

The fin whale (*Balaenoptera physalus*) is a long-lived and wide-ranging baleen whale requiring large-scale, long-term monitoring programmes to identify population trends. Several national and multinational large-scale surveys (e.g. NASS (Lockyer & Pike, 2009), SCANS (Hammond et al., 2017), NAISS (NAMMCO, 2018)) have focussed on assessing long-term changes in distribution and abundance of cetaceans, including fin whales, in the North Atlantic. For instance, in comparison with previous estimates, a substantial increase in fin whale abundance was reported in the Irminger Sea (between Iceland and Greenland), possibly as a result of shifts in distribution and prey availability (Víkingsson et al., 2015). The sum of available abundance estimates from the most recent large-scale surveys adds up to more than 70,000 fin whales in the North Atlantic (NAMMCO, 2018). While fin whales are known to range over the whole North Atlantic basin, they also show strong site fidelity

to specific feeding grounds (Agler et al., 1993; Ramp et al., 2014). Long-term small-scale studies may therefore hold valuable information on changes in local abundances and allow for more detailed investigation into recruitment and survival rates.

A study of fin whales in the northern part of the Gulf of St. Lawrence (GSL) during 2004 to 2010 that applied mark-recapture models to photo-identification data estimated the population at 328 individuals (with 95% confidence interval (CI) of 306-350; Ramp et al., 2014). This study found that non-calf apparent survival probabilities remained stable at 0.955 (95 % CI 0.936-0.969) during the period from 1990 to 2006 but there were indications of a decrease during 2007 to 2010. A combination of lower site fidelity and elevated mortality rates were discussed as potential causes of declining survivorship. Mark-recapture models assume homogeneity in capture probabilities at a given sampling occasion, unless individual variation is explicitly modelled (Lebreton et al., 1992). This assumption is frequently violated in practice in studies of cetaceans because capture probabilities can vary among individuals as a function of intrinsic factors associated with biological or behavioural characteristics (e.g. age, sex, or site fidelity) and of extrinsic factors such as the sampling design (Hammond, 2017). For instance, sampling only a fraction of the distribution when individuals display site fidelity can lead to unequal capture probabilities. Such capture heterogeneity can bias results, typically leading to an underestimation of abundance (Hammond, 1990b). It is unclear to what extent previous estimates of fin whale survival probabilities and abundance were biased due to capture heterogeneity.

The level of connectivity between fin whales in the GSL and neighbouring areas is unresolved. Whaling reports (Sergeant, 1977), contaminant levels (Hobbs et al., 2001), and song structure (Delarue et al., 2009) suggest that the GSL individuals form a distinct population. However, photo-identification and genetic studies do not fully support this hypothesis, instead pointing to exchange with surrounding areas (Bérubé et al., 1998; Coakes et al., 2005). While population identity remains unresolved, several studies suggested that the GSL has been undergoing a substantial change with wide-ranging effects on its fauna (Friesinger & Bernatchez, 2010; Plourde et al., 2014). A shift in the arrival date of fin and humpback (*Megaptera novaeangliae*) whales to their feeding ground in the GSL has been related to earlier winter sea ice break-up linked to a warming climate (Ramp et al., 2015). Significant changes in the ichthyoplankton community structure (Bui et al., 2010), unprecedented warming of the incoming intermediate North Atlantic water (Thibodeau et al., 2010), and higher mortality in harp seals (*Pagophilus groenlandicus*) linked to reduced ice cover (Johnston et al., 2012) are also indicative of ecosystem changes.

The aforementioned lack of recent abundance estimates, the possible decline in survival rates, and ongoing environmental and anthropogenic pressures in the GSL highlight the need for updated estimates of abundance and survival in fin whales. These estimates are crucial to detect local population changes in the GSL, which may otherwise remain undetected in the framework of large-scale surveys. This study aimed to fill this gap in population trends of fin whales in the GSL, providing key information for future assessments of the population status in Atlantic Canadian waters. A long-term data set, consisting of 35 consecutive years of photo-identification surveys in the northern GSL, formed the basis of this study. Our specific objective was to test the hypothesis that there is an ongoing decline in numbers and survival of fin whales in the GSL. Results are discussed in the context of anthropogenic pressures and environmental changes.

The impact of capture heterogeneity on estimates of population parameters is not unique to cetacean individual-based studies and has long been recognised as a potential source of bias in various taxa, e.g. seabirds (Sanz-Aguilar et al., 2010) and pinnipeds (Bradshaw et al., 2003). While many studies acknowledge the problem, few studies have assessed the magnitude of bias introduced by capture heterogeneity. The analysis presented here focussed on reducing the effect of possible sources of bias resulting from capture heterogeneity and temporary emigration to provide robust results. The proposed method used to categorise individuals based on site fidelity indices has the potential for broad applicability to other individual-based studies.

2. MATERIAL AND METHODS

2.1 Study area and field data collection

The study area of approximately 8000 km² was situated in the Jacques Cartier Passage (JCP), located between Anticosti Island and the North Shore in the northern part of the GSL (Fig. 1). The area is characterised by upwelling and high productivity, forming a feeding ground for several baleen whale species (Doniol-Valcroze et al., 2007; El-Sabh, 1976). Since 1982, the Mingan Island Cetacean Study has conducted annual surveys in the area to collect photo-identification data from fin whales. Data collection was conducted from late May/early June until late September/October, with an average of 50 survey days and 13,000 km per year. Surveys were conducted from 7 m long rigid-hulled inflatable boats and aimed to cover a large area, while maximising encounter rates for photo-identification by spending more time in areas with high numbers of individuals. Realised survey effort depended on weather conditions and was discontinued when sea conditions were worse than Beaufort scale 3 or visibility was less than one nautical mile. During the period from 1982 to 2003,

photographs were obtained using standard single lens reflex (SLR) 35mm cameras with black and white film, and from 2004 onwards with digital SLR cameras, with 70-200 mm lenses. From 1990 onwards, skin biopsy samples were collected from free-ranging individuals (Palsbøll et al., 1991) for molecular determination of sex from the DNA extracted from skin samples using the ZFX/ZFY chromosomes following the methodology described in Bérubé and Palsbøll (1996a, 1996b).

Figure 1. Location of the study area in the Jacques Cartier Passage, situated between Anticosti Island and the North Shore on the East coast of Canada. Opportunistic photo-identification data were available for Gaspé (GASP), the St. Lawrence Estuary (ESTU), and Sept-Îles to Pointe-des-Monts (SIPM)

2.2 Photo-identification data

Photo-identification (photo-ID) is a method in which individual animals are recognised from images of their natural markings, providing capture histories of individuals (Hammond, 1990a). Photo-ID methodology has been successfully used in previous studies of fin whales (Agler et al., 1990, 1993; Ramp et al., 2014; Robbins et al., 2007; Whooley et al., 2011). Individual fin whales are identified based on the profile of the dorsal fin and the unique pigmentation pattern of the so-called chevron (Agler et al., 1990). The chevron is a

light 'V'-shaped pigmentation pattern, which extends from the blow holes down both sides of the animal, but is more pronounced on the right side (Fig. 2). In this study, every fin whale was considered individually identifiable from high quality photographs of the shape of the dorsal fin and the pigmentation patterns.

Figure 2. Images used for photo-identification of a fin whale (*Balaenoptera physalus*) in the Gulf of St. Lawrence. (Top) Chevron pattern on left-side flank. (Bottom) Dorsal fin. Photograph credit: MICS

After each survey, the best photos of the right side dorsal and right-side chevron were chosen for each individual based on sharpness, angle, coverage and light conditions (contrast). Based on photo quality, pictures were graded from A to D and only individuals with pictures from the highest quality (A and B) categories were matched against the catalogue. In an initial step, researchers matched individuals to individuals already seen during the same season to check for internal duplicates, before matching the individuals seen in a season to the whole catalogue of previously identified individuals. The judgment of three researchers, two of whom had to be experienced in fin whale matching, was required to confirm a match or designate a new individual in order to minimise the chance of mis-identification of individuals. Calves were excluded from mark-recapture analyses because observations of calves are conditional on the presence of their mother.

2.3 Residency in the study area

The complete sighting history for each individual was used to calculate two site fidelity indices: (1) annual sighting rates as the total number of years an individual was seen as a proportion of the total number of years since the first sighting of the given individual and (2) survey sighting rates as the total number of days an individual was seen as a proportion of the total number of survey days carried out since the first sighting of the given individual. Thus, an annual sighting rate of one indicated that an individual had at least one confirmed identification each year since the first sighting. The survey sighting rates were related to seasonal residency patterns; individuals identified multiple times in a single season scored higher than individuals sighted only once. Individuals first identified after 2011 were excluded from the analysis because insufficient time had passed to estimate a robust site fidelity index.

Agglomerative hierarchical cluster (AHC) analysis was used to categorise individuals based on the two site fidelity indices using the *hclust* function in R (vers. 3.4.3, R Core Team, 2015). AHC analysis was chosen over alternative clustering and ordination methods because it follows a bottom-up approach that does not require prior specification of the expected number of clusters. The method has been applied to study residency patterns in other marine vertebrates (Daly et al., 2014; Zanardo et al., 2016). The site fidelity indices were standardised relative to the median and the median absolute deviation using the *scale* function in R, in order to enable comparisons of the two indices. The AHC analysis requires specification of an agglomerative clustering algorithm and measure of dissimilarity. Here, Ward's method was applied as the clustering algorithm because of its known robustness and competitiveness with other clustering methods (Cao et al., 1997; Murtagh & Legendre, 2014; J. H. J. Ward, 1963). Ward's method was formulated based on Euclidean distance, which was applied as a measure of dissimilarity to create a distance matrix. The AHC analysis compares all distances between all the observations and new clusters are formed by pairing the closest observations. This process is repeated until a single cluster remains. The cluster solution was displayed as a dendrogram, which was inspected visually to choose the number of site fidelity groups (see below).

As a complement to the above analyses, confirmed opportunistic matches of fin whales between the JCP and adjacent areas were considered as a means to improve the understanding of the ranging capacities of the animals within and among seasons.

2.4 Mark-recapture analyses

Cormack-Jolly-Seber (CJS; Pollock, Nichols, Brownie, & Hines, 1990) models were fitted to estimate apparent survival probabilities (Φ) and recapture probabilities (p), and the POPAN formulation for the Jolly-Seber model (Schwarz & Arnason, 1996) was employed to estimate the abundance of the super-population N . Here, the super-population is defined as the total number of individuals that were in the study area at some point from 2010 to 2016. CJS and POPAN models were fitted using the R package RMark (vers. 2.2.2, Laake & Rexstad, 2008). Each field season was considered a single sampling occasion, resulting in a total of 35 capture-recapture occasions from 1982 to 2016.

Goodness-of-fit (GOF) tests implemented in the software U-CARE (vers. 2.3.2, Choquet, Lebreton, Gimenez, & Pradel, 2005) were applied to assess the fit of a fully parameterised CJS model to the data and to identify unequal survival or recapture probabilities, for example as a result of transients (Pradel et al., 1997) or trap-dependence (trap-happiness or trap-shyness; Pradel, 1993). Transients were defined as individuals with a single sighting, thus having a zero probability of survival after their initial capture (Pradel et al., 1997). Over-dispersion in the data was estimated as the ratio, $\hat{c}$, of the overall Pearson χ^2 statistic to its number of degrees of freedom.

Following the methodology described by Ramp et al. (2014), CJS models were fitted to estimate apparent survival and recapture probabilities of sexed animals from 1990 to 2015. Information on the sex of individuals was limited to a fraction of the data set from 1990 to 2015. To account for potential bias introduced by limiting the dataset to biopsied individuals, individuals were assumed to enter the population during the year they were biopsied and all previous sightings discarded (Nichols et al., 2004). The probability of apparent survival Φ_t is the product of two components: (1) the probability that an individual survives from occasion t to $t+1$ and (2) the probability that the individual returns to the study area (site fidelity). Candidate models were built based on different combinations of effects on survival and recapture probabilities following the notation of Lebreton et al. (1992): constant over sampling occasions ($\cdot$), fully time-dependent (t), linear temporal trend (T), sex (s), and trap-dependence (m). The inclusion of immediate trap-dependence in the models of recapture probabilities was justified by the lack of fit in the Test2.CT component of the GOF test (U-CARE Test2.CT, $\chi^2 = 53.40$, $df = 23$, $p < 0.001$). The effect of trap-dependence was incorporated as an individual time-varying covariate using dummy variables (0 and 1), which allowed capture probabilities to vary depending on whether the individual was captured on the previous occasion or not (Huggins, 1989). No

transient effect (U-CARE Test3.SR, $\chi^2 = 8.92$, $df = 17$, $p = 0.94$) or over-dispersion (overall $\chi^2 = 154.51$, $df = 152$; $\hat{c} = 1.01$) was detected in the data. In addition to the strictly linear temporal trend, a more flexible temporal trend with multiple inflection points (knots) was explored using the *bs()* function in the R *splines* package (Altukhov et al., 2015). The optimal number of knots was chosen by comparing models with one to six knots based on the Akaike Information Criterion corrected for small sample size (AIC_C, Anderson, Burnham, & White, 1994). The model with three knots was retained. Additive (+) and interaction (:) effects were also considered in the form of p_{t+m} and $\Phi_{s:T}$.

Two potential sources of bias in survival estimation were assessed: temporary emigration and capture heterogeneity. As long as temporary emigration is random, survival estimates in CJS models remain unbiased (Schaub et al., 2004); however, problems arise when non-random (Markovian) temporary emigration occurs, which can introduce severe bias, particularly at the end of the time series (terminal bias: Kendall, Nichols, Hines, & Mar, 1997; Langtimm, 2009). Especially in the case of long-lived, highly mobile species, Markovian temporary emigration from the study area may not be uncommon (Langtimm, 2009). As a result, the increased uncertainty about the fate (death or temporarily unavailable for capture) of individuals at the end of the time series can make the interpretation of temporal trends in survival probabilities difficult (Peñaloza et al., 2014). As suggested by Langtimm (2009), we truncated the original capture histories and reanalysed the data over shorter time periods in order to assess whether the original data set was subject to terminal bias.

The assumption of equal capture probabilities may be violated due to differences in site fidelity patterns. To investigate the effect of heterogeneous site fidelity patterns, we estimated apparent survival probabilities for the different site fidelity clusters (i.e. core regulars and occasional visitors (see below)) as identified by the AHC analysis. CJS models were fitted to the categorised capture histories from all non-calf individuals (sexed and unsexed) from 1990 to 2016. As was the case for the AHC analysis, individuals that entered the data set during the last five years of the study were excluded.

Because there was little support for sex-specific survival rates (see below), sighting histories from all non-calf individuals (sexed and unsexed) identified during 2010 to 2016 were used to provide an abundance estimate of the super-population N using POPAN. In addition to the apparent survival Φ and recapture p probability parameters, the POPAN formulation also estimates the probability of entry (*pent*) from the super-population into the study area, as a result of immigration and/or birth. We hereafter refer to this as recruitment. The parameters Φ , p , and *pent* were allowed to be constant (.), time-dependent (t), or to follow

a linear temporal trend (T). A CJS model was used as an approximation for GOF testing, because U-CARE does not support GOF tests of POPAN models. While there was no evidence for an effect of trap-dependence (U-CARE Test2.CT; $\chi^2 = 4.87$, $df = 4$, $p = 0.301$), the GOF tests indicated the presence of transients in the data set (U-CARE Test3.SR; $\chi^2 = 23.80$, $df = 5$, $p < 0.001$). To account for a potential transient effect due to the inclusion of all individuals, we fitted models with separate survival for the interval following the first sighting of a whale by creating a time-varying covariate called *trans* (cf. Félix, Castro, Laake, Haase, & Scheidat, 2011; Laake & Rexstad, 2008). For each individual, seven (one for each year) covariates were created with 1 for an animal's first sighting and 0 for all other occasions. After accounting for transience, the over-dispersion factor was estimated to be $\hat{c} = 1.4$ and the model selection criterion (QAIC_C) and estimated standard errors were adjusted accordingly. Additive (+) and interaction (:) effects were also considered for the survival model ($\Phi_{trans+T}$ and $\Phi_{trans:T}$). Because the estimate previously published by Ramp et al. (2014) did not include a transient effect, the POPAN models with transient effect were rerun with the 2004 to 2010 data to provide a reference estimate for comparison.

Model selection of candidate CJS and POPAN models was based on AIC_C and Quasi-likelihood AIC_C (QAIC_C, Burnham & Anderson, 2002), respectively. Model averaged estimates were computed based on the AIC_C or QAIC_C weight of the models.

3. RESULTS

In total, 5,191 identifications of 507 individual fin whales were made from 1982 to 2016. The number of identified individuals in the catalogue increased steadily since 1982, marked by increased effort during 1992 and 1993, as well as the introduction of digital SLR cameras in 2004 (Fig. 3). After a pronounced increase in new identifications during 2004 to 2008, the rate of new identifications decreased after 2008. Sex was determined for 196 individuals, of which 74 were females and 122 males. Since 2004, a total of 78 calves was reported, but the number decreased sharply after 2008 to almost none since 2013 (Sullivan-Lord et al., in prep). Forty-one individuals, categorised as calves on their first sighting, were excluded from mark-recapture analyses.

Figure 3. Discovery curve of the cumulative number of identified individuals in the catalogue from 1982 to 2016 (points), with bar plots showing the number of previously identified and new individuals seen each year.

3.1 Cluster Analysis

The AHC analysis separated individuals into two distinct categories (Fig. 4). Out of the 462 individuals, the sighting histories of 128 individuals were characterised by high yearly and survey sighting rates, forming the core of individual fin whales that frequent the study area regularly, hereafter referred to as core regulars. The second group comprised the remaining 334 individuals, which showed very low site fidelity indices and are hereafter referred to as occasional visitors. This group included transient individuals that were only seen once, as well as individuals with a sparse re-sighting history in the study area. This clustering solution was confirmed by significant differences in mean yearly (two-sample $t_{159.15} = -21.50$, $p < 0.001$) and survey (two sample $t_{138.88} = -19.63$, $p < 0.001$) sighting rates between the two categories. The core regulars comprised 31 females and 63 males, compared to 37 females and 58 males among the occasional visitors. These sex ratios did not differ significantly between the two groups (2-sample test for equality of proportions; $\chi^2 = 0.49$, $df = 1$, $p = 0.48$).

Figure 4. Dendrogram visualising results of agglomerative hierarchical cluster analysis, where every tip of a branch represents one individual. Individuals can be split in two categories: a high site fidelity group (core regulars; yellow) and a low site fidelity group (occasional visitors; blue). The sample size (n), mean yearly and survey sighting rates (SR) with standard errors (SE) are given for each group.

3.2 Exchange rates with adjacent areas

Limited photo-identification data from outside the JCP were available to gain an insight into the movement patterns of fin whales in the GSL (Table 1). Despite restricted survey effort in the Estuary (ESTU), Gaspé (GASP), and Sept-Iles et Pointe-des-Monts (SIPM), 24.5% ($n=129$) of the individuals were identified in at least two areas in the GSL. Fifty-one individuals were recorded in multiple areas in the same year.

3.3 Estimated apparent survival rates during 1990 to 2015

Model support (weight) was limited to four candidate models (Table 2: models 1-4), all of which accounted for time and trap dependence in the recapture probabilities; models without the interaction term of p_{t+m} (models 5-12) had no support. The two models for survival based on temporal trends (models 1 and 3) had more support than the equivalent model without a trend (models 2 and 4). Survival models without sex (models 1 and 2) carried more weight than those with sex (models 3 and 4). Model averaged estimates of apparent survival and recapture probabilities are shown in Figure 5. A clear negative trend in estimated apparent survival was apparent since the start of the study (Fig. 5a). An initial decline was followed by a period of little change between 1998 and 2008, followed by a sharp

decline. The median overall estimate of survivorship was 0.946 (95% CI 0.910-0.967). There was little difference in estimates of survival between sexes. Recapture probabilities varied considerably among years (Fig. 5b). Elevated probabilities were observed from 2004 and onwards, coinciding with the transition to digital photography.

Table 1. Number of individuals (*N*) identified within a single area or across multiple areas.

Area	<i>N</i>
Matched individuals within areas	
ESTU	2
GASP	13
JCP	381
SIPM	2
Total	398
Matched individuals between areas	
ESTU + GASP	1
ESTU + JCP	26
ESTU + SIPM	2
GASP + JCP	43
JCP + SIPM	28
ESTU + GASP + JCP	14
ESTU + GASP + SIPM	1
ESTU + JCP + SIPM	5
GASP + JCP + SIPM	7
ESTU + GASP + JCP + SIPM	2
Total	129

Note. Location of additional areas shown in Figure 1. In JCP identifications were made on 821 survey days, compared to opportunistic effort of 91 survey days in GASP, 32 in SIPM, and unknown number of surveys in ESTU. ESTU: St. Lawrence Estuary; GASP: Gaspé; JCP: Mingan Islands and Jacques Cartier Passage; SIPM: Sept-Îles to Pointe-des-Monts.

Table 2. Cormack-Jolly-Seber models fitted to data from 1990 to 2015 for estimation of survival rate Φ .

Model	npar	AIC _C	Δ AIC _C	weight	Residual Deviance
1. $\Phi_{(T)}p_{(t+m)}$	30	2015.80	0.00	0.46	1953.04
2. $\Phi_{(.)}p_{(t+m)}$	27	2017.22	1.43	0.23	1960.99
3. $\Phi_{(s:T)}p_{(t+m)}$	29	2017.23	1.43	0.23	1956.65
4. $\Phi_{(s)}p_{(t+m)}$	28	2019.15	3.36	0.09	1960.76
5. $\Phi_{(T)}p_{(t)}$	29	2049.99	34.20	0.00	1409.62
6. $\Phi_{(s:T)}p_{(t)}$	28	2052.48	36.68	0.00	1414.28
7. $\Phi_{(.)}p_{(t)}$	26	2058.85	43.05	0.00	1424.98
8. $\Phi_{(s)}p_{(t)}$	27	2060.62	44.82	0.00	1424.59
9. $\Phi_{(.)}p_{(m)}$	3	2136.46	120.66	0.00	2130.43
10. $\Phi_{(s)}p_{(m)}$	4	2138.43	122.63	0.00	2130.37
11. $\Phi_{(s:T)}p_{(m)}$	5	2139.99	124.19	0.00	2129.90
12. $\Phi_{(T)}p_{(m)}$	6	2141.45	125.66	0.00	2129.33

Note. Models are ordered in ascending order of their Akaike Information Criterion corrected for small sample sizes (AIC_C); npar: number of parameters; Δ AIC_C: difference in AIC_C in relation to model with lowest AIC_C; p : recapture probability; T : linear temporal trend; t : time (sampling occasion); m : trap-dependence; s : sex; $(.)$: constant.

Figure 5. Model-averaged (a) apparent survival Φ and (b) recapture probabilities p with 95% confidence intervals from the Cormack–Jolly–Seber models listed in Table 2.

Truncation of the data set to shorter time periods strongly suggested a terminal bias due to non-random temporary emigration (Langtimm, 2009; Fig. 6). When sighting histories were truncated by three, six, and nine years, the apparent survival estimates of the last one to three years were lower than the estimates for the same period with the full data set. The large proportion of occasional visitors identified during the AHC analysis might be the cause of the terminal bias.

To test the hypothesis of terminal bias caused by divergent site fidelity patterns, CJS models were fitted separately to the sighting histories of the core regulars and the occasional visitors (Supporting information; Table S1 + S2). As expected, the recapture probabilities of the high site fidelity core regulars were significantly higher than those of the low site fidelity occasional visitors (Fig. 7b), indicating that the assumption of recapture homogeneity was violated in the previous model where all individuals were pooled together (see Fig. 5b). Apparent survival probabilities were overall lower for the occasional visitors and showed a constant negative trend (Fig. 7a). For the highly site faithful core regulars, apparent survival probabilities were close to one before declining from 2005 and onwards.

Figure 6. Temporal trend in survival probabilities of the full 25-year period (black) and of capture histories truncated to 22 (blue), 19 (yellow), and 16 (red) years. Arrows indicate the last survival value of truncated time series. The truncation of capture histories was used to investigate the presence of terminal bias in survival probabilities. Based on time dependent CJS model $\phi_t p_{t+m}$.

Figure 7. Time-series of model-averaged (a) apparent survival Φ and (b) recapture probabilities p with 95% confidence intervals. Cormack-Jolly-Seber models (Supporting information; Table S1 + S2) were fitted separately to sighting histories of core regulars and occasional visitors.

3.4 Estimated super-population size

The most supported model included the transient effect and temporal trend for the probability of survival Φ , with time dependent recapture probability p and a linear temporal trend for recruitment $pent$ (Table 3 model 1). All candidate models which included the transient effect in the survival model (models 1-9) had greater support (based on QAIC_C weight) than comparable models without the transient effect (models 10-12), highlighting the importance of this additional parameter. The probabilities of apparent survival and recruitment steadily decreased over time, with recruitment almost reaching zero probability by the end of the time series (Fig. 8). Recapture probabilities reached a minimum of 0.3 in 2014 and increased to ~0.6 during the last two years of the study. The model-averaged estimate of super-population size N was 291 (95% CI 270-312), reflecting the estimate of abundance of the population which contributed individuals to the study area in 2010 to 2016. The same models fitted to the 2004 to 2010 data resulted in a model averaged N of 335 (95% CI 321-348) from 2004 to 2010 (Supporting information; Table S3).

Table 3. Selection of POPAN models fitted to data from 2010 to 2016 for estimation of super-population size N .

Model	npar	QAIC _C	ΔQAIC _C	weight	QDeviance
1. $\Phi_{(trans+T)}p_{(t)}pent_{(T)}N_{(.)}$	13	908.06	0.00	0.51	881.43
2. $\Phi_{(trans+T)}p_{(t)}pent_{(.)}N_{(.)}$	12	910.52	2.47	0.15	885.99
3. $\Phi_{(trans)}p_{(t)}pent_{(T)}N_{(.)}$	12	910.94	2.88	0.12	886.41
4. $\Phi_{(trans:T)}p_{(t)}pent_{(T)}N_{(.)}$	12	911.44	3.38	0.09	886.91
5. $\Phi_{(trans+T)}p_{(t)}pent_{(t)}N_{(.)}$	17	912.75	4.69	0.05	877.70
6. $\Phi_{(trans:T)}p_{(t)}pent_{(.)}N_{(.)}$	11	913.65	5.60	0.03	891.20
7. $\Phi_{(trans)}p_{(t)}pent_{(.)}N_{(.)}$	11	913.89	5.83	0.03	891.44
8. $\Phi_{(trans:T)}p_{(t)}pent_{(t)}N_{(.)}$	16	915.95	7.89	0.01	883.01
9. $\Phi_{(trans)}p_{(t)}pent_{(t)}N_{(.)}$	16	915.95	7.89	0.01	883.01
10. $\Phi_{(.)}p_{(t)}pent_{(T)}N_{(.)}$	11	920.22	12.16	0.00	-550.11
11. $\Phi_{(T)}p_{(t)}pent_{(T)}N_{(.)}$	12	921.60	13.54	0.00	-550.81
12. $\Phi_{(.)}p_{(t)}pent_{(.)}N_{(.)}$	10	923.06	15.00	0.00	-545.20

Note. Models are ordered based on the Quasi-likelihood AIC_C (QAIC_C). *pent*: probability of recruitment; *trans* : transient effect. See Table 2 for other abbreviations. Full model list in Supporting information, Table S4.

Figure 8. Model-averaged probabilities of apparent survival Φ (yellow), capture p (blue) and recruitment $pent$ (red) with 95% confidence intervals for the POPAN models from 2010 to 2016 (Table 3).

4. DISCUSSION

Robust estimates of abundance and survival rates provide valuable information on population status, but they remain difficult to obtain for wide-ranging, mobile species. This study stems from a photo-identification database for fin whales in the JCP spanning 35 years. A mark-recapture analysis revealed a decline in apparent survival rates from 1990 to 2015. The deterioration in the condition of the population implied by this finding was supported by three additional observations: (1) a negative trend in recruitment from 2010 to 2016, (2) a significant decline in the super-population size from an estimated 335 (95% CI 321-348) animals in 2004 to 2010 to 291 (95% CI 270-312) animals in 2010 to 2016, and (3) a sharp drop in the number of reported calves since 2008 with almost none since 2013. Before discussing possible explanations and implications of these findings, we first assess to what extent individual heterogeneity in site fidelity and movement patterns (e.g. non-random temporary emigration) could have influenced these results.

Open population models, such as the CJS and POPAN models used in this study, make two assumptions that require close scrutiny: (1) every marked animal present in the population at time (t) has the same probability of recapture (p_t) and (2) all marked individuals have the same survival probability from one sampling occasion to the next (Hammond, 1990b; Lebreton et al., 1992). These assumptions are often unrealistic in wildlife studies due to inherent individual heterogeneity (Hammond, 1990b), but here several measures were applied to relax them. We accounted for trap-dependency in the CJS recapture models and for a transient effect in the POPAN survival models to minimise potential bias. A pattern of trap-dependence can appear in the data when parts of the study area are more frequently surveyed when animals have been detected, when individuals have higher recapture probabilities because they spend more time in more accessible parts of the study area, or when recapture probabilities are affected by life history (Pradel & Sanz-Aguilar, 2012). Transient individuals were less likely to be biopsied, which is probably why no transient effect was found when limiting the dataset to biopsied individuals only. Compared to Ramp et al.'s (2014) estimate ($N = 328$; 95% CI 306-350), the inclusion of a transient effect did not alter the estimate of the super-population size from 2004 to 2010 ($N = 335$; 95% CI 321 - 348), but was slightly more precise.

Despite accounting for trap-dependency, there were strong indications of deviations from equal recapture probabilities in the first CJS model due to heterogeneity in the degree of site fidelity. Schaub et al. (2004) showed that while the U-CARE Test2.CT component was initially developed to detect immediate trap response behaviour; a significant test could also be indicative of Markovian temporary emigration. The inclusion of the time-varying trap-

dependence variable (m) only approximately adjusts for temporary emigration because recapture probabilities are made dependent on sightings during the previous capture occasion (Schaub et al., 2004). However, Markovian temporary emigration is likely to be a lot more complex and may depend on other factors, such as prey availability. The AHC analysis revealed a range of site fidelity patterns, with two broad categories for core regulars and occasional visitors. As expected, the core regulars displayed higher probabilities of recapture compared to the occasional visitors. Hence, ignoring divergent site fidelity patterns equates to ignoring capture heterogeneity. Considering that apparent survival probabilities are a combination of true survival and permanent emigration, which in turn may be linked to site fidelity, estimates of survival rates may be biased when differences in site fidelity (and therefore recapture probability) are ignored. In particular, temporal variation in site fidelity could lead to misleading trends in apparent survival probabilities.

Another side effect of Markovian temporary emigration patterns is terminal bias in apparent survival estimates. Truncation of the time series of data, as suggested by Langtimm (2009), continued to show lower survival estimates at the end of the truncated time series, indicative of terminal bias. True survival and temporary emigration rates have both been shown to influence how far back in time the bias will propagate, where animals with high true survival and temporary emigration rates are most strongly affected by terminal bias (Langtimm, 2009). The negative trends in estimated survival were still evident when individuals were grouped into separate categories based on their site fidelity patterns, but occasional visitors showed a steady long-term decline, while the survival of core regulars only dropped sharply in the final years of the study. It remains difficult to judge to what extent this drop was a result of remaining terminal bias. Models with a robust design (RD) can account for random temporary emigration and mitigate some of the concomitant bias (Kendall et al., 1997; Peñaloza et al., 2014). The RD requires individuals to be sampled at primary occasions, open to gains and losses, and closed secondary occasions. While the assumption of closure can be relaxed under specific conditions, Kendall (1999) found that estimators were biased when movement was non-random. In our case preliminary analyses rejected the assumption of closure during shorter sampling periods (months) over summer (results not shown). The reason for this is considerable intra-seasonal movement in and out of the study area. Due to the violation of the assumption of closure and the suspected presence of non-random temporary emigration, the RD model was considered inappropriate for this dataset. The Barker model (Barker, 1997) requires information on sightings between primary sampling periods, which was not available at the time of writing, but collaborations with other research institutions could make such an analysis possible in the future.

Such collaborative work would be particularly beneficial in the light of what we have learned from the results of this study. The increasing discovery curve (Fig. 3) suggests that the JCP contains only a fraction of the animals in the GSL population. The limited data on photo-ID matches among different study areas in the GSL highlight a high rate of interchange of individuals among areas. The high proportion of occasional visitors could be an indication that individuals are attracted to the JCP at times of high productivity. Coakes et al. (2005) described the occurrence of unusually high numbers of fin whales off Nova Scotia in 1997, including individuals from the GSL and Gulf of Maine, which coincided with higher levels of herring, sand lance and euphausiid abundance. Concurrently, these authors reported a lower abundance of fin whales in the GSL in 1997. Estimates for the JCP have previously been considered representative for the GSL (Ramp et al., 2014); however, these results indicate that only about a quarter of the individuals (27.7%) show high site fidelity to the area, with the majority of fin whales using the JCP on an irregular basis, possibly depending on prey availability.

The problems encountered in the mark-recapture analysis are not unique to this study. We therefore caution researchers to consider possible effects of capture heterogeneity, introduced by divergent site fidelity patterns in their study population, and the effect of terminal bias when analysing their data and interpreting the results of long-term survival trends of long-lived, highly mobile species. When alternative models (RD or Barker) are not applicable, the proposed categorisation of individuals using cluster analysis offers a flexible alternative to minimise bias while providing additional insights into population demography. The grouping based on AHC analysis may also offer an alternative to 'time since marking' (TSM) or 2 age-class models. TSM models have been proposed to account for transients (animals seen only once) by estimating different survival rates for the first sampling interval compared to subsequent intervals (Pradel et al., 1997). However, site fidelity patterns can range along a continuum and by only accounting for transients, capture heterogeneity caused by individuals with low site fidelity may stay unaccounted for. In contrast, the AHC approach offers greater flexibility in defining groups based on their visitation patterns.

The median unisex estimate of survivorship of 0.946 (95% CI 0.910-0.967) was comparable to the estimate provided by Ramp et al. of 0.955 (95% CI 0.936-0.969). While the drop in apparent survival estimates in the later years of the study is likely subject to some terminal bias, the inference of a deterioration in population status is supported by the negative trend in recruitment and the significant decline in super-population size, implying that a lower number of fin whales used the JCP at any point between 2010 to 2016 compared to 2004 to

2010. The decline in survival could partly be the result of higher rates of permanent emigration compared to immigration rates.

In the period of 2004 to 2010, 20 dead fin whales were reported in the GSL, compared to six animals for 2010 to 2016 (Quebec Marine Mammal Emergency Network Call Center, pers. comm.). These numbers are underestimates of true mortality rates because an unknown number of carcasses were missed or unreported. A documented cause of fin whale mortality is vessel collisions. Fin whales are the most commonly reported species in the current global vessel-strike data set maintained by the Scientific Committee of the International Whaling Commission (Douglas et al., 2008; Laist et al., 2001; Panigada et al., 2006; Van Der Hoop et al., 2013). Such high mortality rates are likely unsustainable for a population of fewer than 300 individuals and could, in combination with the lack of recruitment, explain the observed decline in the super-population size.

An alternative explanation is that the observed changes could be caused by varying environmental conditions affecting prey availability. Individuals may have permanently emigrated from the JCP in favour of a different feeding ground. A gradual shift in distribution could explain lower recruitment and a decrease in the super-population size. While significant changes in the ecosystem of the GSL have been reported (Bui et al., 2010; Johnston et al., 2012; Ramp et al., 2015), it is not clear how fin whale prey availability changed over the study period or whether changes in prey distribution could have caused a shift in distribution away from the JCP in recent years. A shift in distribution would result in a concomitant increase in abundance in neighbouring areas, which has not been confirmed (GREMM, pers. comm.), but large areas remain unsurveyed.

The new information presented here is important to consider in future conservation plans for fin whales in the GSL. Priority should be given to determining the underlying cause(s) of the observed decline, which we hypothesise to be the result of anthropogenic mortality events (e.g. vessel collisions, entanglements), changes in prey availability, or a combination of these factors. Failure to address these issues could result in an ongoing decline of fin whales in the GSL with unknown impacts on the balance of the GSL ecosystem.

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Authors' contributions

AS, CR, RS, PSH conceived the initial ideas of the study and designed the methodology; AC, CR, JD, MB, PJP and RS collected photo-identification data and/or skin samples; MB and PJP conducted the analysis to sex the individuals; JD, AC, CR, RS processed the photo-ID data; AS analysed the data; AS and PSH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

R code, capture histories and sex of individual fin whales to estimate survival rates and abundance are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pv93760>.

SUPPLEMENTARY INFORMATION

Cormack-Jolly-Seber (CJS) models were fitted separately to individuals classified as core regulars or occasional visitors by the agglomerative hierarchical clustering analysis. After accounting for trap-dependence in the models fitted to the capture histories of core regulars (U-CARE Test2.CT, $\chi^2 = 75.10$, $df = 24$, $p < 0.001$), the over-dispersion factor was estimated to be $\hat{c} = 1.24$ (overall $\chi^2 = 70.7$, $df = 57$). The model selection criterion (QAIC_c) and standard errors were adjusted accordingly (Table S1). No $\hat{c}$ adjustment was necessary for the models fitted to the occasional visitor group ($\chi^2 = 87.22$, $df = 82$, $\hat{c} = 1.06$; Table S2). In both groups, the model for survival with a linear temporal trend ($\Phi_{(T)}$) and recapture probabilities accounting for time and trap dependence ($p_{(t+m)}$) held most of the weight.

Table S1. Model selection for CJS models fitted to capture histories from 1990 to 2016 for group of core regular individuals. See Table 2 for abbreviations.

model	npar	QAICc	Δ QAICc	weight	QDeviance
1. $\Phi_{(T)}p_{(t+m)}$	29	1857.19	0.00	0.97	1797.20
2. $\Phi_{(.)}p_{(t+m)}$	28	1863.86	6.67	0.03	1806.00
3. $\Phi_{(T)}p_{(t)}$	28	1876.04	18.85	0.00	1423.55
4. $\Phi_{(.)}p_{(t)}$	27	1892.16	34.97	0.00	1441.79
5. $\Phi_{(t)}p_{(t+m)}$	53	1904.65	47.46	0.00	1791.90
6. $\Phi_{(t)}p_{(t)}$	52	1923.68	66.49	0.00	1418.56
7. $\Phi_{(T)}p_{(m)}$	4	1966.51	109.32	0.00	1958.47
8. $\Phi_{(.)}p_{(m)}$	3	1967.65	110.47	0.00	1961.63
9. $\Phi_{(t)}p_{(m)}$	28	2011.31	154.12	0.00	1953.45

Table S2. Model selection for CJS models fitted to capture histories from 1990 to 2016 for group of occasional visitors. See Table 2 for abbreviations.

model	npar	AICc	Δ AICc	weight	Deviance
1. $\Phi_{(T)}p_{(t+m)}$	29	2814.53	0.00	0.77	2754.20
2. $\Phi_{(.)}p_{(t+m)}$	28	2817.43	2.89	0.18	2759.26
3. $\Phi_{(T)}p_{(t)}$	28	2820.41	5.88	0.04	1517.39
4. $\Phi_{(.)}p_{(t)}$	27	2826.34	11.81	0.00	1525.47
5. $\Phi_{(t)}p_{(t+m)}$	53	2849.85	35.32	0.00	2735.94
6. $\Phi_{(t)}p_{(t)}$	52	2854.29	39.76	0.00	1497.83
7. $\Phi_{(.)}p_{(m)}$	3	2997.16	182.63	0.00	2991.13
8. $\Phi_{(T)}p_{(m)}$	4	2998.38	183.84	0.00	2990.32
9. $\Phi_{(t)}p_{(m)}$	28	3017.75	203.22	0.00	2959.58

To get comparable estimates to the period 2010-2016, a POPAN model with transient effect was fitted to data from 2004 to 2010 to estimate the super-population size N . A CJS model

was fitted for approximate GOF testing in U-CARE. After accounting for a transient effect (U-CARE Test3.SR, $\chi^2 = 16.04$, $df = 5$, $p = 0.007$), there was no sign of over-dispersion left in the data ($\chi^2 = 14.87$, $df = 14$, $\hat{c} = 1.06$) and no $\hat{c}$ adjustment was applied (Table S3).

Table S3. Model selection for POPAN 2004 to 2010.

model	npar	AICc	Δ AICc	weight	Deviance
1. $\Phi_{(trans:T)}p_{(t)}pent_{(t)}N_{(.)}$	16	1726.64	0.00	0.72	1693.97
2. $\Phi_{(trans+T)}p_{(t)}pent_{(t)}N_{(.)}$	17	1729.64	3.00	0.16	1694.88
3. $\Phi_{(trans+T)}p_{(.)}pent_{(t)}N_{(.)}$	11	1730.36	3.71	0.11	1708.03
4. $\Phi_{(trans:T)}p_{(t)}pent_{(T)}N_{(.)}$	12	1741.31	14.67	0.00	1716.93
5. $\Phi_{(trans:T)}p_{(.)}pent_{(t)}N_{(.)}$	10	1742.08	15.44	0.00	1721.81
6. $\Phi_{(T)}p_{(.)}pent_{(t)}N_{(.)}$	10	1744.44	17.79	0.00	-787.38
7. $\Phi_{(trans+T)}p_{(t)}pent_{(T)}N_{(.)}$	13	1744.63	17.99	0.00	1718.19
8. $\Phi_{(T)}p_{(t)}pent_{(t)}N_{(.)}$	16	1744.77	18.12	0.00	-799.46
9. $\Phi_{(trans)}p_{(t)}pent_{(t)}N_{(.)}$	16	1747.66	21.02	0.00	1714.99
10. $\Phi_{(.)}p_{(t)}pent_{(t)}N_{(.)}$	15	1749.73	23.08	0.00	-792.42
11. $\Phi_{(T)}p_{(t)}pent_{(T)}N_{(.)}$	12	1758.99	32.34	0.00	-776.95
12. $\Phi_{(trans)}p_{(t)}pent_{(T)}N_{(.)}$	12	1762.61	35.97	0.00	1738.23
13. $\Phi_{(trans:T)}p_{(t)}pent_{(.)}N_{(.)}$	11	1763.74	37.10	0.00	1741.42
14. $\Phi_{(.)}p_{(t)}pent_{(T)}N_{(.)}$	11	1764.38	37.74	0.00	-769.49
15. $\Phi_{(trans+T)}p_{(.)}pent_{(T)}N_{(.)}$	7	1764.96	38.31	0.00	1750.82
16. $\Phi_{(trans+T)}p_{(t)}pent_{(.)}N_{(.)}$	12	1767.20	40.55	0.00	1742.81
17. $\Phi_{(.)}p_{(.)}pent_{(t)}N_{(.)}$	9	1767.63	40.98	0.00	-762.14
18. $\Phi_{(trans)}p_{(.)}pent_{(t)}N_{(.)}$	10	1769.33	42.69	0.00	1749.06
19. $\Phi_{(trans:T)}p_{(.)}pent_{(T)}N_{(.)}$	6	1777.94	51.29	0.00	1765.83
20. $\Phi_{(T)}p_{(.)}pent_{(T)}N_{(.)}$	6	1779.08	52.43	0.00	-744.58
21. $\Phi_{(T)}p_{(t)}pent_{(.)}N_{(.)}$	11	1782.38	55.74	0.00	-751.49
22. $\Phi_{(trans)}p_{(t)}pent_{(.)}N_{(.)}$	11	1785.75	59.11	0.00	1763.43
23. $\Phi_{(.)}p_{(t)}pent_{(.)}N_{(.)}$	10	1788.31	61.67	0.00	-743.51
24. $\Phi_{(trans+T)}p_{(.)}pent_{(.)}N_{(.)}$	6	1797.69	71.04	0.00	1785.58
25. $\Phi_{(.)}p_{(.)}pent_{(T)}N_{(.)}$	5	1803.50	76.86	0.00	-718.12
26. $\Phi_{(trans)}p_{(.)}pent_{(T)}N_{(.)}$	6	1805.16	78.52	0.00	1793.06
27. $\Phi_{(T)}p_{(.)}pent_{(.)}N_{(.)}$	5	1811.31	84.67	0.00	-710.31
28. $\Phi_{(trans:T)}p_{(.)}pent_{(t)}N_{(.)}$	5	1818.83	92.19	0.00	1808.76
29. $\Phi_{(.)}p_{(.)}pent_{(.)}N_{(.)}$	4	1844.10	117.45	0.00	-675.51
30. $\Phi_{(trans)}p_{(.)}pent_{(.)}N_{(.)}$	5	1845.29	118.64	0.00	1835.21

Table S4. Full list of POPAN models considered for recapture histories from 2010 to 2016.

model	npar	QAICc	Δ QAICc	weight	QDeviance
1. $\Phi_{(trans+T)}p_{(t)}pent_{(T)}N_{(.)}$	13	908.06	0.00	0.51	881.43
2. $\Phi_{(trans+T)}p_{(t)}pent_{(.)}N_{(.)}$	12	910.52	2.47	0.15	885.99
3. $\Phi_{(trans)}p_{(t)}pent_{(T)}N_{(.)}$	12	910.94	2.88	0.12	886.41
4. $\Phi_{(trans:T)}p_{(t)}pent_{(T)}N_{(.)}$	12	911.44	3.38	0.09	886.91
5. $\Phi_{(trans+T)}p_{(t)}pent_{(t)}N_{(.)}$	17	912.75	4.69	0.05	877.70
6. $\Phi_{(trans:T)}p_{(t)}pent_{(.)}N_{(.)}$	11	913.65	5.60	0.03	891.20
7. $\Phi_{(trans)}p_{(t)}pent_{(.)}N_{(.)}$	11	913.89	5.83	0.03	891.44
8. $\Phi_{(trans:T)}p_{(t)}pent_{(t)}N_{(.)}$	16	915.95	7.89	0.01	883.01
9. $\Phi_{(trans)}p_{(t)}pent_{(t)}N_{(.)}$	16	915.95	7.89	0.01	883.01
10. $\Phi_{(.)}p_{(t)}pent_{(T)}N_{(.)}$	11	920.22	12.16	0.00	-550.11
11. $\Phi_{(T)}p_{(t)}pent_{(T)}N_{(.)}$	12	921.60	13.54	0.00	-550.81
12. $\Phi_{(.)}p_{(t)}pent_{(.)}N_{(.)}$	10	923.06	15.00	0.00	-545.20
13. $\Phi_{(T)}p_{(t)}pent_{(.)}N_{(.)}$	11	923.83	15.78	0.00	-546.50
14. $\Phi_{(.)}p_{(t)}pent_{(t)}N_{(.)}$	15	925.02	16.96	0.00	-553.69
15. $\Phi_{(T)}p_{(t)}pent_{(t)}N_{(.)}$	16	926.30	18.25	0.00	-554.51
16. $\Phi_{(trans+T)}p_{(.)}pent_{(.)}N_{(.)}$	6	935.21	27.15	0.00	923.06
17. $\Phi_{(trans)}p_{(.)}pent_{(.)}N_{(.)}$	5	935.33	27.27	0.00	925.23
18. $\Phi_{(trans)}p_{(.)}pent_{(T)}N_{(.)}$	6	936.10	28.04	0.00	923.96
19. $\Phi_{(trans+T)}p_{(.)}pent_{(T)}N_{(.)}$	7	936.19	28.13	0.00	922.00
20. $\Phi_{(trans)}p_{(.)}pent_{(t)}N_{(.)}$	10	938.35	30.30	0.00	917.98
21. $\Phi_{(trans+T)}p_{(.)}pent_{(t)}$	11	938.48	30.42	0.00	916.03
22. $\Phi_{(trans:T)}p_{(.)}pent_{(T)}N_{(.)}$	6	940.22	32.16	0.00	928.07
23. $\Phi_{(trans:T)}p_{(.)}pent_{(.)}N_{(.)}$	5	940.24	32.18	0.00	930.13
24. $\Phi_{(trans:T)}p_{(.)}pent_{(t)}N_{(.)}$	10	942.40	34.34	0.00	922.02
25. $\Phi_{(.)}p_{(.)}pent_{(.)}N_{(.)}$	4	946.61	38.55	0.00	-509.34
26. $\Phi_{(.)}p_{(.)}pent_{(T)}N_{(.)}$	5	946.99	38.93	0.00	-510.99
27. $\Phi_{(T)}p_{(.)}pent_{(.)}N_{(.)}$	5	948.59	40.53	0.00	-509.39
28. $\Phi_{(T)}p_{(.)}pent_{(T)}N_{(.)}$	6	948.70	40.64	0.00	-511.33
29. $\Phi_{(.)}p_{(.)}pent_{(t)}N_{(.)}$	9	949.18	41.12	0.00	-517.01
30. $\Phi_{(T)}p_{(.)}pent_{(t)}N_{(.)}$	10	950.86	42.80	0.00	-517.40

CHAPTER

03

3

Spatio-temporal patterns in fin whale (*Balaenoptera physalus*) habitat use in the northern Gulf of St. Lawrence²

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ABSTRACT

Significant ecosystem changes in the Gulf of St. Lawrence (GSL), Canada, have had far-reaching effects at all trophic levels. The abundance of fin whales (*Balaenoptera physalus*) has declined significantly in the northern GSL over the past decade. This study aimed to test the hypothesis that the observed decline was correlated to changing environmental conditions. Cetacean sighting data from 292 surveys, resulting in 2986 fin whale encounters from 2007 to 2013, were used to fit two separate generalised additive models in terms of (1) bathymetric and oceanographic variables (the proxy model) and (2) modelled krill biomass (the prey model). The concept of 'handling time' was introduced to correct for time off search effort, applicable to other studies relying on opportunistically sampled data. While a positive correlation between krill biomass and fin whale numbers was found, the performance of the proxy model (24.2 % deviance explained) was overall better than the prey model (11.8 %). Annual predictive maps derived from the final proxy model highlighted two key areas with recurrently high relative fin whale abundance and a significant overlap with shipping lanes. While both models provided evidence for an annual decline in relative fin whale abundance, static bathymetric features were the most important predictors of habitat use and no correlation between dynamic variables and the decline was found. High resolution prey data and a better understanding of the feeding ecology of fin whales are proposed to further investigate the predator-prey relationship and decline of fin whales in the GSL.

1. INTRODUCTION

Rapid ecosystem changes in relation to changing environmental conditions have been reported in a wide variety of ecosystems (e.g. Fossheim et al., 2015; Hoegh-Guldberg et al., 2007; Sahade et al., 2015; Thomson et al., 2015). Changes in environmental conditions may affect species directly by challenging their physiological tolerance levels or indirectly by disrupting vital interspecies interactions (Tylianakis et al., 2008). Species may respond with changes in abundance or shifts in distribution (Florko et al., 2018).

The Gulf of St. Lawrence (GSL), in eastern Canada, has seen major and potentially far-reaching ecosystem changes over the past decades due to climate change and anthropogenic pressures. In the early 1990s, overfishing culminated in the collapse of Atlantic cod (*Gadus morhua*) and other large demersal fish stocks, marking a fishery-induced regime shift in the ecosystem (Bui et al., 2010; Savenkoff et al., 2007). Simultaneously, unprecedented warming of incoming North Atlantic water, changes in sea surface temperature (SST), salinity and sea ice extent altered the habitat significantly (Plourde et al., 2014; Thibodeau et al., 2010).

Higher mortality rates in response to these ecosystem changes were reported even in higher predators, such as harp seals (*Pagophilus groenlandicus*) and belugas (*Delphinapterus leucas*), highlighting the cascading effects of the changing environmental conditions (Johnston et al., 2012; Plourde et al., 2014).

In this context, this study aimed to investigate the spatio-temporal patterns in fin whale (*Balaenoptera physalus*) distribution and abundance in the northern GSL. Schleimer et al. (2019) found a significant decline in the number of fin whales using this feeding area and evidence of declining survival rates over the past decade. However, a shift in distribution (i.e. permanent emigration) in response to ecosystem changes in the GSL was also proposed as a possible explanation for the decline in numbers. Fin whales in the GSL have been found to shift arrival dates to the feeding ground in the GSL at a rate of one day earlier per year over three decades, linked to earlier winter sea ice break up and higher SST (Ramp et al., 2015). Fin whale distribution has been correlated with the occurrence of thermal fronts in the GSL (Doniol-Valcroze et al., 2007); however, the physical and biological processes that drive intra- and inter-annual variation in distribution of fin whales in the GSL remain poorly understood.

Here, we hypothesised that the observed changes in abundance could be attributed to changes in environmental conditions. To test this hypothesis, spatio-temporal patterns in fin whale distribution were explored within a species distribution model (SDM) framework (Forney et al., 2012; Hazen et al., 2017; Redfern et al., 2006). SDMs aim to identify the underlying factors that drive spatio-temporal trends in species' distribution, offering insight into both the causes of past responses and predictions of future responses to a changing environment (Hazen et al., 2013; Víkingsson et al., 2015). If changes in the environmental conditions in the GSL, as reflected by changes in sea temperature, primary productivity or prey biomass, were at the basis of the observed decline in abundance of fin whales, we expected to detect such a relationship in the SDMs with the retention of dynamic variables in the final model. Extensive survey and effort data collected in the northern GSL over seven summers provided the basis of this study. SDMs frequently use proxy variables that are assumed to be indicative of high productivity and prey distribution (Torres et al., 2008). Here, two separate SDMs were built. The first SDM modelled fin whale relative abundance as a function of commonly used proxy variables for high productivity (including bathymetric and remotely sensed oceanographic variables), while the second SDM used modelled krill biomass as explanatory variable in place of the proxy variables used to derive it (Plourde et al., 2016). Specifically, we wanted to test whether the modelled prey variable would provide better predictive power to a model based on proxy variables to define fin

whale habitat. Euphausiids constitute an important component of fin whale diet in the GSL (Gavrilchuk et al., 2014) and a strong link between fin whale distribution and euphausiid biomass is expected. We wanted to test whether euphausiid biomass derived from a model could serve as informative alternative to high-resolution prey data despite the inherent uncertainty associated with habitat model predictions.

Ideally, cetacean habitat models are built using data derived from systematic surveys specifically designed to estimate cetacean density and abundance. However, given cost and scheduling limitations imposed by such dedicated surveys, there is a growing interest in developing methods to account for the biases associated with non-systematic or opportunistic surveys (e.g. Isojunno, Matthiopoulos, & Evans, 2012; Phillips et al., 2009; Williams, Hedley, & Hammond, 2006). The fin whale data used in the present study were collected as part of a photo-identification study; as such, the survey design differed from conventional systematic cetacean surveys in three ways; (1) surveys were not designed to ensure equal coverage probability, (2) distance-sampling was not implemented, and (3) search effort was interrupted by the collection of sighting-specific data (e.g. photo-identification and biopsy data). The nature of the data prohibited a design-based approach, necessitating a model-based approach, using generalised additive models (GAMs), which does not require random placement of survey lines in the study area. Additionally, the concept of ‘handling time’ was applied to differentiate between time spent collecting sighting-specific data and search effort. The proposed methods are applicable to other studies that rely on opportunistically collected data, such as cetacean data collected during whale watching activities.

2. MATERIALS AND METHODS

2.1 Cetacean survey data

The study area was located in the Jacques Cartier Passage (JCP), between Anticosti Island and the North Shore in the GSL, extending over an area of approximately 8000 km² (Fig. 1). The region covers diverse topographic features, such as the head of the Anticosti Channel, the steep slopes along Anticosti Island, and the shallower plateaus of the North Shore and Banc Parent. Upwelling of cold, nutrient rich waters from the cold intermediate layer place the region among the most productive in the GSL, allowing the ecosystem to sustain a high biodiversity (Bourque et al., 1995; Doniol-Valcroze et al., 2007). During summer months, minke whales (*Balaenoptera acutorostrata*), humpback whales (*Megaptera novaeangliae*), fin whales and harbour porpoises (*Phocoena phocoena*) co-occur in the study area, with

occasional sightings of blue whales (*B. musculus*) and, more recently, North Atlantic right whales (*Eubalaena glacialis*).

Cetacean survey data were collected by researchers from Mingan Island Cetacean Study from June to October in the years of 2007 to 2013. The data used for the purpose of this study consisted of the non-random survey tracks and the position, timing, and group size of each fin whale sighting. Surveys were conducted using rigid-hulled inflatable boats and focussed on the collection of photo-identification data of large rorquals. The survey design is therefore best described in terms of 'whaler-behaviour' meaning that captains targeted areas where they expected to find animals to maximise photo-identification effort. The surveys covered as large an area as possible until groups of whales were found. Boat speed varied between 15 and 20 knots, with occasional stops to scan the horizon with binoculars for blows. For safety reasons, two boats conducted surveys simultaneously, but they generally covered different areas. Surveys were terminated when weather conditions deteriorated to Beaufort scale >3 or visibility <1 nautical mile.

Once an individual or group of whales was detected, the time of the sighting was noted and the animals were approached slowly for collection of photo-identification and sometimes biopsy data. The exact position was recorded at the 'fluke print' where the animal dived after its surfacing sequence. The group size of animals was recorded and individuals were attributed field-ID numbers to keep track of individuals on subsequent sightings. Field-ID numbers and photo-identification data were used to determine whether individuals had already been sighted previously. If individuals were not identifiable, the group was considered to be a new sighting.

2.2 Data processing

2.2.1 Effort quantification

The survey track was recorded using a LOWRANCE LMS-480M GPS unit (precision ≤ 30 m) on each survey boat. The resulting survey tracks were used to calculate survey effort. Due to variable boat speeds and *ad libitum* survey tracks, the length of the survey track was not considered an appropriate measure of effort. Instead effort was defined as the time in seconds spent searching for animals within a grid cell (see below). Timestamps were retrieved from the GPS tracks to estimate the effort spent in each grid cell (see Supplementary Fig. S1).

A grid-based modelling framework was adopted in accordance with previous studies dealing with non-systematic survey designs (Cañadas et al., 2005; Isojunno et al., 2012). The study area was divided into 5 x 5 km grid cells in which the number of fin whale individuals, effort and environmental covariates could be summarised. The size of the grid cells was chosen based primarily on the resolution of available remotely sensed and modelled covariates (Table 1).

Figure 1. Schematic representation of the Gulf of St. Lawrence, with detailed bathymetry of the study area in the Jacques Cartier Passage.

While time identified as ‘off-effort’ was excluded from the calculations, the strong focus on photo-identification and biopsy sampling made further modification of the effort data necessary. When the researchers were concentrating on obtaining photo-identification data and taking biopsy samples, all effort was focused on a single individual or group, rather than searching for new groups. Because the surveys covered all cetacean species encountered, such interruptions of search effort were not limited to fin whale encounters. Because of similar bias, Isojunno et al. (2012) did not consider duration of grid cell visits to be an adequate measure of effort. Here, we corrected the total time spent in each grid cell by removing effort associated with the collection of sighting-specific data. From the survey data it was possible to identify sequential re-sightings of the same group during which such data were taken. The time from the first re-sighting to the last re-sighting of a group was characterised as ‘handling time’ and considered off-effort. A similar approach has been used to calculate search effort of whalers, where the chasing and processing of caught whales was considered ‘handling time’ and was excluded from the general search effort (Sigurjónsson,

1988; Sigurjónsson & Gunnlaugsson, 2006). This approach more accurately reflected time spent searching for fin whales and allowed us to use time as an offset in our models.

2.2.2 Environmental Data

Environmental data were chosen based on (1) their importance in previous cetacean species distribution models and (2) their availability at a sufficiently fine spatial resolution with respect to the 25 km² grid resolution of the sightings and effort data (Table 1). The data set was subdivided into months to allow seasonal and inter-annual variation in time-variable covariates (SST, chlorophyll *a* [chl *a*], krill biomass) to be incorporated. Month was chosen as an appropriate time period to minimise gaps in remotely sensed data, which tend to have significantly fewer missing data due to cloud cover when summarised per month compared to daily or weekly resolutions. Fin whale sighting and survey effort data were pooled for each month of the field season, resulting in a maximum of 35 (five months x seven years) temporal sub-units per grid cell. Greene and Pershing (2000) proposed a conceptual model linking North Atlantic Oscillation (NAO), physical environmental conditions, and zooplankton in the northwest Atlantic. This distant potential link was explored in our analyses by including NAO indices (NAOIs) as explanatory variables. Hurrell's PC-based NAOI was used in this study for monthly and winter NAOI (Hurrell et al., 2003). Previous studies have shown that abundance of balaenopterids typically lag behind maximum primary productivity by several weeks (Croll et al., 2005; Ramp et al., 2015; Visser et al., 2011). The possible effect of a temporal lag in the response of fin whale distribution to proxy variables was assessed by including composite spring SST and chl *a* concentrations and lagged winter NAOIs.

In the absence of high-resolution euphausiid data covering the entire study area/period, krill biomass was derived from a krill habitat model as described in Plourde et al. (2016). Briefly, Plourde et al. (2016) modelled krill biomass spatial and temporal distribution in eastern Canadian waters as a function of static (bathymetry and slope) and dynamic (SST, chl *a*, sea level height anomaly) environmental variables in a GAM framework. High-resolution quantification of euphausiid biomass was available from multifrequency acoustic data collected from surveys in the GSL (including the JCP) and adjacent waters since 2000 (McQuinn et al., 2015). The final euphausiid biomass model explained 24.5 % of deviance and was used to get monthly predictions of krill biomass at 5 x 5 km resolution in the JCP for the present study. Due to the spatial overlap of both studies, no extrapolations beyond the range of explanatory variables were necessary.

2.3 Data analysis

The relationship between the number of fin whale individuals in each grid cell (response variable) and the explanatory variables was modelled using GAMs (Hastie & Tibshirani, 1990; Wood, 2017), which are commonly used to study spatial and temporal drivers in cetacean distribution because of their flexibility (Becker et al., 2016; Isojunno et al., 2012; Redfern et al., 2006, 2017). Only grid cells with search effort were used to build the model. GAMs were fitted in the R (v. 3.2.3; R Core Team, 2015) package *mgcv* (v. 1.8-25; Wood, 2017).

Two separate models were built to model temporal and spatial patterns in fin whale distribution. The first model (the proxy model) included all static and dynamic environmental proxy variables (all variables listed in Table 1, except for krill biomass), including month and year. The second model (the prey model) included only modelled krill biomass, month and year, thus excluding the remaining proxy variables (most of which were used in the model to predict krill biomass). In both models, the number of individual fin whales per grid cell was modelled as a negative binomial distribution with logarithmic link function. The response variable was characterised by a high frequency of zeros (3207 grid cells without sightings compared to 312 grid cells with sightings) and the negative binomial error distribution provided the best fit to the data (Supplement S2).

The negative binomial distribution has been used in previous studies with similar types of data (i.e. count data with many zeros and overdispersion; Virgili, Racine, Authier, Monestiez, & Ridoux, 2017; Warton, 2005). The natural logarithm of monthly search effort was included as an offset term in the model to account for variable search effort across the study area. Only the first encounter of a fin whale individual/group was counted towards the monthly sum of fin whales in each grid cell to avoid the inclusion of duplicate sightings. Sightings data collected on the same day from different survey boats were treated independently because the spatial coverage differed between boats.

Table 1. Candidate explanatory variables for models to predict fin whale relative abundance in the Jacques Cartier Passage, Gulf of St. Lawrence.

Variable	Description	Resolution
Static variables		
Depth^a	Water depth (metres) at grid cell centre	1 arc-min
Slope^a	Slope of seafloor (degrees) calculated in QGIS from bathymetry	1 arc-min
Aspect^a	Slope orientation (0° to 360°) calculated in QGIS from bathymetry	1 arc-min
DistCoast^a	Distance to nearest coastline (metres)	1 arc-min
Dynamic proxy variables		
SST^b	Monthly average sea surface temperature (°C)	4 km
Spring SST^b	Seasonal composite of average spring (21 March - 21 June) sea surface temperature (°C)	4 km
Chl <i>a</i>^c	$\text{Log}(x + 1)$ transformed monthly average chlorophyll <i>a</i> concentration (mg m ⁻³)	4 km
Spring chl <i>a</i>^c	$\text{Log}(x + 1)$ transformed seasonal composite of average spring (21 March - 21 June) chlorophyll <i>a</i> concentration (mg m ⁻³)	4 km
NAOI^d	Monthly Hurrell North Atlantic Oscillation index (NAOI)	
WinterNAOI^d	Winter NAOI for the winter (December to March) preceding sampling season	
WinterNAOIlag1^d	Winter NAOI with one-year lag	
WinterNAOIlag2^d	Winter NAOI with two-year lag	
Year	Survey year (2007-2013)	
Month	Survey month (June-October)	
Dynamic prey variable		
Krill biomass^e	$\text{Log}(x + 1)$ transformed modelled monthly krill biomass (g m ⁻²)	5 km

Sources: ^aETOPO1 1 Arc-Minute Global Relief Model

^b Aqua-MODIS Level-3 sea surface temperature (4µ nighttime)

^c Aqua-MODIS Level-3 chlorophyll concentration (OCx algorithm)

^d National Center for Atmospheric Research Staff (Eds). The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (PC-based).

^e Plourde et al. (2016)

Prior to model fitting, explanatory variables were inspected for collinearity using the *pairs* function from the *AED* package in R, which generates a correlation matrix for pair-wise comparison between variables (Zuur et al., 2009). Two variables were deemed collinear if the estimated Pearson correlation coefficient exceeded 0.6. No collinearity was detected among covariates (Supplement 3, Fig. S3). Chl *a* and krill biomass values were log transformed ($\log(X + 1)$) to reduce skewness in the data. Field observations suggested that fin whales fed in shallower waters on the North Shore in June and July; interaction terms of month with depth and with aspect were thus considered to explore whether the data supported these relationships.

Restricted maximum likelihood (REML) was used for smoothing parameter estimation (Marra & Wood, 2011). The gamma term, which acts as an additional penalty, was set to 1.4 to reduce over-fitting in cases with relatively few observations per variable (Kim & Gu, 2004; Wood, 2006). Full models with and without interaction terms were fitted with penalised cubic regression splines and tensor products (*ti*) for interaction terms. A cyclic regression spline was fitted to aspect (0-360°) to match start and end points. Shrinkage spline smooths were used for covariate selection. The shrinkage approach penalises the null space of the smooth function, reducing the degrees of freedom of unsupported covariates to zero, allowing multiple terms to be dropped from the full model in a single step (Marra & Wood, 2011).

Models with and without interaction terms were compared using Akaike's information criterion (AIC; Akaike, 1973; Wood, Pya, & Säfken, 2016), percentage of deviance explained, and average squared prediction error (ASPE). To calculate the latter, a five-fold cross-validation was applied to assess the performance of candidate models in predicting novel data. Data were randomly split into five subsets. Models were fitted to 80% of the data for model training and the remaining 20% of the data were subsequently used for validation of predictions based on the trained model. ASPE was calculated as the mean squared difference between predicted and observed fin whale numbers in the validation subset. This cross-validation was run five-times in total and the mean ASPE was retained for model selection.

The final chosen model was refitted with the complete data set. If terms with an approximate *P*-value >0.05 remained in the model after shrinkage, the covariate with the least significant *P*-value was dropped from the model. If the exclusion of the variable did not increase the AIC score, the reduced model was retained. The relative covariate importance was estimated with the R function *varImpBiomod* (Thuiller et al., 2009). Model residual plots were examined visually to verify that assumptions of normality and variance homogeneity

were met (Figs. S4 & S5). Spatial autocorrelation of model residuals was assessed using a variogram (Zuur et al., 2009).

2.4 Prediction

The final proxy and prey models were used to compute predictions of relative abundance (individuals/hour) in each grid cell. Predictive maps were generated for each year, fixing the offset term to one hour of effort in each grid cell per month, in the open source GIS software package Quantum GIS (QGIS v. 2.18.1; QGIS Development Team, 2016). Because the model yielded separate predictions for each month, the mean relative abundance per year was plotted. To assess prediction uncertainty, coefficients of variation (CV) were calculated based on posterior simulation. From the posterior distributions of the model coefficients, 1000 coefficient vectors were simulated using *mvnrm* from the R MASS library (Venables & Ripley, 2002) and were used to generate 1000 predictions. The mean and CV were calculated from these 1000 predictions. The performance of the proxy and prey models were evaluated by comparing the percentage deviance explained and the predictive maps derived from the final models.

3. RESULTS

Sightings and effort data from 292 dedicated cetacean surveys were available to investigate temporal and spatial patterns in fin whale habitat use in the JCP. In total, 1878 hours were spent on effort, of which 510 hours were characterised as handling time during which the researchers were collecting photo-ID or biopsy data, leaving 1368 hours of corrected effort (Table 2, Fig. 2). Overall, 2986 individual fin whales were recorded on effort, with an average group size of 2.19 animals (SE = 0.05). Average annual encounter rates and median group sizes decreased over the study period (Table 2).

Table 2. Summary of annual survey effort (in hours) and the number of fin whale sightings with information on the median (and maximum) group sizes of the fin whale encounters.

Year	Uncorrected effort	Handling time	Corrected effort	Fin whale sightings	Sightings per corrected hour	Median group size
2007	206.1	37.3	168.8	527	3.12	2 (9)
2008	280.2	81.5	198.7	674	3.39	2 (14)
2009	325.6	112.1	213.5	488	2.29	2 (8)
2010	252.6	70.5	182.1	508	2.79	2 (10)
2011	170.1	59.1	111.0	177	1.60	1 (6)
2012	297.7	89.1	208.6	296	1.42	1 (8)
2013	346.1	60.4	285.7	316	1.11	1 (14)
Total	1878.4	510.0	1368.4	2986

Figure 2. Distribution of total survey effort in the Jacques Cartier Passage in minutes per 25 km² grid cell over the seven survey years (June to October, 2007 to 2013), followed by the amount of handling time and the derived corrected effort per grid cell.

3.1 Proxy fin whale distribution models

Out of the five models fitted with proxy variables, the model which included an interaction term of aspect and month performed best in terms of AIC, percentage deviance explained and ASPE (Table 3). Distance to coast, chl *a*, spring chl *a*, spring SST, NAOI, and lagged winter NAOIs were shrunk to zero degrees of freedom by the shrinkage regression splines and simultaneously dropped from the model (Model 1.3 Table 3). Winter NAOI was subsequently dropped from the model, because it was the only term with an approximate *P*-value > 0.05 and very low effective degrees of freedom (edf = 0.19). The resulting final proxy model explained 24.2 % of deviance.

Table 3. Model selection of proxy and prey fin whale models with and without interaction terms.

Variables	θ	REML	AIC	%Dev	r^2	ASPE
1. Proxy model						
1.1 Penalised model*	0.17	1068.7	2963.4	20.6	0.38	29.59
1.2 Penalised model +ti(depth,month)	0.18	1067.5	2953.4	23.1	0.36	28.83
1.3 Penalised model +ti(depth,year)	0.17	1068.5	2963.1	21.1	0.39	27.72
1.4 Penalised model +ti(aspect,month)	0.18	1065.0	2944.4	23.7	0.43	25.72
1.5 Penalised model +ti(aspect;year)	0.17	1068.4	2961.9	21.5	0.37	28.50
2. Prey model						
2.1 s(krill) +s(month) +s(year)	0.12	1143.6	3185.2	7.6	0.21	34.29
2.2 s(krill) +s(month) +s(year) +ti(krill,month)	0.13	1138.3	3161.8	11.8	0.23	33.07
2.3 s(krill) +s(month) +s(year) +ti(krill,year)	0.12	1143.2	3184.0	8.1	0.21	34.03

Note. *Full penalised model includes all variables described in Table 1, except for krill biomass: s(Depth)+ s(Slope)+ s(Aspect)+ s(DistCoast)+ s(SST)+ s(SpringSST)+ s(Chla)+ s(SpringChla)+ s(NAOI)+ s(WinterNAOI)+ s(WinterNAOIlag1)+ s(WinterNAOIlag2)+ s(year)+ s(month) with automated variable selection using shrinkage smoothers. Model selection was based on Akaike's Information Criterion (AIC), percentage of deviance explained (%Dev), and mean average squared prediction error (ASPE) from a five-fold cross-validation. θ : theta parameter from negative binomial *nb()* error distribution; REML: restricted maximum likelihood. Selected models are shown in **bold**.

Among the covariates retained in the final model, water depth and aspect were of the highest importance, with fin whales occurring in greater numbers in deeper waters, over steep, and northward facing slopes (Fig. 3). Higher numbers were also recorded at SST greater than 12°C. Temporal trends suggested a peak in fin whales at the onset of the survey season in June, followed by a decline until September, and a second peak at the end of the season in October. The affinity to northward facing slopes changed by month, showing that occurrence at southward facing slopes was less likely in August and September, compared to June, July and October. The negative yearly trend that was already reported for the annual fin whale encounter rates was also reflected in the final model.

Figure 3. Smooth functions fitted in the final proxy-fin whale model. Positive values of the smoothed function indicate a positive effect on the response variable. Tick marks on the horizontal axis show the distribution of observations, while the smoother terms with estimated degrees of freedom (edf) are shown on the vertical axes. Shaded areas represent 95% confidence intervals. Last plot shows the 2-D interaction between aspect and month (5.06 edf, cold colours represent negative effect).

3.2 Prey fin whale distribution models

The prey model that included an interaction term between krill biomass and month had the lowest ASPE and AIC score and highest percentage of deviance explained (11.8 %) among all three built models (Table 3). Krill biomass had the highest importance among the model covariates, followed by month and year. The intra- (month) and inter-seasonal (year) patterns followed the same trends as described for the proxy model (Fig. 4). Fin whale numbers increased with higher modelled krill biomass, although the interaction term indicated that fin whales also occurred in areas with lower krill biomass at the onset of the season (June and July).

Figure 4. Smooth functions fitted in the final prey-fin whale model. Positive values of the smoothed function indicate a positive effect on the response variable. Tick marks on the horizontal axis show the distribution of observations, while the smoother terms with estimated degrees of freedom (edf) are shown on the vertical axes. Shaded areas represent 95% confidence intervals. First plot shows the 2-D interaction between krill biomass and month (4.63 edf).

Figure 5. Predictive maps of relative annual fin whale abundance (individuals per hour effort) from the proxy fin whale model. Each map shows the average annual relative abundance of fin whales in each grid cell; dots: reported sightings of fin whale groups made during the surveys in that year.

Figure 6. Predictive maps of relative annual fin whale abundance (individuals per hour effort) from the prey fin whale model. Each map shows the average annual relative abundance of fin whales in each grid cell; dots: reported sightings of fin whale groups made during the surveys in that year.

3.3 Prediction

Annual predictive maps of average fin whale occurrence generated from the final proxy and prey fin whale models are shown in Figs. 5 & 6, with CV in Supplement 4 (Figs. S6 & S7). From the proxy model, two main areas with consistently high predicted relative abundance of fin whales were identified: the western end of the Anticosti Channel and the area north of Banc Parent (see Fig. 1 for locations). The area off Banc Parent coincides with the southern branching traffic shipping lanes. The predictive maps indicated a potential third high density area on the northern edge of the Laurentian Channel. However, this area of very high predicted relative abundance lies at the very southwestern edge of our survey area and could represent an ‘edge effect’ because the area is the deepest in the surveyed area with little effort extending that far. A clear annual decline in fin whale numbers was evident from the predictive maps.

Predictions from the prey model favoured a more even spatial distribution of fin whales across the JCP. The head of the Anticosti Channel to the east and the southwestern area of the study area seemed to have overall the highest predicted numbers, but the strong signal of the annual negative trend masked areas with consistently high numbers.

4. DISCUSSION

SDMs were fitted to understand the extent to which the observed decline in fin whale numbers was a result of changing environmental conditions in the northern GSL. The proxy and prey models both identified the negative annual trend in the number of fin whale individuals, but the proxy model had overall a better predictive performance than the prey model. Here, we discuss the link between the observed decline in fin whales and the spatio-temporal patterns that were revealed by the SDMs.

Over the study period, the majority of sightings clustered around the head of the Anticosti Channel and north of Banc Parent with some inter-annual variability. This distribution was best reflected in the predictive maps of the proxy model, while the prey model largely failed to highlight those high-density areas. The static bathymetric features in the areas with consistently high predicted fin whale numbers, characterised by deep water and steep, northward facing slopes, were the most important predictors in the proxy model. Among all the dynamic covariates (chl *a*, SST, NAOI), which could explain the inter-annual variability in sightings, only SST was retained in the final proxy model. Fin whale numbers increased in waters with higher SST, suggesting that cooling of SST could have led to the observed annual decline. However, a trend analysis showed that the GSL is undergoing warming of SST, with the northeastern Gulf warming at a faster pace than the southern part

of the Gulf (Galbraith et al., 2012; Larouche & Galbraith, 2016). In our study area, both the lowest and highest average SST in the study area were recorded in 2007 and 2008, respectively, which were also the years with the highest encounter rates (Fig. S8). Since 2012, near-record temperatures of both surface and deep layers of the GSL were found to correlate with variations in plankton phenology and fish abundance (Brosset et al., 2018; Plourde et al., 2015). While results presented here suggest that a direct correlation between decreasing fin whale abundance and SST is unlikely, it remains unclear to what extent cascading effects of a warming Gulf could have impacted fin whale abundance and/or distribution indirectly.

The final proxy model explained 24.2 % of the variability in the data, indicating that important explanatory variables were missing from the model. On a feeding ground, a strong predator-prey relationship is expected in baleen whales (Piatt et al., 1989; Ressler et al., 2015). No real-time, high-resolution euphausiid data were collected during the cetacean surveys, so we used modelled krill biomass to test how well it explained fin whale relative abundance compared to a model using proxy covariates. While the prey model found a positive relationship between modelled krill biomass and fin whale numbers, the model performed poorly overall compared to the proxy model in terms of percentage of deviance explained and predictive power. The modelled krill biomass variable was thus not a suitable alternative to the proxy variables in this study. The uncertainty associated with the krill biomass covariate (predicted from a model that explained 24.5% of deviance (Plourde et al., 2016), could have decreased its power as a predictor on a fine spatial scale. This does not preclude a better predictive performance at larger spatial scales. Previous models found differing relationships between fin whale and euphausiid abundance, possibly due to differences in spatial scales (Zerbini et al., 2016). Laidre et al. (2010) highlighted the importance of high spatio-temporal synchrony in the collection of prey and cetacean data to quantify their relationship. We therefore recommend to explore the performance of modelled krill biomass as predictor of baleen whale distribution at broader spatial scales in the GSL.

Another factor that could have contributed to the lower performance of the prey model is the generalist diet of fin whales. While euphausiids are an integral part of their diet, fin whales are also known to switch prey depending on availability (Gavrilchuk et al., 2014; Ressler et al., 2015). The inclusion of interaction terms in both models indicated that habitat use changed as the season progressed. The higher number of fin whales found on southward facing slopes and at lower krill biomass at the beginning of the season (June-July) coincided with the rolling of capelin (*Mallotus villosus*) along the North Shore (MPO, 2003). To fully quantify the complex predator-prey relationship in fin whales, we need to gain a better

understanding of their feeding ecology, especially threshold values at which prey switching occurs, and obtain higher (spatial and temporal) resolution data from all potential prey species. In the absence of such data, it cannot be excluded that inter-annual variability in prey availability was, at least partly, the cause of the observed annual decline in fin whale numbers in the northern GSL.

In addition to environmental variability, anthropogenic pressures could affect habitat use and relative abundance. The high-density area identified north of Banc Parent coincided with the southern branch of the shipping lanes. In fact, more than a fifth (22.6 %) of all fin whale sightings in this study occurred inside the shipping corridor, posing a considerable risk of ship collisions and noise pollution. Fin whales are the most commonly reported species in the current global vessel strike data set maintained by the Scientific Committee of the International Whaling Commission (Van Der Hoop et al., 2013; Van Waerebeek & Leaper, 2008). Based on marine mammal stranding records in the GSL from 1994 to 2008, ship collision was the most common anthropogenic trauma for fin whales (22%; Truchon et al. 2018). Shipping traffic is projected to increase in the GSL with the opening of the Northwest Passage (Pizzolato et al., 2016). The predicted areas of high fin whale density described here should be included in future risk assessments to mitigate the potential impact of shipping on fin whales (Redfern et al., 2013). Recommended measures could include vessel speed limits and area avoidance recommendations, which were shown to significantly reduce ship strikes with North Atlantic right whales (Laist et al., 2014).

While the modelling conducted could not provide a clear indication of the cause of the annual fin whale decline, it did offer valuable insights into spatio-temporal patterns of fin whale habitat use in the northern GSL. Importantly, the predictions derived from the proxy model highlighted two key areas with recurrently occurring high fin whale abundance. The bathymetric features which characterise those areas were in line with previous findings, which have also found water depth and slope to be important predictors of fin whale occurrence in the Mediterranean Sea (Azzellino et al., 2012; Panigada et al., 2005; Pennino et al., 2016), in the northeastern Atlantic (Víkingsson et al., 2015), and the Bay of Fundy (Ingram et al., 2007; Woodley & Gaskin, 1996). Krill and capelin aggregate along shelf breaks and steep slopes as a result of tidal currents and upwelling in the GSL and St. Lawrence Estuary (Cotté & Simard, 2005; Simard et al., 2002). The two high fin whale density areas coincide with the two areas of above average krill biomass accumulation identified in the JCP by large-scale hydroacoustic surveys (McQuinn et al., 2015). A potential third high density area was predicted along the northern slopes of the Laurentian Channel, which received little survey effort during this study. This predicted high density

area could be an edge effect (i.e. an artefact); future surveys of this area are needed to identify whether or not this area is important habitat for fin whales.

This study has shown how data collected on surveys primarily designed for other purposes can be adapted for habitat modelling analysis. However, this *ad hoc* adaptation of the data leads to a number of concessions. In the absence of distance-sampling and a design ensuring equal coverage probability, it was not possible to estimate absolute density or abundance throughout the study area using design-based methods. While the model-based approach used here accounted for uneven distribution of effort through the inclusion of an offset term, we were able to describe only relative variability in abundance and distribution. The focus on sampling individuals rather than space further compromised search effort data. Such a disruption of search effort could lead to bias in the effort quantification and the inclusion of duplicate sightings, when previously encountered animals catch up with the survey boat. The particular setup of this study allowed us to identify duplicate sightings from the photo-identification data and to correct for handling time based on detailed field notes. Without standardised sampling design, data from opportunistic platforms generally require data-specific solutions. However, the data described here share many similarities with data collected from other platforms of opportunity, such as whale watching boats. We therefore propose that the correction of effort for handling time is applicable to other data sets compromised by disrupted search effort, and its application could allow hitherto unused data to provide useful information on distribution and habitat use.

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SUPPLEMENTARY INFORMATION

1. Effort Calculation

The GPS unit had different sampling settings, including sampling locations at a set temporal interval and an automatic mode, during which positions were recorded at random time-interval when the boat was changing direction. However, the GPS units on the boats only recorded positions in latitude and longitude, without timestamp. Because time was identified as the most appropriate measure of effort for this study, the first step consisted in associating timestamps to the GPS locations for the calculation of effort. During the survey, precise timestamps and positions were recorded manually for events such as survey start, survey stop, sightings and changes in survey conditions. For each survey track, these recorded timestamps were associated to the nearest point of the survey track collected on the same day and boat (Fig. S1). Associations that were made with positions farther than 100m apart were discarded. Once these timestamps from the survey data were associated to the survey track, the sampling interval could be estimated by dividing the time difference between two timestamps by the number of positions recorded by the GPS unit. Depending on the setting, the GPS unit recorded positions at a 5, 10, or 30 second interval. On an unknown number of surveys, the GPS unit ran on the default automatic mode. For those days it was impossible to reconstruct the timestamp and all associated sighting and effort data were excluded from future analysis. Once the sampling interval was determined, the timestamps were reconstructed for all remaining GPS positions. Data from 292 surveys were retained for the habitat modelling.

Figure S1. Example of timestamp association procedure from survey on 5 Aug 2008. The time interval divided by the number of intermediate GPS positions provides a sampling interval of 30 sec ($=4\text{min}/8$), allowing the calculation of timestamps for all intermediate GPS location.

2. Error Distribution Selection

The response variable was characterised by a high frequency of zeros (3207 grid cells without sightings compared to 312 grid cells with sightings), requiring careful choice of the error distribution. Quantile-quantile plots were used to compare the performance of three different error distributions, namely overdispersed Poisson (quasi-Poisson), negative binomial, and Tweedie error distributions for the fin whale occurrence model (Figs S2 & S3). All three error structure have been suggested to deal with overdispersed count data and differ mainly by their mean-variance relationship (Miller et al., 2013; Ver Hoef & Boveng, 2007; Warton, 2005). Quasi-Poisson and negative binomial share the same number of parameters, but the linear mean-variance function of the Quasi-Poisson distribution puts more weight on large counts while small counts are more heavily weighted in the negative binomial distribution due to its quadratic mean-variance function (Ver Hoef & Boveng, 2007). In addition to the mean (μ) and dispersion ($\emptyset$) parameters, the Tweedie distribution

has a third power (p) parameter, offering additional flexibility to model count data (Miller et al., 2013). The Tweedie mean-variance relationship is described as $var(Y) = \varnothing\mu^p$ (Miller et al., 2013). Setting p to 1 gives a quasi-Poisson distribution.

Figure S2. Quantile-Quantile plots of proxy model with three different error distributions. The negative binomial error distribution provided the best fit.

3. Model validation

Collinearity between candidate explanatory variables was evaluated using the `pairs()` function in the AED package. Based on the 0.6 cut-off value, there was no evidence for significant collinearity that required further investigation (Fig. S3).

Figure S3. Pairplot of candidate explanatory variables, with the upper panel showing estimated pair-wise correlation coefficients. R-code based on Zuur et al. (2009).

Residual plots were investigated to assess assumptions of variance homogeneity and independent errors. There was no indication for variance heterogeneity or autocorrelation for the proxy-fin whale model (Fig. S4) but some indication of autocorrelation in the prey-fin whale model (Fig. S5).

Figure S4. Diagnostic residual plot for proxy-fin whale occurrence model. The horizontal band on the semi-variogram of residuals, with distance on the x-axis and semi-variance on the y-axis, indicates spatial independence (Zuur et al. 2009).

Figure S5. Diagnostic residual plot for prey-fin whale occurrence model. The horizontal band on the semi-variogram of residuals, with distance on the x-axis and semi-variance on the y-axis, indicates spatial independence (Zuur et al. 2009).

4. Uncertainty distribution of model predictions

Figure S6. Coefficients of variation (CV) of annual average predictions from the proxy-fin whale model.

Figure S7. Coefficients of variation (CV) of annual average predictions from the prey-fin whale model.

5. Summary of annual trends

Figure S8. Average annual sea surface temperatures (SST) and modelled krill biomass over all grid cells.

CHAPTER

04

4

Population genetic structure in a low divergence species: a multi-faceted approach to studying North Atlantic and Mediterranean Sea fin whales (*Balaenoptera physalus*)

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ABSTRACT

Low levels of genetic divergence still pose challenges to studies aiming to characterise population structuring due to limited statistical power and confounding effects from divergence times and gene flow. In this study, a multi-faceted approach was employed to gain insights into the population genetic structuring in a species with low genetic divergence; the North Atlantic and Mediterranean Sea fin whales (*Balaenoptera physalus*). This study highlights the benefits of employing both coalescent- and kinship-based approaches to complement inferences drawn from fixation indices. A break in gene flow was detected among North Atlantic and Mediterranean Sea fin whales based on 20 microsatellite loci and mitochondrial DNA sequences collected from ~1,600 fin whale samples. Within the North Atlantic, fixation indices and kinship-based analyses suggested a stepping-stone model of population divergence likely due to recurrent gene flow among neighbouring regions. Of 133 inferred parent-offspring dyads, 15 comprised individuals sampled in different areas, indicative of contemporary connectivity. Deviations from drift-migration-mutation equilibrium were detected in coalescent-based assessments, suggesting that North Atlantic fin whales have undergone a post-glacial population expansion whereas Mediterranean Sea fin whales have declined during this period. The application of complementary population genetic approaches enabled multi-faceted and detailed insights into both the past and present population genetic structure in a species with wide ranges.

1. INTRODUCTION

Population differentiation is an inherently dynamic process, shaped by spatio-temporal changes in gene flow, selection, and genetic drift (Wright, 1931). The contemporary population genetic structure, i.e. the current spatial distribution of genetic variation, is therefore a product of past as well as current processes (Ibrahim et al., 1996). Consequently, the contemporary, spatial distribution of intra-specific genetic diversity is often employed to make inferences about past demographic changes and connectivity or contemporary population genetic structuring (Beichman et al., 2018; Fraser et al., 2009; Hewitt, 2000). Conversely, current levels of population structuring may be masked by the effects of past demographic, evolutionary, and environmental processes (Gaggiotti et al., 2009; Hewitt, 2000). Disentangling past and contemporary processes that shaped the distribution of genetic diversity is therefore key to understand population dynamics.

Populations characterised by low levels of genetic divergence pose a particular challenge due to limited statistical power and confounding effects from divergence times and gene flow (Bossart & Prowell, 1998; Palsbøll et al., 2010; Waples, 1998; Waples & Gaggiotti, 2006).

Low levels of genetic divergence can reflect high contemporary rates of gene flow; however, they can also be a product of recent divergence from a common ancestral population and low contemporary rates of gene flow (Nielsen & Wakeley, 2001; Palsbøll et al., 2004). Failure to distinguish among competing causes of low genetic divergence can lead to erroneous conclusions about behavioural and/or ecological drivers of current population structuring, with potentially wide-reaching implications for population management and conservation.

The choice of the right analytical approach therefore becomes key to elucidate the contemporary population genetic structure, particularly for low divergence species (Nielsen & Wakeley, 2001; Palsbøll et al., 2004, 2010; Waples, 1998). Importantly, inferences are likely to benefit from combining a multitude of approaches, rather than relying on a single statistic, like F_{ST} (Wright, 1943) or analogue fixation indices (e.g. Excoffier, Smouse, & Quattro, 1992; Hedrick, 2005; Nei, 1972; Weir & Cockerham, 1984). These well-established fixation indices are widely employed to estimate genetic divergence and allow sound inferences about population connectivity when divergence is high. However, moderate to high levels of gene flow (i.e. $N_e m > 10$, where N_e denotes the effective population size and m represents the probability that an individual is an immigrant) reduce the effect size and consequently statistical power and accuracy of fixation indices (Palsbøll et al., 2010; Taylor & Dizon, 1996; Waples & Gaggiotti, 2006). Fixation indices cannot distinguish among competing demographic histories and assume drift-migration-mutation equilibrium (Excoffier et al., 2009; Nielsen & Wakeley, 2001). In other words, biologically relevant levels of population structuring may be misinterpreted if relying solely on fixation indices especially when the level of genetic divergence is low (Crandall et al., 2019; Marko & Hart, 2011).

Employing multiple, complementary analytical approaches that capture different aspects and time-scales of population genetic divergence may provide additional insights into the dynamic nature of population structuring (Pearse & Crandall, 2004). Accordingly, fixation indices can be complemented with other population genetic approaches that; (1) do not solely rely on statistical power, i.e. P -values (Waples, 1991); (2) provide insights into past deviations from migration-drift-mutation equilibrium (e.g. due to the population expansions and declines; Ibrahim et al., 1996); or (3) yield estimates of gene flow at the relevant timescale. Coalescent-based approaches are capable of facilitating inferences of past changes in N_e as well as fluctuations in m at moderate rates of gene flow (Beerli & Felsenstein, 2001; Kingman, 1982; reviewed by Kuhner, 2009). In contrast, kinship-based approaches aim at inferring contemporary population connectivity (e.g. Escoda, González-Esteban, Gómez, & Castresana, 2017; Fountain et al., 2018; Frantz, Pope, Etherington,

Wilson, & Burke, 2010; Palsbøll et al., 2010; Peery et al., 2008; Planes, Jones, & Thorrold, 2009; Wang, 2014). These approaches are ultimately drawing inferences from the relative degree of co-ancestry within and among populations, either among individuals (e.g. kinship-based approaches) or gene copies (e.g. fixation indices and coalescent-based approaches). However, individual approaches differ by the timescales they apply to; kinship-based assessments yield contemporary estimates of dispersal and abundance during the few recent generations while the coalescent-based approaches integrate over the entire intra-specific genealogy. Therefore, combining fixation indices, coalescent- and kinship-based approaches holds the potential of providing a more dynamic insight into the scale and processes leading to the contemporary population structure, especially in populations at low levels of divergence (Crandall et al., 2019; Iacchei et al., 2013).

North Atlantic and Mediterranean Sea fin whales (*Balaenoptera physalus*) represent an illustrative case of low levels of population genetic divergence. Earlier work by Bérubé et al. (1998) suggested that North Atlantic fin whales likely underwent an exponential expansion after the Last Glacial Maximum (LGM). Accordingly, the estimated degree of genetic divergence was low among fin whales sampled at high latitude summer aggregations and in the Mediterranean Sea, seemingly reflecting high contemporary rates of gene flow. However, the low degree of genetic divergence among regions may also be the result of recent population structuring at low levels of gene flow (Berube et al., 1998). Kinship-based analyses could potentially indicate whether contemporary fin whale summer aggregations are structured at finer spatio-temporal scales. To this end, this study aimed at conducting a large-scale genetic assessment of fin whales in the North Atlantic and Mediterranean Sea, employing *F*-statistics in combination with coalescent- and kinship-based approaches.

In common with most baleen whales, fin whales have been observed to undertake long-distance movements to a varying degree depending on the location (Edwards et al., 2015; Geijer et al., 2016). Fin whales inhabiting the enclosed bodies of water, such as the Mediterranean Sea (Notarbartolo di Sciara et al., 2003) and the Gulf of California (Bérubé et al., 2002; Urbán et al., 2005) appear to be largely resident, undertaking seasonal migrations between relatively proximate summer and winter areas. In contrast, fin whales in the (eastern) North Atlantic appear to undertake comparatively longer seasonal migrations (Silva et al., 2013). While the summer distribution is well known with high densities observed in the Irminger Sea and off northwestern Spain (Hammond et al., 2017; Víkingsson et al., 2015), most fin whale breeding grounds remain unknown. Mating and calving are generally presumed to take place on low latitude or offshore breeding grounds

during winter (Edwards et al., 2015; Mitchell, 1974; Romagosa et al., 2020; Simon et al., 2010).

Previous work by Bérubé et al. (1998) detected significant levels of genetic heterogeneity among mitochondrial control region (mtCR) DNA sequences collected from 407 fin whales sampled in the Mediterranean Sea and the North Atlantic. The degree of genetic divergence estimated from six microsatellite loci was low (F_{ST} ranging from zero to 0.007), but significant levels of heterogeneity were detected among the most distant sampling areas. Overall the study indicated a population genetic structure characterised by a stepping-stone model resulting in isolation-by-distance (IBD; Wright 1943), supporting the notion of a 'patchy continuum' originally proposed by Sergeant (1977). However, the number and distribution of samples prevented an assessment of population structuring among proximate areas. Bérubé et al. (1998) did not find support for Mitchell's (1974) proposal of two or more discrete fin whale aggregations in the western North Atlantic put forward to explain differences in whaling depletion rates.

In this study, analyses of nuclear and mitochondrial genetic markers supported the qualitative inferences drawn by Bérubé et al. (1998), i.e. some deviations from panmixia among North Atlantic high-latitude, summer fin whale aggregations, as well as between North Atlantic and Mediterranean Sea fin whales. Coalescent-based analyses revealed contrasting demographic histories in the North Atlantic and Mediterranean Sea as well as asymmetric rates of gene flow. Kinship-based analyses revealed finer-scale population structuring among western North Atlantic fin whales despite overall low levels of genetic divergence.

2. METHODS

2.1 Sample collection

Tissue samples were collected from 15 different areas in the North Atlantic, the Strait of Gibraltar, and the Mediterranean Sea from 1982 to 2018 (Figure 1). Samples from the resident Gulf of California fin whale population (Bérubé et al., 2002; Gilmore, 1957; López et al., 2019; Rivera-León et al., 2019) were included to serve as an out-group. Most samples were collected as skin biopsies from free-ranging animals, using a crossbow and bolt with a biopsy tip (Palsbøll et al., 1991). A few samples originated from stranded animals or were collected as sloughed skin. Samples from Iceland, Spain (Galicia) and West Greenland were collected during whaling operations. All samples were collected in accordance with

domestic and international laws and regulations. All tissue samples were conserved in a 5M NaCl solution with 30% dimethylsulphoxide at -20°C or -80°C.

2.2 Laboratory analyses

2.2.1 DNA extraction and sex determination

Total-cell DNA was extracted from tissue samples either by standard phenol:chloroform extractions (Sambrook et al., 1989) or using the Qiagen DNeasy™ Blood and Tissue Kit (Qiagen Inc.) according to the manufacturer's instructions. Extracted DNA was re-suspended in 1x TE buffer (10mM Tris-HCl, 1mM EDTA, pH 8.0). The sex of each sample was determined from extracted DNA by molecular sex determination as described in Bérubé and Palsbøll (1996a) and Bérubé and Palsbøll (1996b) and by co-amplification of a SRY specific marker (Bérubé et al., in prep).

One negative and four positive controls were included with every 96 DNA extractions for all amplifications. A total of 96 randomly selected samples were re-analysed to estimate consistency rates in genotyping and sequencing.

2.2.2 Mitochondrial control region DNA sequencing

The first 450 base pairs (bps) of the 5' end of the mtCR were amplified and sequenced using the oligo-nucleotide primers MT4F (Árnason et al., 1993) and BP16071R (Drouot et al., 2004). The initial polymerase chain reactions (PCR) amplifications were performed in 20 µL reaction volumes consisting of 0.2 µM of dNTP, 67mM Tris-HCl (pH 8.8), 2mM MgCl₂, 17mM NH₄SO₄, 10mM β-mercaptoethanol, 0.1µM of each primer, 0.4 units of *Taq* DNA polymerase and 10-20 ng of genomic DNA. The thermocycling conditions were: 2 min at 94°C, followed by 25 cycles at 94°C (15 sec), 54°C (30 sec) and 72°C (120 sec). The sequencing of the PCR products was performed as described in Huijser et al. (2018) and the order of sequencing products was resolved using an ABI Prism™ 3730 (Applied Biosystems Inc.). The resulting DNA sequences were aligned using CLUSTALW (v.1; Thompson, Higgins, & Gibson, 1994) with default settings as implemented in MEGA (v.7.0.26; Kumar, Stecher, & Tamura, 2016); these were checked manually.

2.2.3 Microsatellite loci genotyping

The genotypes were determined at the following 20 microsatellite loci: EV037 and EV094 (Valsecchi & Amos, 1996), GATA028, GATA098, GATA417, and TAA023 (Palsbøll, Bérubé, et al., 1997), GT011 (Bérubé et al., 1998), GT023, GT211, GT271, GT310, and

GT575 (Bérubé et al., 2000), AC087 and CA234 (Bérubé et al., 2005), GATA25072, GATA43950, GATA5947654, GATA6063318, GATA91083 (Bérubé et al., in prep), and EV001 (Valsecchi & Amos, 1996). The oligo-nucleotide primer employed to genotype the latter locus was modified for this study due to the presence of null alleles: EV001A (5'-GCT GGG GAC ACA AAC AAA AGC TC-3'). Samples were genotyped in multiplex PCR reactions, using the MM2X™ Multiplex kit Plus (Qiagen Inc.) in 5µL reaction volumes. The thermocycling conditions were: 2 min at 94°C, followed by 35 cycles at 94°C (30 sec), 57°C (90 sec) and 72°C (30 sec) followed by a final cycle at 68°C (10 min). The PCR products were separated by capillary electrophoresis using an ABI Prism™ 3730 (Applied Biosystems Inc.). The size of the amplification products was estimated using the Genescan ROX-500 size standard (Applied Biosystems Inc.) and GENEMAPPER™ (v. 4.0; Applied Biosystems Inc.).

2.3 Data analyses

The probability of identity between unrelated individuals (P_{ID}) and full siblings (P_{ID-sib} ; Waits, Luikart, & Taberlet, 2001) was estimated in CERVUS (v. 3.0.7; Kalinowski, Taper, & Marshall, 2007; see Supplementary Material 1). Within-partition duplicate samples (DNA samples inferred as collected from the same individual at multiple occasions) were excluded from subsequent data analyses (Supplementary Material 1). Deviations of sex ratios from parity were assessed using a χ^2 test. The potential bias caused by the inclusion of samples from genetically related individuals was considered, i.e. correlated sampling of two closely related individuals, such as calf-of-the-year together with its mother (Wang, 2018; Waples & Anderson, 2017). Therefore, samples collected on the same day from female-female or female-male dyads with identical mtCR haplotypes that were inferred to be related as parent and offspring (see below) were assumed to represent correlated samples of cow and calf dyads. Accordingly, one individual from each dyad was removed.

2.3.1 Analyses of mtCR DNA sequences

Haplotype (h) and nucleotide (π) diversity was estimated in DNASP (v. 6.10.01; Rozas et al., 2017). Pairwise-comparisons were assessed using Weir & Cockerham's θ (hereafter Weir's θ , Weir & Cockerham, 1984) and Φ_{ST} (Excoffier et al., 1992). The probability of the observed estimate of Weir's θ , assuming samples were drawn from the same underlying distribution, was estimated from the proportion of 10,000 random permutations of the observed data that yielded a similar, or more extreme, estimate of Weir's θ as implemented in the *strataG* package (v. 2.0.2; Archer, Adams, & Schneiders, 2017) in R (v.3.6.0; R Core

Team, 2019). The specific mutation model employed to estimate Φ_{ST} was selected from an assessment conducted using JMODELTEST (v. 0.1.1; Posada, 2008) and the Akaike Information Criterion for model selection (Akaike, 1973). Confidence intervals for both Weir's θ and Φ_{ST} were estimated from 1,000 bootstrap samples (sampling nucleotide sites with replacement; Felsenstein, 1985). A hierarchical bottom-up approach was employed combining non-heterogeneous, spatio-temporal proximate samples in a sequential manner between sex, sampling years and areas. Samples were combined when no statistically significant heterogeneity was detected (using Weir's θ as test statistic and sample sizes above 30). Within single sampling areas, sample partitions with fewer than 30 samples were combined, with the caveat of potentially missing heterogeneity within sampling areas. Sampling areas with fewer than 30 samples were kept as separate sample partitions. Effects of multiple simultaneous tests were corrected by applying a false discovery rate (FDR, Benjamini & Hochberg, 1995) at $\alpha = 0.05$.

2.3.2 Analysis of multi-locus genotypes

Multi-locus genotypes were assessed in MICRO-CHECKER (v. 2.2.3; Van Oosterhout, Hutchinson, Wills, & Shipley, 2004) to detect possible large-allele dropout. Deviations from the expected Hardy-Weinberg (HW) genotype proportions were assessed using Fisher's exact tests based on 1,000 Monte Carlo permutations, implemented in the *pegas* R package (v. 0.10; Paradis, 2010). Linkage disequilibrium was assessed using a standardised index of association $\bar{r}_d$ (Agapow & Burt, 2001) as implemented in the *poppr* R package (v. 2.5.0; Kamvar, Tabima, & Grünwald, 2014). The probability of the observed value of $\bar{r}_d$ was estimated as the proportion of 999 permutations (of alleles at all loci) that yielded a similar or more extreme value of $\bar{r}_d$ (Kamvar et al., 2014). Genetic diversity was estimated as the rarefied allelic richness and expected heterozygosity using the *diveRsity* R package (v. 1.9.9.; Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013). The degree of genetic divergence was estimated using Weir's θ and Jost's D (Jost, 2008) as implemented in *strataG*. Bias corrected 95% confidence intervals were estimated from 1,000 bootstrap replicates across loci in *diveRsity* (Keenan et al., 2013).

N_e was estimated from the degree of linkage disequilibrium as implemented in NeEstimator (v. 2.1; Do et al., 2014) using a rare allele frequency threshold of 0.02 (values at 0.05 and 0.01 were also evaluated). Ninety-five percent confidence intervals of N_e were estimated by jackknifing over samples as implemented in NeEstimator (Jones et al., 2016). The Bayesian clustering approach implemented in the software STRUCTURE (v. 2.3.4.; Pritchard, Stephens, & Donnelly, 2000) was employed to estimate the most likely number of distinct,

genetic clusters (K). A no-admixture model with correlated allele frequencies was employed, using sampling location as prior. A detailed description of the methodology (with an additional analysis employing the admixture model) is provided in Supplementary Material 2 (Figures S3 & S4).

2.3.3 Isolation-by-distance

A stepping-stone model was assessed using a Mantel test (Mantel, 1967; Rousset, 1997) as implemented in the *adeigenet* R package (v. 2.1.1; Jombart, 2008). Geographic distances were log transformed shortest oceanic distance (in km) and inter-area genetic distances were approximated as the linearised genetic distances (Weir's $\theta / (1 - \text{Weir's } \theta)$; Rousset, 1997). Oceanic distances were estimated as the shortest oceanic path between sampling areas using GEOMAPAPP (v. 3.6.8; Ryan et al., 2009). Estimations were conducted with and without the most distant sampling areas. The probability of the observed estimate of the correlation value was estimated from 9,999 permutations. Monmonier's maximum difference algorithm (Monmonier, 1973) was applied to assess deviations from IBD (Manni et al., 2004) using the *adeigenet* package and a Delaunay triangulation (Brassel & Reif, 1979). Sampling area coordinates were adjusted for oceanic distances by applying multi-dimensional scaling (Manni et al., 2004).

2.3.4 Coalescent-based estimations

Genetic diversity ($\theta = N_e \mu$, where μ denotes the generational mutation rate per nucleotide site) and $N_e m$ were estimated using the coalescent-based Bayesian approach implemented in MIGRATE-N (v. 3.6.6; Beerli & Felsenstein, 2001). Random sub-samples of 200 mtCR DNA sequences (without replacement) were generated to ensure even sample sizes. A detailed description of the analysis parameter values is listed in the Supplementary Material, section 3. Briefly, the final Markov chain comprised 100 replicate chains, each at 1.25×10^8 iterations, with sampling every 500th iteration during the last 7.5×10^7 iterations. The estimate of gene flow $M_{j \rightarrow i}$ (i.e. $M = m/\mu$ from population j into population i) was converted into $N_f m_{j \rightarrow i}$ by multiplying $M_{j \rightarrow i}$ with 0.5 times θ_i (the estimated value of θ for population i), where N_f denotes the effective female population size. The time units reported by MIGRATE-N were transformed into years assuming a generation time of 32.45 years (the average generation time for fin whales estimated by Taylor et al. (2007) and Pacifici et al. (2013)) and two different annual mutation rates for the mtCR at 5.2×10^{-8} (Alter & Palumbi, 2009) and at 8.5×10^{-9} (Baker et al., 1993) per nucleotide site (estimated for humpback whales).

2.3.5 Kinship-based analyses

Pairwise relatedness coefficients (r) were estimated using the *related* R package (v. 1.0; Pew, Muir, Wang, & Frasier, 2015). The performance of four estimators was compared against simulated datasets of related individuals to assess which estimator yielded the most accurate r given the observed data (see Supplementary Material 4; Pew et al., 2015). Assessments of the relative difference in r within and between sampling partitions included only dyads above a pre-determined r value. The chosen threshold value was the value of r for which 99% of dyads were unrelated. The threshold value was determined from 400 simulated dyads of individuals of known relatedness (i.e. unrelated, half-siblings, full-siblings, parent-offspring (PO)) from the observed allele frequencies (Pew et al., 2015).

Estimates of r were employed to assess if the Strait of Gibraltar (GB) fin whale samples on average were more closely related to the Mediterranean Sea (MED; $\bar{r}_{GB-MED}$) or eastern North Atlantic (NEA; $\bar{r}_{GB-NEA}$). The probability of the observed difference (D , equal to $\bar{r}_{GB-MED} - \bar{r}_{GB-NEA}$) was estimated as the proportion of 1,000 randomised data sets with a similar or more extreme estimate of D . Each randomised data set was generated by randomly re-sampling (without replacement) the observed genotypes using observed sample sizes (cf. Valenzuela, Sironi, Rowntree, & Seger, 2009).

The statistical power to discern PO from full-sibling dyads was estimated using the power for relationship inference (PW_R) as implemented in KININFOR (v. 1.0; Wang, 2006, see Supplementary Material 5).

Candidate PO dyads were identified using the maximum likelihood approach implemented in ML-RELATE (Kalinowski et al., 2006). Dyads most likely to be related as PO were considered candidate PO dyads. Additional candidate PO dyads were identified among dyads with estimates of r above 0.42 (the lowest r estimate among candidate PO dyads identified from likelihoods) to account for possible genotyping errors or large allele dropout at one or two (of 20) loci.

The relatedness category likelihood ratios (LOD score) were employed to determine the optimal α -level for the FDR. A detailed description of the FDR procedure is provided in the Supplementary Material section 6.

An assessment of heterogeneity in the spatial distribution of PO dyads was conducted by comparing the observed and expected number of PO dyads for which the two individuals were sampled in different areas (Økland et al., 2010). The expected distribution of the number of such between-area PO dyads was estimated from randomised 1,000 data sets.

Each randomised data set was generated by randomly assigning individuals (without replacement) to a sampling area at sample sizes equal to the observed. The probability of the observed number of between-area PO dyads data was estimated as the proportion of random data sets with a similar or more extreme number of between-area PO dyads.

3. RESULTS

In total 1,659 nuclear 20-locus microsatellite genotypes and 1,651 mtCR DNA sequences (each 450 bps) were generated (Table 1). The genotype inconsistency rate was estimated at 0.2%. P_{ID} and P_{ID-sib} was estimated at 7.7×10^{-25} and 2.6×10^{-9} , respectively for the combined North Atlantic and Mediterranean Sea samples; sufficiently low to safely assume that samples with identical 20-loci genotypes were collected from the same individual (Table 1).

A total of 273 duplicate genotypes was detected, including four between-area duplicated samples. Three fin whales were sampled both in the Strait of Gibraltar and the northwestern Mediterranean Sea. The most geographically distant match was a fin whale sampled off Norway in 2003, and later off the Azores in 2017. While ~30% of all duplicate samples were collected during the same year, the majority (~70%) of duplicate samples were collected in different years. The longest time interval between duplicate samples was 25 years (Gulf of St. Lawrence, 1990 and 2015, Figure S1). All but one sample from a given individual was kept in each data partition during data analysis. Twenty-seven likely cow and calf dyads were sampled in the same area and on the same day (i.e. non-independent sampling of genetically similar individuals). Only one individual was retained from these dyads. The final data set comprised 1,423 20-loci genotypes and 0.71% missing data.

The overall sex ratio did not differ significantly from parity (0.97 males: 1 female, $\chi^2 = 0.2$, d.f. = 1, $P > 0.5$). However, sex ratios differed significantly among sampling areas ($\chi^2 = 60.5$, d.f. = 12, $P < 0.001$; see Figure S6 and Supplementary Material 7).

3.1 Mitochondrial diversity and divergence

A total of 46 segregating sites defined 108 mtCR haplotypes in 1,376 unique multi-locus genotypes. Heteroplasmy was detected in 14 individuals. Both haplotypes were retained for individuals with a single-site heteroplasmy. The North Atlantic sample, Mediterranean Sea (incl. the Strait of Gibraltar) and Gulf of California samples contained 102, 12 and four mtCR haplotypes, respectively. The estimated haplotype and nucleotide diversity was lowest in the Gulf of California ($n = 43$, $h = 0.29 \pm 0.03$ 95% CI, $\pi = 0.001 \pm 0.0003$ 95% CI, see Rivera-León et al., 2019 for details), followed by the Mediterranean Sea ($n = 207$, $h =$

0.49 ± 0.005 , $\pi = 0.004 \pm 0.0004$), and the North Atlantic ($n = 1125$, $h = 0.95 \pm 0.0002$, $\pi = 0.012 \pm 0.0004$; Table 1).

A

B

Figure 1. (A) Sampling areas depicted as shaded area with the number of parent-offspring (PO) dyads sampled in those areas (total within-within PO dyads = 118). Arrows depict the number of PO dyads with members sampled in different areas; MA, Mid-Atlantic; GM, Gulf of Maine; GL, Gulf and Estuary of St. Lawrence; WG, West Greenland; IS, Iceland; FO, Faroe Islands; NO, Norway; SV, Svalbard; AZ, Azores; IR, Ireland; SP, Atlantic Spain; CI, Canary Islands; GB, Strait of Gibraltar; ME, Mediterranean Sea; (B) Number of PO dyads expected under the null-expectation within and between GL and GM. Blue lines show observed number of PO dyads and the corresponding P -value.

There was no evidence for significant levels of heterogeneity (between sex and years) within sampling areas. JMODELTEST identified Tamura & Nei (1993)'s model as the most probable mutation model (model weight of 69.9%) and so it was employed in the estimation of Φ_{ST} . The highest pairwise estimates of genetic divergence included the outgroup, i.e. the Gulf of California. The divergence between the Gulf of California and the Mediterranean Sea samples was between 0.57 (Weir's θ , 95% CI: 0.57-0.8) and 0.78 (Φ_{ST} , 95% CI: 0.61-0.91); and between 0.29 (Weir's θ , 95% CI: 0.29-0.39) and 0.55 (Φ_{ST} , 95% CI: 0.41-0.72) to the North Atlantic sample.

Table 1. Summary statistics of mitochondrial control region DNA sequences and nuclear multi-locus genotypes.

Area	mtDNA control region			nuclear multi-locus genotypes							
	<i>N</i>	π	<i>h</i>	<i>N</i>	<i>A_R</i>	<i>H_o</i>	<i>H_e</i>	$\bar{r}_d$	$p(\bar{r}_d)$	<i>P_{ID}</i>	<i>P_{ID-sib}</i>
MA	16	0.01±0.0029	0.9±0.0289	15	4.94	0.77	0.77	9.99E-03	0.152	1.77E-23	4.31E-09
GM	95	0.011±0.0012	0.9±0.0026	109	4.83	0.79	0.78	-5.45E-04	0.86	6.28E-24	3.73E-09
GL	353	0.011±0.0006	0.92±0.0005	354	4.9	0.78	0.78	4.07E-03	0.003*	2.85E-24	3.27E-09
WG	63	0.012±0.0016	0.95±0.0027	54	4.81	0.77	0.77	2.02E-02	0.275	5.70E-24	3.80E-09
IS	244	0.013±0.0009	0.96±0.0008	267	4.97	0.77	0.79	-5.48E-04	0.855	6.83E-25	2.64E-09
FO	15	0.013±0.0038	0.99±0.011	16	4.91	0.76	0.76	5.01E-03	0.195	5.89E-23	5.90E-09
NO	61	0.013±0.0017	0.96±0.0034	64	4.92	0.8	0.77	-5.78E-04	0.635	3.94E-24	3.85E-09
SV	7	0.011±0.0053	0.95±0.0571	6	4.85	0.8	0.71	-1.15E-02	0.74	9.15E-20	3.00E-08
AZ	101	0.011±0.0012	0.94±0.0025	103	4.93	0.78	0.78	7.31E-03	0.167	1.76E-24	3.10E-09
IR	27	0.012±0.0025	0.74±0.0289	28	4.88	0.8	0.77	7.62E-03	0.062	2.33E-23	4.89E-09
SP	138	0.012±0.0011	0.92±0.0028	155	4.97	0.77	0.79	-1.51E-03	0.774	5.50E-25	2.46E-09
CI	5	0.015±0.0088	0.9±0.1168	5	4.82	0.79	0.72	-2.25E-02	0.796	1.80E-19	3.00E-08
GB	53	0.005±0.0008	0.47±0.0217	55	4.89	0.77	0.77	1.96E-02	0.164	2.30E-24	3.05E-09
ME	154	0.004±0.0004	0.49±0.0069	159	4.86	0.78	0.78	6.59E-03	0.165	1.92E-24	3.14E-09
GC	43	0.001±0.0003	0.29±0.026	33	3.02	0.5	0.49	5.05E-02	0.001*	1.05E-11	1.58E-05

Note. Sampling areas (area) denoted by MA, Mid-Atlantic; GM, Gulf of Maine; GL, Gulf and Estuary of St. Lawrence; WG, West Greenland; IS, Iceland; FO, Faroe Islands; NO, Norway; SV, Svalbard; AZ, Azores; IR, Ireland; SP, Atlantic Spain; CI, Canary Islands; GB, Strait of Gibraltar; ME, Mediterranean Sea; GC, Gulf of California. *N*, sample size; *h*, haplotype diversity (95% confidence intervals); π , nucleotide diversity (95% confidence intervals); *A_R*, allelic richness; *H_o*, observed heterozygosity; *H_e*, expected heterozygosity; $\bar{r}_d$, standardised index of linkage association; $p(\bar{r}_d)$, *p* – value for $\bar{r}_d$; * denotes significant linkage disequilibrium; *P_{ID}*, probability of identity; *P_{ID-sib}*, sibling probability of identity.

The average degree of divergence among the Mediterranean Sea sample and North Atlantic sample areas was an order of magnitude higher than among North Atlantic sampling areas (Figure 2a and Supplementary Material 8). The estimate of divergence among North Atlantic sample areas was 0.17 (Weir's θ , 95% CI: 0.11-0.25) and 0.13 (Φ_{ST} , 95% CI: 0.06-0.18). The divergence between the Strait of Gibraltar and the Mediterranean Sea samples did not differ significantly from zero, i.e. the confidence intervals of both Weir's θ and Φ_{ST} included zero (Figure 2a and Supplementary Material 8). The same was the case between Iceland, Norway, the Azores and West Greenland within the North Atlantic.

Figure 2. Population divergence estimates based on (a) Weir's θ (Weir & Cockerham, 1984) and Φ_{ST} for mtDNA sequences and (b) Weir's θ and Jost's D for multi-locus genotypes. Colour gradient reflects magnitude of divergence (view scale on right, number estimates given in Supplementary Material, Table S1 & S2). Abbreviations of sampling areas as in Table 1. * denotes statistically significant differentiation after Benjamini-Hochberg correction.

3.2 Genetic diversity and divergence at nuclear microsatellite loci

No statistically significant deviations from the expected Hardy-Weinberg genotype proportions were detected within sampling areas after applying a FDR (Waples, 2015). A significant degree of linkage disequilibrium was observed in the Gulf of St. Lawrence and Gulf of California (cf. Rivera-León et al., 2019) samples after applying FDR (Table 1).

The highest level of genetic divergence was estimated between the Gulf of California and Mediterranean Sea samples (Weir's θ 0.2, 95% CI: 0.16-0.24; Jost's D 0.39, 95% CI: 0.26-0.54) and between the Gulf of California and North Atlantic fin samples (Weir's θ 0.19, 95% CI: 0.15-0.22; Jost's D 0.37, 95% CI: 0.24-0.51). Several pairwise estimates of Weir's θ between the Mediterranean Sea and some North Atlantic sampling areas were significantly

larger than zero (overall Weir's θ 0.005, 95% CI: 0.003-0.006; Jost's D 0.012, 95% CI: 0.006-0.018; Figure 2b and Supplementary Material 8). A few cases of significantly positive degrees of divergence were also detected among comparisons between western and eastern North Atlantic sampling areas (Figure 2b).

The estimate of N_e inferred from the degree of linkage for the combined North Atlantic sample was 4,304 (95% CI: 2,966 – 7,510) and 444 (95% CI 300 – 787) for the Mediterranean Sea sample. Because generations overlap, these estimates represent the effective number of breeders that produced the sample set (Waples & Do, 2008). Estimates of N_e for each sampling area in the North Atlantic failed to produce estimates with a finite upper confidence band, except for the Gulf of St. Lawrence sample where most samples were collected ($N_e = 547$, 95% CI: 427 – 741).

The most probable number of clusters (K) was three (for both the log-likelihood & Evanno's ΔK ; Figure S2, Supplementary Material 2) partitioning the samples into a Mediterranean Sea, western North Atlantic, and eastern North Atlantic cluster, respectively (Figure 3a). The West Greenland samples, at the intersection of the two North Atlantic clusters were admixed (between the eastern and western North Atlantic). Lower levels of admixture were suggested for the Azores, Ireland, and Strait of Gibraltar samples (Figure 3a).

3.3 Isolation-by-distance assessment

The Mantel test revealed a significant degree of IBD in case of both the mtCR (Mantel $r = 0.52$, $P < 0.001$) and nuclear microsatellite loci (Mantel $r = 0.42$, $P < 0.001$) in the combined North Atlantic and Mediterranean Sea sample (Supplementary Material, Figure S7). No significant difference was observed between females (Mantel $r = 0.41$) and males (Mantel $r = 0.47$, Fisher's z (1925) = -0.44, $P = 0.66$, Supplementary Material, Figure S8). The significant correlation between genetic divergence and geographic distance remained among samples within the North Atlantic (i.e. excluding Mediterranean and Strait of Gibraltar samples, Figures 3b and 3c). The correlation coefficient among the North Atlantic samples decreased appreciably when the most distantly located samples were excluded (i.e. Norway, Gulf of Maine). The Monmonier-based assessment suggested a larger-than-expected change in genetic divergence between the Mediterranean Sea (including the Strait of Gibraltar) and the North Atlantic for the mtCR (Figure 3d).

Figure 3. (A) Bar plot of individual admixture proportions for priors of K between 2 - 4. Location abbreviations given in Table 1. Relationship between pairwise linearised Weir's θ and oceanic distances based on (B) mitochondrial control region DNA sequences (Mantel $r = 0.67$, $P < 0.001$) and (C) nuclear multi-locus genotypes (Mantel $r = 0.48$, $P < 0.006$) in North Atlantic samples only. (D) Delaunay triangulations among sampling regions (thin black lines) and the location of a comparatively elevated degree of gene divergence detected using Monmonier's algorithm (thick black line).

3.4 Coalescent-based analyses

Coalescent-based estimates of θ and Nm suggested very different demographic histories for North Atlantic and Mediterranean Sea (including the Strait of Gibraltar) fin whales. The mode of the posterior distribution of θ estimated for the North Atlantic samples was at 0.056 (95% highest posterior density interval (HPDI): 0.037 – 0.088) compared to 0.002 for the Mediterranean Sea samples (95% HPDI: 0 – 0.007). Depending on the generational mutation rate (1.04×10^{-6} or 2.76×10^{-7} per nucleotide site), N_e (i.e. θ_i/μ) was estimated at 53,700 (95% HPDI: 35,400 – 84,500) or 202,200 (95% HPDI: 133,300 – 318,400) for North Atlantic fin whales and at 2,200 (95% HPDI: 0 – 6,300) or 8,400 (95% HPDI: 0 – 23,700) for Mediterranean Sea fin whales. The migration rate (number of female migrants per generation) from the North Atlantic into the Mediterranean Sea was estimated at 0.5 (95% HPDI: 0 – 10.9) versus 12.7 (95% HPDI: 2.7 – 42.4) in the opposite direction. The skyline plot of N_e suggested contrasting trends in abundance in the two oceans (Figure 4,

Supplementary Material, Figure S10). The estimated skyline plot suggested that the North Atlantic fin whale population increased exponentially during the past 5,000 years (or 30,000 years, depending on the chosen mutation rate, Figure 4, Supplementary Material, Figure S10). In contrast, the skyline plot of N_e for the Mediterranean Sea suggested a decrease in abundance during the same time period (Figure 4, Supplementary Material, Figure S10). Similarly, the migration rates were also inferred as increasing during the past 3,000 (or 20,000 years, depending on the mutation rate, Figure 4, Supplementary Material, Figure S10).

Figure 4. Trajectories of effective population size N_e and number of effective female immigrants per generation N_fm for the North Atlantic and Mediterranean Sea fin whales with 95% highest posterior density intervals assuming an annual mutation rate at 5.2×10^{-8} per nucleotide site (Alter & Palumbi, 2009).

3.5 Kinship-based analyses

The dyadic likelihood estimator (Milligan, 2003) provided the best fit to the observed data (Pearson's correlation 0.91; Figure S5). Average pairwise estimates of r among related dyads ($r > 0.23$) was higher within sampling areas ($r = 0.43$) than between sampling areas ($r = 0.39$, $P < 0.001$). Although no significant differentiation (based on fixation indices) was detected among central/eastern North Atlantic (West Greenland, Iceland, Azores, Faroe Islands, Norway) sampling regions, the average estimate of r was significantly higher within regions compared to between regions ($P < 0.001$). The average estimate of r between the Strait of Gibraltar and Mediterranean Sea was significantly higher than the estimate for the Strait of Gibraltar and the eastern North Atlantic ($P < 0.001$). Overall, between-sampling area relatedness correlated (negatively) with oceanic distances (Z-statistic = 31.9, $P = 0.029$; Figure S9).

The statistical power to discern between full sibling and PO relationships was estimated at 0.98 for the 20 microsatellite loci assuming no genotyping errors. A total of 184 candidate PO dyads was identified among the North Atlantic and Mediterranean Sea samples. Applying an FDR significance level of 0.1, 51 PO dyads were deemed false positives (Supplementary Material 6). Among the 133 remaining PO dyads, both members of 118 dyads were sampled in the same area. The members in the remaining 15 dyads were sampled in different sampling area, at distances between members ranging from 1,400 to 3,300 kms (Figure 1a). These 15 between-sampling area PO dyads included four female-female dyads, seven mixed sex dyads, and four male-male dyads. The within-sampling area PO dyads included 41 female-female, 56 mixed sex, and 21 male-male dyads. These proportions deviated significantly from the expected ratios given a 1:1 sex ratio (i.e. 0.25 female-female, 0.5 mixed, 0.25 male-male; $\chi^2 = 7.09$, d.f. = 2, $P = 0.029$).

The number of PO dyads within and between the Gulf of Maine and St. Lawrence was assessed for spatial heterogeneity. This assessment was limited to the Gulf of Maine and St. Lawrence due to the extensive number of biopsy samples collected in two adjacent areas. The observed number of between-sampling area PO dyads ($n = 5$) differed significantly from the null expectation (median $n = 33$, $P_{[PO, GL-GM]} < 0.001$, Figure 1b). The numbers of observed PO dyads within both areas (75 in the St. Lawrence and 10 in the Gulf of Maine) were consequently significantly higher than expected ($P_{[PO, GL]} < 0.001$, $P_{[PO, GM]} < 0.035$). The observed number of male-male PO dyads was also significantly higher within the Gulf of St. Lawrence ($P < 0.005$, $n = 19$) and hence significantly lower between areas ($P = 0.006$, $n = 2$).

compared to random expectations (Figure S11). No male-male dyads were observed in the Gulf of Maine sample.

4. DISCUSSION

The present study demonstrates the benefits of applying a multi-faceted approach to assess population genetic structure in a low-divergence species. Fixation indices, coalescent- and kinship-based approaches are, to some extent, complementary in terms of which spatial and temporal scale they capture and hence may provide a more dynamic insight into the processes leading and maintaining contemporary population genetic structure. Coalescent-based analyses revealed contrasting long-term demographic histories and asymmetric gene flow was inferred in the North Atlantic and Mediterranean Sea. The spatial distribution of related individuals in the North Atlantic was consistent with a stepping-stone model, resulting in IBD. Accordingly, the overall low ocean-scale genetic divergence indicates recent demographic expansion and stepwise gene flow among fin whales from proximate summer feeding areas, resulting in increasing genetic divergence with greater geographical distance.

The challenges inherent in low levels of population differentiation have long been recognised in studies of marine species (Palumbi, 2003; Waples, 1998; R. D. Ward et al., 1994; Whitlock & McCauley, 1999). Common pitfalls include the inference of biologically significant population structure from rejecting panmixia alone and the understatement of study limitations (Palsbøll et al., 2007, 2010; Taylor & Dizon, 1996; Waples, 1998; Waples & Gaggiotti, 2006). High apparent genetic connectivity inferred from fixation indices is not necessarily analogous to demographic interdependence (Lowe & Allendorf, 2010; Waples & Gaggiotti, 2006).

Complementary approaches, such as the coalescent- and kinship-based approaches presented here, therefore allow contextualised estimates of genetic differentiation. Coalescent-based methods were previously employed to relate low levels of divergence (pairwise $F_{ST} < 0.2$ for mtCR) in southern right whales (*Eubalaena australis*) to a demographic history marked by isolation followed by secondary contact (Carroll et al., 2018). Crandall et al. (2019) highlighted the advantages of coalescent genealogy sampler, using a model-selection framework, to identify underlying stepping-stone models in high gene flow species ($Nm = 100$). Complementary to the historical context provided by coalescent-based approaches, kinship-based approaches provide a means to detect contemporary population structure even when genetic divergence is low (Frantz et al., 2010; Palsbøll, 1999; Palsbøll et al., 2010; Peery et al., 2008; Planes et al., 2009).

Previous studies have estimated contemporary dispersal rates using kinship-based methods, by integrating individual-based models and the spatial distribution of close relatives (Escoda et al., 2017, 2019; Fountain et al., 2018; Hall et al., 2009; Peery et al., 2008; Wang, 2014). The high spatio-temporal variation in sampling effort precluded such an analysis in the present study. Direct estimates of gene flow can greatly strengthen inferences drawn from measures of differentiation (Marko & Hart, 2011); however, they require a careful study design (cf Peery et al., 2008). Ten percent of the PO dyads detected in this study comprised members sampled in different regions. If these dispersal events resulted in gene flow, this would be indicative of some contemporary gene flow among North Atlantic fin whale sampling areas. In that case, the observed low levels of genetic divergence would unlikely be the result of recent divergence and low contemporary gene flow.

The recaptures of individuals and close-kin in different areas were consistent with previous reported long-range movements by fin whales in the eastern North Atlantic (Lydersen et al., 2020; Mikkelsen, 2007; Silva et al., 2013). Telemetry studies tracked individuals from the Azores to eastern Greenland and western Iceland on their northward spring migration (Silva et al., 2013) and from the Faroe Islands to the British Isles in autumn (Mikkelsen, 2007). One individual was tracked from Svalbard, Norway, to the warm waters off Morocco in autumn, stopping numerous times along its track along the edge of the continental shelf, e.g. off Ireland (Lydersen et al., 2020). These dispersal patterns are likely linked to seasonal migrations from high latitude summer feeding areas to low latitude winter areas (Baines et al., 2017; Kellogg, 1928; Lydersen et al., 2020; Silva et al., 2013). While capture-recapture data do not provide the same spatio-temporal resolution of movements as telemetry, our match of an individual biopsied off Norway and then again in the Azores represents a previously undocumented link between these two areas. A migratory link between the northeast and central Atlantic was previously suggested from analyses of stable isotopes (Silva et al., 2019) and behavioural observations (Baines et al., 2017). The observed recaptures of close-kin and low levels of genetic differentiation in the present study are consistent with such a migratory link among fin whales from the central and northeast Atlantic, although none of the results presented here or in previous studies provided estimates of actual dispersal rates.

The level of genetic divergence between the North Atlantic and Mediterranean Sea at mitochondrial ($\Phi_{ST} = 0.12$) and nuclear ($\theta = 0.005$) loci was markedly and significantly lower compared to the estimated divergence between ocean basins, such as the Gulf of California and the North Pacific Ocean (coastal California) which were estimated at 0.19 (Φ_{ST} , mtCR) and between 0.17 - 0.21 (F_{ST} , nuclear loci; (Archer et al., 2019; Bérubé et al.,

1998, 2002; Rivera-León et al., 2019). Despite low levels of genetic divergence among North Atlantic fin whale samples, some genetic sub-structuring was detected between sampling areas in the western (i.e. Gulf of Maine and St. Lawrence, mtCR Weir's $\theta = 0.006$) and eastern North Atlantic (Figure 2). The overall population genetic structure of North Atlantic fin whales was in part (Mantel $r = 0.67$) explained by a stepping-stone model of gene flow, implying recurrent gene flow among neighbouring regions and evident as increased differentiation with oceanic distance. Accordingly, the kinship-based approach detected higher average levels of genetic relatedness among fin whales within sampling areas than expected under panmixia; even among samples where conventional homogeneity tests failed to detect significant levels of heterogeneity. Ninety-eight percent of the inter-annual, individual recaptures were within the same sampling areas, confirming previous behavioural observations of strong seasonal site fidelity to specific feeding grounds (Agler et al., 1990; Ramp et al., 2014; Whooley et al., 2011), as well as the results of the analyses of morphology and chemical tracers (Borrell et al., 2018; Hobbs et al., 2001; Mitchell, 1974; Sanpera et al., 1996; Vighi et al., 2016, 2019), which suggested some degree of population structuring. However, most recaptures were detected in sampling areas with a long-term and sustained high effort, notably in the Gulf of St. Lawrence, the Gulf of Maine, and the Ligurian Sea (France/Italy). It therefore remains to be confirmed whether a behavioural component, e.g. maternally directed site fidelity, is also contributing to the population genetic structure in other North Atlantic regions. Stevick et al. (2006) detected more long-distance movements among the eastern North Atlantic humpback whales (compared to the western North Atlantic), which was attributed to a less predictable prey distribution. Similar movement patterns in fin whales in relation to prey distribution and predictability could explain lower levels of genetic differentiation in the eastern North Atlantic, compared to the western North Atlantic.

While the observed genetic divergence overall was consistent with a stepping stone model, there was also some evidence for “discrete” clusters in the Bayesian cluster analysis. However, Bayesian clustering methods are designed to divide multi-locus genotypes into discrete clusters and hence unable to capture the genetic structure of a stepping stone model (Frantz et al., 2009). The observed clustering in the North Atlantic (i.e. separate western and eastern North Atlantic clusters) may be an artefact created by an underlying IBD pattern, which could explain the apparent admixture in the West Greenland samples.

The extent of gene flow among fin whales between the western and eastern North Atlantic could not be resolved in the present study. A fin whale tagged in Newfoundland in 1979 was later recovered off western Iceland in 1988 (Sigurjónsson et al., 1991). This recapture

represented the only evidence of dispersal between the western and central North Atlantic. Another, 57 (of a total of 296) tags were recovered within the East Greenland-Iceland region where they were tagged, leading Víkingsson and Gunnlaugsson (2006) to conclude that mixing between the western and central North Atlantic likely was very low. Of 25 fin whales tagged in Svalbard, none of the migrants showed any transatlantic tendencies (Lydersen et al., 2020). In the present study, an attempt to estimate gene flow among western and eastern North Atlantic fin whales using MIGRATE-N failed to converge.

Extensive sampling efforts in the western North Atlantic allowed a more in-depth investigation of population divergence among fin whales from two adjacent feeding grounds. Fixation indices and kinship-based approaches suggested weak genetic substructuring among fin whales from the Gulf of Maine and the Gulf of St. Lawrence. Previous studies reported evidence in favour of a small, distinct population in the Gulf of St. Lawrence based upon rates of whaling stock depletion, acoustic song patterns and heavy metal loads (Delarue et al., 2009; Hobbs et al., 2001; Mitchell, 1974; Sergeant, 1977). The observed frequency of PO dyads within the Gulf of Maine and St. Lawrence was significantly higher than expected under the null expectation. Previous fin whale studies have reported maternally-directed site fidelity to summer feeding grounds (Clapham & Seipt, 1991), which could explain the higher-than-expected proportion of female-female PO dyads. However, the number of male-male PO dyads detected in the Gulf of St. Lawrence and the low number of such pairs between the two feeding areas suggest that individuals from the Gulf of St. Lawrence are more likely to mate with each other than with Gulf of Maine whales. Limited exchange with neighbouring summer feeding areas could make the Gulf of St. Lawrence fin whales more vulnerable, particularly considering a recent decline in abundance (Schleimer et al., 2019) and the discovery of vastly underestimated entanglement rates (Ramp et al., 2021).

A comparatively, and substantially lower rate of gene flow was detected between North Atlantic and Mediterranean Sea fin whales, in accordance with previous genetic studies (Bérubé et al., 1998; Palsbøll et al., 2004). The gene flow between North Atlantic and Mediterranean Sea was asymmetrical with the lowest rate out from the Mediterranean Sea into the North Atlantic. Despite an extensive dataset, the presence of unsampled, so-called ghost populations, may affect the estimation of gene flow and effective population sizes (Beerli, 2004; Slatkin, 2005). The effective rate of gene flow of North Atlantic fin whales into the Mediterranean Sea was estimated at 0.5 (95% HPDI: 0 – 10.9) females per generation, which is low from an ecological/ conservation perspective, and may be insufficient to buffer a decline in abundance, e.g. due to cumulative anthropogenic stressors (Fossi et al., 2010,

2016; Panigada et al., 2006, 2011). For example, the minimum annual, fatal ship collision rate during the 1990s in the Mediterranean Sea was estimated at 1.7 whales/year (Panigada et al., 2006).

The precise location of the boundary between the North Atlantic and Mediterranean fin whales has been debated extensively (Castellote et al., 2012; Gauffier et al., 2018; Giménez et al., 2013, 2014; Notarbartolo di Sciara et al., 2016). Northeastern North Atlantic fin whales are assumed to enter and exit through the Strait of Gibraltar and range as far east as the Balearic Islands, where they presumably overlap with the resident Mediterranean population (Notarbartolo di Sciara et al., 2016). The presumed distribution is consistent with reported isotope (Bentaleb et al., 2011; Giménez et al., 2013; Ryan et al., 2013), and acoustic (Castellote et al., 2012) findings. However, a recent acoustic study conducted off southwest Portugal detected two different acoustic song patterns, which were assumed to represent Mediterranean Sea and eastern North Atlantic fin whales, respectively (Pereira et al., 2020). In this study, Strait of Gibraltar fin whales clustered with the Mediterranean Sea fin whales. The recapture of two individuals in the Strait of Gibraltar that were previously sampled in the Ligurian and Sardinian Sea as well as the identification of four PO dyads with members sampled in the Ligurian Sea and the Strait of Gibraltar further support the notion that the range of the Mediterranean Sea fin whales includes the Strait of Gibraltar. The seemingly different conclusions on the identity of the Strait of Gibraltar individuals drawn from this and previous studies could reflect differences in sampling in relation to seasonal migration patterns. Stable isotope signatures (Gauffier et al., 2020) and acoustic recordings off southwest Portugal (Pereira et al., 2020) revealed strong seasonal differences. Most biopsy samples from the Strait of Gibraltar included in this study were collected during the summer, and hence provide no insights regarding the oceanic affinity of fin whales in this area during the winter.

Differentiation between the North Atlantic and the Mediterranean Sea was also evident in terms of the long-term changes in abundance. In addition to recurrent gene flow among fin whales from different regions, population expansion likely contributed to the overall low levels of divergence in the North Atlantic. The rate of genetic drift is reduced in expanding populations (relative to a constant sized population), which, in turn, results in lowered genetic divergence (Excoffier et al., 2009; Huijser et al., 2018; Waxman, 2012). As outlined by Bérubé et al. (1998), the current high latitude fin whale feeding grounds only became accessible to fin whales after the LGM (ca. 19-20,000 years ago, Clark et al., 2009). Foote et al. (2013) linked the population expansion observed in the genetic diversity of bowhead whales (*Balaena mysticetus*) to the onset of the Holocene epoch (ca. 11,650 years ago) and

concomitant increase in core suitable habitat. Reduced sea ice coverage, along with large-scale changes in ocean productivity, likely resulted in an expansion of fin whale populations in the North Atlantic following the LGM (Cabrera, 2018). In contrast to the past expansion of fin whales in the North Atlantic, fin whales in the Mediterranean Sea appeared to have undergone a long-term, post-LGM population decline. The environmental conditions in the Mediterranean Sea following the LGM were likely unfavourable to fin whales. Sea surface temperatures increased in the western Mediterranean Sea by 8°C after the LGM, resulting in a shift towards oligotrophic conditions (Kuhlemann et al., 2008). These environmental changes proposed as an explanation for the absence of some cold-water adapted cetacean species, such as the harbour porpoise (*Phocoena phocoena*, Fontaine et al., 2014), from the Mediterranean Sea.

Sergeant (1977) suggested that the North Atlantic fin whale population structure was best described as “patchy continuum”, which was consistent with the findings in the genetic analyses reported by Bérubé et al. (1998). The results presented here also support a population structure characterised by elevated fine-scale within-region relatedness, as well as connectivity among neighbouring regions. While fin whales have the capacity for wide-ranging movements, their propensity for site fidelity was evident in low, but significant, heterogeneity among areas. The movement behaviour of fin whales encompasses a wide spectrum of strategies (Geijer et al., 2016), which was reflected in the present study as heterogeneous distribution of genetic variation in combination with detections of apparent connectivity among populations.

Low levels of population differentiation can arise from various demographic histories and patterns of population connectivity, which may be challenging to discern among using a single-analysis approach. The multi-faceted approach presented here, combining traditional fixation indices, coalescent- and kinship approaches, provided a more dynamic insight into the population structure of a species with high dispersal potential. Coalescent-based analyses revealed contrasting demographic histories in the North Atlantic and Mediterranean Sea. Long-term population expansions in the North Atlantic may have contributed to the overall low levels of divergence observed among North Atlantic fin whales. Individual and kinship-based approaches complemented inferences drawn from fixation indices, suggesting a population structure captured by the stepping-stone model likely due to recurrent gene flow among neighbouring regions.

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SUPPLEMENTARY INFORMATION

1. Probability of identity and duplicate sampling

Methods

The probability of identity between unrelated individuals (P_{ID}) and full siblings (P_{ID-sib} ; Waits, Luikart, & Taberlet, 2001) was estimated using CERVUS (v. 3.0.7; Kalinowski, Taper, & Marshall, 2007). The expected number of pairs of individuals with identical genotypes by chance was estimated by multiplying the number of pairwise comparisons ($(N * (N - 1))/2$) by P_{ID} or P_{ID-sib} for unrelated and related pairs, respectively. P_{ID-sib} was also employed to estimate the minimum number of loci required to discern among different individuals. The threshold number of matching loci was determined from P_{ID-sib} , as the probability which resulted in less than one pair of different individuals matching at all loci.

Results

The estimated P_{ID} in the fin whale samples from the North Atlantic and the Mediterranean Sea was 7.7×10^{-25} , i.e. sufficiently low to discriminate among unrelated individuals. The data also provided sufficient power to discern among full siblings at a P_{ID-sib} of 2.6×10^{-9} . The expected numbers of pairs of individuals with identical genotypes by chance in the North Atlantic and Mediterranean Sea were estimated at 1×10^{-18} for unrelated and 3.5×10^{-3} for related individuals. Based upon a threshold level of 7.6×10^{-7} , matching at five and 14 loci were sufficient to discern among unrelated and related individuals, respectively. Accordingly, two samples were considered to be potential duplicate samples from the same individuals when their multi-locus genotypes matched on 14 or more loci. A total of 273 duplicate samples were identified among the 1,659 unique multi-locus genotypes.

Figure S1. Frequency of duplicate sampling occurring at different temporal intervals (in years). Over 80 duplicate samples were taken during the same year (0 years interval). The longest time interval between sampling events of a single individual was 25 years, which occurred in the GL, where an individual was biopsied in 1990 and again in 2015. Colours reflect the sampling region, including the four between-region matches (MIX). AZ = Azores, CI = Canary Islands, FO = Faroe Islands, GB = Strait of Gibraltar, GC= Gulf of California, GL = Gulf and Estuary of St. Lawrence, GM = Gulf of Maine, IL = Iceland, IR = Ireland, MA= Mid-Atlantic States, ME = Ligurian Sea and Balearic Islands, NO = Norway, SP = Atlantic Spain, WG = West Greenland.

2. Detailed *STRUCTURE* methodology and supplementary results

Methods

The Bayesian clustering approach as implemented in the software package *STRUCTURE* (v. 2.3.4.; Pritchard, Stephens, & Donnelly, 2000) was employed to determine the most likely number of distinct genetic clusters K in the North Atlantic and Mediterranean Sea. The parameter λ was inferred from an initial run with $K = 1$, burn-in comprised 50,000 Markov-Chain Monte-Carlo (MCMC) iterations, followed by 100,000 MCMC iterations. We employed a no-admixture model with correlated allele frequencies, using sampling location as prior. The final estimation was conducted with a burn-in period at 100,000 iterations followed by 400,000 iterations, with a fixed prior for K from one to eight. Three independent estimates, based upon fifteen replicates, were performed for each value of K to

assess consistency among runs. The estimated posterior probability of the data given a value of K $LnP(D|K)$ (Pritchard et al., 2000) and the *ad hoc* statistic ΔK (Evanno et al., 2005) were employed to determine the most probable number of clusters. Clusters were aligned using CLUMPP (v.1.1.2; Jakobsson & Rosenberg, 2007) with plots assembled in the *pophelper* R package (v. 2.3.0; Francis, 2017).

Results

Figure S2. Log $LnP(D|K)$ (L) and derivatives of Bayesian clustering solutions for values of K from one to eight. (A) Mean $L(K)$ ($\pm$ standard deviation SD) over 15 runs for each K value. (B) Rate of change in $LnP(D|K)$ (mean $\pm$ SD) calculated as first derivative $L'(K) = L(K) - L(K - 1)$. (C) Absolute values of the second order rate of change of the likelihood distribution (mean $\pm$ SD) calculated according to the formula: $|L''(K)| = |L'(K + 1) - L'(K)|$. (D) Evanno's ΔK calculated as $\Delta K = m|L''(K)| / s[L(K)]$. The uppermost level of structure (here $K=3$) is inferred from the modal value of this distribution.

Supplementary STRUCTURE analysis with admixture model

The Bayesian clustering approach implemented in the software STRUCTURE (ver. 2.3.4.) was repeated using the admixture model with correlated allele frequencies with sampling location as a prior. The parameter λ was inferred as 0.57 from an initial run with $K = 1$, a burn-in of 50,000 Markov-Chain Monte-Carlo (MCMC) iterations, followed by 100,000 MCMC iterations. The population-specific ancestry prior and $\alpha = 1/K$ were applied in accordance with recommendations outlined by Wang (2017). The final model was run with a burn-in period of 100,000 MCMC followed by 400,000 iterations for each K value, ranging from one to eight. Three independent runs of fifteen replicates were performed for each value of K to assess consistency among runs. The estimated posterior probability for the data $\text{Ln}P(D|K)$ for each K was assessed to determine the most likely number of plausible clusters.

Results from the three independent runs of 15 replicates were all consistent and the number of clusters K that was the most likely given the data was $K = 1$ (Figure S3). The difference between $K = 1$ and $K = 2$ was not substantial, but the plot of admixture proportions for $K = 2$ did not support a clear differentiation into two distinct clusters (Figure S4).

Figure S3. Mean of estimated probability of data is shown for each number of clusters K with standard deviations. The mean and standard deviations were calculated by combining the results from the three independent runs of the 15 replicates for each K after checking that the results did not differ significantly among the three independent runs.

Figure S4. Bar plot of admixture proportions for each individual fin whale as determined by STRUCTURE under the scenario of $K = 2$. MA: mid-Atlantic, GM: Gulf of Maine, GL: Gulf of St. Lawrence, WG: West Greenland, IL: Iceland, PT: Azores, FO: Faroe, NE: Norway, EI: Ireland, SP: northern Spain, CI: Canary Islands, GB: Strait of Gibraltar, IT: Italy and southern France.

3. Detailed MIGRATE-N methodology

Relative effective population sizes ($\theta = N_e\mu$) and levels of historical gene flow ($M = m/\mu$), where μ represents the generational mutation rate (per nucleotide site), for fin whales sampled in the North Atlantic and the Mediterranean Sea were quantified using the coalescent-based Bayesian inference approach as implemented in MIGRATE-N (v. 3.6.6; Beerli & Felsenstein, 2001). Random sub-samples of 200 mtDNA sequences (without replacement) were generated to ensure identical sample sizes from all sampling regions. The transition/transversion ratio was inferred from the most probable mutation model (i.e. model with lowest AIC score) in JMODELTEST (v. 0.1.1; Posada, 2008). Preliminary analyses with fewer MCMC iterations using F_{ST} estimates as starting values, were conducted to determine prior ranges for (θ) and M and starting values for the estimation (i.e. with more iterations). The final Markov Chain scheme consisted of 100 replicates, each comprising a single MCMC at 1.25×10^8 iterations, sampling at every 500th iteration during the last 7.5×10^7 iterations. A static heating scheme of four chains at temperatures of 1.0, 1.5, 3.0, and 1,000,000, respectively, was employed. Trace and density plots were visually checked to assess mixing. Effective sample sizes (ESS), adjusted for autocorrelation. ESS above 4000 were considered an index for adequate MCMC chain lengths. In addition to assessing the consistency of the posterior probability distributions between runs, convergence was also assessed using the potential scale reduction factor R , as described by Gelman & Rubin (1992) and implemented in the *coda* package (v. 0.19-1; Plummer, Best, Cowles, & Vines, 2006).

4. Relatedness estimator comparison

Figure S5. Comparison of four relatedness estimators implemented in the *related* R package using simulated datasets of individuals with known relationships. L&R, Lynch & Ritland (1999); M, Milligan (2003); Q&G, Queller & Goodnight (1989); W, Wang (2002). The dyadic likelihood estimator by Milligan (2003) provided the best fit to the data (Pearson's correlation at 0.91).

5. Detailed KININFOR methodology

The power of the microsatellite loci to discriminate PO pairs from full-siblings, was inferred using the Power for Relationship Inference (PW_R) was computed in KININFOR (v. 1.0; Wang, 2006). The primary and null hypotheses were specified as full-siblings ($\Delta_1 = 0.5$, $\Delta_2 = 0.25$) and PO ($\Delta_1 = 1$, $\Delta_2 = 0$), respectively. One million pairs of 20 loci genotypes were simulated for each relationship category, sampling from the empirical microsatellite allele frequencies and assuming a prior Dirichlet distribution of (1,1,1) for Δ_0 , Δ_1 , Δ_2 . The significance level was set at 0.05.

6. False-Discovery-Rate application to parent-offspring pair identification

The LOD score was estimated for each candidate PO dyad to compare the null hypothesis of unrelated to the alternative hypothesis of half siblings following the rationale outlined by Skaug et al. (2010). FDR procedure was applied in the following manner: for each candidate PO dyad, P -values were estimated by comparing their LOD score to a distribution of LOD scores from 500 simulated datasets. Simulated genotypes were generated by permutation based upon empirical sample sizes and allele frequencies following the script by Skaug et al. (2010). From a range of significance levels between 0.001 and 0.9, the chosen FDR significance level was with fewest false positives and false negatives. Female-female pairs inferred as PO dyads with different mtDNA haplotypes were deemed false positives. Known cow-calf pairs (from field observations) were employed to confirm the genetic inference of PO dyads to control for false negatives.

Using the above approach and mitochondrial haplotypes of 55 female-female candidate PO dyads and 18 known cow and calf relationships sampled in the Gulf of St. Lawrence, an FDR significance level of 0.1 was applied, leading to the removal of 51 PO pairs with the highest P -values.

7. Sex ratio differences among sampling areas

Overall, the sex ratio did not differ significantly from parity (0.97 males: 1 female, $\chi^2 = 0.2$, d.f. = 1, $P > 0.5$). However, sex ratios differed significantly from parity among sampling regions ($\chi^2 = 60.5$, d.f. = 12, $P < 0.001$). In the Gulf of Maine (1.8 males: 1 female), Gulf of St. Lawrence (1.4 males: 1 female) and the Faroe Islands (4.3 males: 1 female), sex ratios were biased towards males, while in the Atlantic Spain sample, the sex ratio was biased towards females (0.4 males: 1 female; Figure S6). Sex ratios in the remaining regions did not differ significantly from parity.

In the Gulf of St. Lawrence, fin whales have been observed to aggregate in large male-dominated groups. Because large groups are more readily detected and easier to approach and sample, Bérubé, Berchok, & Sears (2001) suggested that the male-bias in sampling arose from biased sampling of these male dominated groups, noting that no deviations from a 1:1 sex ratio were detected in singles and pairs. In the Gulf of Maine, fin whales are rarely observed in large groups and preferential detection/sampling of groups can thus not explain the male bias in this region (J. Robbins, pers. comm.).

Figure S6. Comparison of the proportion of females among sampling regions with 95% confidence intervals. Horizontal line shows 1:1 sex ratio. See Figure S1 for region abbreviations.

8. Pairwise *F*-statistics estimates

Table S1. Pairwise *F*-statistics for mtDNA control region sequences with θ (B. S. Weir & Cockerham, 1984) shown above diagonal and Φ_{ST} below diagonal. In bold are shown the estimates whose confidence interval did not include zero (significant *P*-value after applying *FDR*). See Figure S1 for region abbreviations.

	MA	GM	GL	WG	IS	FO	NO	IR	SP	AZ	GB	ME
MA		0.006	0.018	0.027	0.025	0.018	0.044	0.166	0.07	0.029	0.357	0.369
GM	0.004		0.006	0.034	0.033	0.022	0.049	0.147	0.071	0.038	0.282	0.308
GL	0	0.007		0.015	0.021	0.014	0.029	0.103	0.045	0.02	0.212	0.224
WG	0.02	0.052	0.014		0.004	0.001	0.004	0.072	0.017	0	0.198	0.222
IS	0.014	0.017	0.007	0.004		0	0.002	0.063	0.011	0	0.167	0.182
FO	0.051	0	0.033	0.1	0		0	0.083	0.014	0.001	0.276	0.291
NO	0.017	0.028	0.019	0.003	0	0		0.054	0.004	0	0.175	0.2
IR	0.018	0.044	0.028	0.005	0.061	0.052	0.027		0.021	0.05	0.056	0.075
SP	0.058	0.019	0.061	0.027	0.005	0.002	0	0.043		0.005	0.121	0.137
AZ	0.022	0.006	0.025	0	0	0	0	0.019	0.001		0.161	0.182
GB	0.28	0.203	0.112	0.086	0.118	0.221	0.149	0.047	0.071	0.094		0
ME	0.32	0.204	0.198	0.121	0.128	0.279	0.156	0.186	0.028	0.097	0	

Table S2. Pairwise estimates of Weir & Cockerham's θ (Weir & Cockerham, 1984) inferred from multi-locus genotypes above diagonal and estimates of Jost's *D* below diagonal. Bold typeface denotes estimates whose confidence interval exclude zero (significant *P*-value after applying *FDR*). See Figure S1 for region abbreviations.

	MA	GM	GL	WG	IS	FO	NO	IR	SP	AZ	GB	ME
MA		0.0014	0.0022	0.0000	0.0006	0.0040	0.0010	0.0032	0.0018	0.0016	0.0024	0.0056
GM	0.0039		0.0014	0.0024	0.0043	0.0068	0.0062	0.0059	0.0043	0.0039	0.0086	0.0095
GL	0.0044	0.0024		0.0016	0.0021	0.0038	0.0031	0.0034	0.0027	0.0017	0.0083	0.0079
WG	0.0029	0.0061	0.0031		0.0008	0.0032	0.0010	0.0022	0.0013	0.0008	0.0059	0.0049
IS	0.0029	0.0086	0.0045	0.0032		0.0012	0.0000	0.0019	0.0000	0.0005	0.0051	0.0049
FO	0.0149	0.0110	0.0057	0.0064	0.0057		0.0001	0.0068	0.0010	0.0010	0.0077	0.0077
NO	0.0039	0.0127	0.0057	0.0028	0.0002	0.0036		0.0032	0.0000	0.0000	0.0061	0.0060
IR	0.0058	0.0117	0.0083	0.0064	0.0051	0.0120	0.0059		0.0001	0.0016	0.0068	0.0050
SP	0.0043	0.0086	0.0052	0.0028	0.0003	0.0045	0.0015	0.0012		0.0006	0.0052	0.0036
AZ	0.0048	0.0079	0.0034	0.0026	0.0012	0.0042	0.0007	0.0038	0.0015		0.0055	0.0046
GB	0.0092	0.0156	0.0096	0.0122	0.0089	0.0121	0.0114	0.0170	0.0077	0.0088		0.0045
ME	0.0090	0.0207	0.0188	0.0097	0.0113	0.0169	0.0114	0.0094	0.0078	0.0099	0.0046	

9. Additional isolation-by-distance results

Figure S7. The correlation between pairwise estimates of Weir & Cockerham's θ (Weir & Cockerham, 1984) and oceanic distance based on (a) mtDNA sequences ($r = 0.52$, $P < 0.001$) and (b) multi-locus genotypes ($r = 0.42$, $P < 0.002$) among North Atlantic and Mediterranean Sea fin whales.

Figure S8. The correlation between linearised Weir & Cockerham's θ (Weir & Cockerham, 1984) and oceanic distances among males and females. The slopes did not differ significantly between sexes (Fisher's z (1925) = -0.44 , $P = 0.66$).

Figure S9. Relationship between genetic relatedness and oceanic distance (log-transformed), (Z -statistic = 31.9, $P < 0.029$).

10. Additional *MIGRATE-N* results

Figure S10. Alternative timeline using an annual mutation rate of 8.5×10^{-9} (Baker et al., 1993) per nucleotide site.

11. Expected vs observed father-son dyads in western North Atlantic

Figure S11. Distribution of number of father-son pairs expected to be sampled within the Gulf of St. Lawrence (GL), between the Gulf of St. Lawrence and the Gulf of Maine (GM), and within the Gulf of Maine, as expected under a random-mixing scenario. Blue line shows the observed number of father-son pairs and P -values.

CHAPTER

05

5

Paleo-climate driven changes in effective population size and connectivity define the global genomic diversification process of a highly mobile pelagic species

Anna Schleimer, Martine Bérubé, Per J. Palsbøll

ABSTRACT

Pleistocene climate forcing affected the demographic history and contemporary population genetic structuring in a wide range of taxa. Previous studies on the effects of past climatic changes in the marine domain have been mainly focused on coastal and polar species. Here, we assessed the hypothesis that Pleistocene glacial-interglacial cycles affected the population connectivity and effective population sizes of a globally distributed, highly dispersive pelagic species, the fin whale (*Balaenoptera physalus*). We employed genome-wide single nucleotide polymorphisms to assess contemporary global population genetic structure and to perform demographic model selection. Population divergence among fin whales from the North Pacific and North Atlantic was best explained by a demographic model with secondary contact, implying a period of gene flow possibly during the last interglacial (~125 thousand years ago). The demographic histories of Northern and Southern Hemisphere fin whales were characterised by a two-epoch model with asymmetric connectivity and changes in effective population sizes. The asymmetric demographic responses could be indicative of asynchronous climate change between hemispheres and/or stronger impacts of climate forcing on habitat availability in the Northern Hemisphere. The timing of demographic events, and hence their co-occurrence with major climatic events, depended greatly on the assumed mutation rate; however, the dominant expansion signals were inferred to have occurred prior to the Last Glacial Maximum. The results of this study add to the growing body of literature highlighting that past climate forcing did not only affect shallow coastal and polar habitats, but also noticeably impacted populations in offshore, open ocean ecosystems.

1. INTRODUCTION

Contemporary species have persisted through past periods of substantial and rapid environmental change, with wide-ranging effects on key aspects, such as habitat availability and inter-specific dynamics (Burger & Lynch, 1995; Pease et al., 1989). The Pleistocene glacial-interglacial cycles during the last 2.6 million years exemplify rapid ecosystem changes at a global scale, which, in turn, subjected the biota to repeated expansions and contractions in distribution and intra-specific connectivity (Graham et al., 1996). Environmental-driven changes in habitats in turn affected abundance and connectivity among sub-populations and the spatio-temporal configuration of intra-specific genetic diversity, which is mirrored in the genetic make-up of contemporary populations (Harpending et al., 1998). Consequently, the contemporary partition of con-specific genetic diversity may inform about past demographic changes and the correlation with major

environmental transitions, providing fundamental insights into the response of Earth's biota to past climate changes (Fraser et al., 2009; Stange et al., 2018).

During the repeated cycles of the Pleistocene, biogeographical ranges generally shifted to the equator during glacial periods and expanded poleward during interglacial periods (Fraser et al., 2012; Hewitt, 2000; Lorenzen et al., 2011; O'Corry-Crowe, 2008). However, the demographic response varied among species due to intrinsic factors, such as dispersal capacity, physiological tolerance limits, and life history traits, and extrinsic factors, such as ecological conditions, geographical context, and inter-specific competition (Burrows et al., 2011; Graham & Grimm, 1990; Hewitt, 2000; Lorenzen et al., 2011). Marine species were long believed to be disproportionally less impacted by glacial-interglacial climate changes compared to terrestrial and freshwater communities (Dawson & Hamner, 2008; Foltz et al., 2008; Hewitt, 2000). However, a growing body of evidence suggests that the Pleistocene glaciation cycles explain contemporary population genetic structure and biogeographic ranges in a wide variety of marine biota (Avice, 2000; Cabrera, 2018; Fraser et al., 2012; J. X. Liu et al., 2011; Maggs et al., 2008; Pastene et al., 2007).

The oceanographic conditions during glaciation periods differed markedly from the present, as exemplified by estimated changes in sea-ice extent and temperatures during the last glacial maximum (LGM, ~ 27-23 thousand year ago (kya); Hughes & Gibbard 2015). The North Atlantic was covered with extensive perennial sea-ice along eastern Canada and Greenland and the waters in the central North Atlantic and Norwegian Sea open during the warm season (de Vernal et al., 2006). In the central and eastern North Atlantic the winter sea-ice extended ten degrees farther south (to ~55°N) during the LGM compared to ~65°N today (de Vernal et al., 2006). The mid-latitudinal North Atlantic waters and western Mediterranean Sea were six to ten degrees Celsius cooler (Waelbroeck et al., 2009). North Pacific cooled to a lesser degree. Parts of the Northwest Pacific were possibly slightly warmer than present conditions (Waelbroeck et al., 2009). The winter sea-ice in the Bering Sea extended beyond its current limit, but likely did not reach the south-central part of the sea (Matul, 2017). In the Southern Ocean, winter sea-ice was displaced northward by 7-10° in latitude, converting to a ~100% increase of the sea ice field compared with modern conditions (Gersonde et al., 2005). The polar front extended north to ~45°S resulting in austral summer temperatures two to six degrees Celsius below current levels (J. B. Anderson et al., 2002; Waelbroeck et al., 2009).

The lower sea-surface temperature and increased sea-ice cover during the LGM affected ocean circulation and stratification (Costa et al., 2018). Proxy data suggest comparatively lower levels of primary productivity at high latitudes during glaciations. In contrast, the

rates of upwelling and cooler temperatures at lower latitudes resulted in an increase in primary productivity (Costa et al., 2018; Foster & Sexton, 2014; Hernández-Almeida et al., 2019; Radi & De Vernal, 2008; E. Thomas et al., 1995). The primary productivity increased at high latitudes, and decreased at lower latitudes when global temperatures increased after the LGM (Costa et al., 2018).

In the Northern Hemisphere, latitudinal postglacial range shifts and population expansions have been reported in several marine taxa (Foote, Kaschner, et al., 2013; Maggs et al., 2008; O’Corry-Crowe, 2008; Palsbøll, Heide-Jørgensen, et al., 1997). Briggs (1970) hypothesised that the comparatively larger change in post-LGM temperatures in the North Atlantic may have resulted in more drastic range shifts relative to the North Pacific. In the Southern Hemisphere, comparatively few species succeeded in recolonising polar regions from lower latitude refuges following deglaciation, possibly due to the isolating effect of the Antarctic Circumpolar Current (De Bruyn et al., 2009; Fraser et al., 2009, 2012). While species’ responses were strongly influenced by their dispersal capacity and habitat requirements (T. L. Cole et al., 2019), those factors are often insufficient to account for the contrasting phylogeographic patterns observed among closely related species with similar life history traits (Bargelloni et al., 2003). Given these complex species-specific responses to past climatic oscillations and ocean-basin differences in oceanographic conditions, much remains to be learnt about the demographic responses of pelagic species to changing environmental conditions.

The present study employed genome-wide variation to gain insights into the response of fin whales (*Balaenoptera physalus*) to past glaciations at a global scale. Fin whales have a global distribution and are mainly observed in areas with a high primary productivity during the summer and at lower latitude during the winter (Cotté et al., 2009; López et al., 2019; Mizroch et al., 2009; Scales et al., 2017; Sergeant, 1977; Silva et al., 2013), with a likely equatorial hiatus (Edwards et al., 2015). Several recent studies have reported apparent changes in fin whale arrival time and distribution on high-latitude summer feeding grounds in the North Atlantic, possibly in response to contemporary environmental changes due to global warming (G. E. Davis et al., 2020; Ramp et al., 2015; Víkingsson et al., 2015). On a longer time-frame, genetic analyses uncovered genetic diversity consistent with rapid, post-LGM population expansions in the North Atlantic likely as a consequence of habitat expansions and elevated levels of marine productivity (Bérubé et al. 1998; chapter 4 in this thesis). Population connectivity and effective population sizes (N_e) are two key population parameters which most likely were affected by the changes in habitat availability and productivity due to glaciation cycles, as reported in other marine taxa (Alter et al., 2015; T.

L. Cole et al., 2019; Curtis et al., 2009; Foote, Kaschner, et al., 2013; Palumbi & Kessing, 1991; Pastene et al., 2007).

Here, we employed trends in genetic diversity θ as a proxy for changes in demography, i.e. N_e and population connectivity. Differences in local climatic and geographical contexts during the Pleistocene glaciation cycles were hypothesised to have influenced fin whale demographic histories heterogeneously, ultimately shaping the contemporary global genetic population structure. During the glaciations, fin whales likely persisted in glacial refugia in mid- and low-latitude waters. Such a constriction in range toward the equator placed Northern and Southern Hemisphere populations in closer proximity and hence facilitated inter-hemisphere connectivity. The reduction in available habitat was likely mirrored by a reduction in N_e . Conversely, interglacial periods would have reinforced the divergence among fin whales from different hemispheres through the reduction of inter-hemisphere connectivity. An ice-free Arctic Sea would have allowed direct dispersal between the North Pacific and North Atlantic (Mckeon et al., 2016), as previously suggested in the cases of gray (*Eschrichtius robustus*; Alter et al., 2015) and bowhead whales (*Balaena mysticus*; Foote, Kaschner, Schultze, Garilao, Ho, Post, Higham, Stokowska, Van Der Es, et al., 2013). The postglacial increase in available habitat likely caused an increase in N_e (Borreagaard & Rahbek, 2010).

We employed analyses of genome-wide genetic variation in fin whales from the North Pacific, North Atlantic, Southern Ocean, as well as the seas of the Gulf of California and Mediterranean Sea, to infer the likelihood of alternative climate-based hypotheses of past population divergence and connectivity. Differential climatic and geographical contexts were expected to have led to heterogeneous demographic responses in fin whales.

2. METHODS

2.1 Sample collection

Skin biopsy samples were collected from fin whales in five different oceans and seas; (1) the eastern North Pacific ($N = 6$), (2) the Gulf of California ($N = 10$), (3) the Southern Ocean (Antarctic Peninsula; $N = 6$), (4) the North Atlantic ($N = 113$), and (5) the Mediterranean Sea ($N = 37$; Fig. 1). Samples were collected as skin biopsies from free-ranging fin whales using a crossbow and a bolt with a biopsy tip (Palsbøll et al., 1991). Tissue samples were conserved in a saturated NaCl solution with 30% dimethylsulphoxide and stored at either -20°C or -80°C until DNA extraction.

Figure 1. Sampling areas and schematic representation of proposed effects of climate variability on fin whale populations. Interglacial periods are hypothesised to promote differentiation among hemisphere, but facilitate gene flow via the Arctic Ocean. Conversely, glacial periods are hypothesised to facilitate gene flow between hemispheres.

2.2 Laboratory analyses

Total-cell DNA was extracted from tissue samples either by phenol:chloroform extractions (Sambrook et al., 1989) or with the Qiagen DNeasy™ Blood and Tissue Kit (Qiagen Inc.) according to the manufacturer's instructions. Extracted DNA was re-suspended in 1x TE buffer (10mM Tris-HCl, 1mM EDTA, pH 8.0) and normalised to 10 ng/μL.

2.3 Data generation

Double digest restriction-site associated DNA (ddRAD; Peterson, Weber, Kay, Fisher, & Hoekstra, 2012) and quaddRAD (Franchini et al., 2017) libraries were comprised of 600 nano grams of extracted DNA from each sample digested with *HindIII* and *MspI*. Fragment sizes between 300 – 400 base pairs (bps) length were sub-selected using a Pippin Prep™ (Sage Inc.). For the ddRAD libraries, each DNA extraction was labelled with unique adapter in-line i5 and i7 barcodes (between 6 – 8 bps) as well as unique i7 only or i7 and i5 indexes of six bps. For both the i5 and i7 adapters, four random bases were inserted between the in-line barcode and restriction site overhang, which were employed to remove PCR-clones (see bioinformatics below). The quaddRAD library was generated as described above except for the addition and sequencing of a i5 index (Franchini et al., 2017). The resulting libraries were sequenced by core facilities on an Illumina HiSEQ™ 2500 sequencer in high throughput mode, as paired-end sequencing of 126 bps.

Sequences were called and indexes de-multiplexed by the core sequencing facilities. The STACKs (v 2.4, Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011) collection of

software was employed to call SNP genotypes. PCR clones were removed (STACKS *clone_filter* script). Reads were demultiplexed based on the i5 and i7 in-line barcodes and adapters low-quality reads were removed (Phred-score below 10 in a 15% read-length window) using the STACKS script *process_radtags*. The resulting fastq sequences were aligned against the published humpback whale (*Megaptera novaeangliae*) genome assembly (v. 1.0, Tollis et al., 2019) using BOWTIE2 (v.2.3.4.3, Langmead & Salzberg, 2012) with the settings *very-sensitive*. Individual SNP genotypes were called using the STACKs script *gstacks* (marukilow SNP model with parameters *var_alpha* at 0.01 and *gt_alpha* at 0.05). The resulting SNP catalogue was filtered using the STACKs *populations* script (-R 0.95, -r 0.95). A thinned dataset was prepared using VCFtools using an interval at 10,000 bps to remove proximate SNPs and hence possibly linked.

2.4 Data analyses

Within-sampling region, inter-library divergence in a subset of sampling locations was employed as means to detect and correct for possible library batch artefacts. Specifically the level of clustering among samples from areas represented in multiple RAD libraries were assessed by principal component analysis (PCA) as implemented in the *adeigenet* R package (Jombart, 2008). Weir & Cockerham's θ (Weir's θ hereafter, 1984) was estimated per-locus using the *diversity* R package (Keenan et al., 2013) to identify potential outlying loci.

2.4.1 Contemporary global population structuring

The population genetic structure was assessed using both Bayesian and likelihood clustering approaches (Guillot et al., 2009). An individual-based PCA was performed with the *glPca* function implemented in the *adeigenet* R package; numbers of alleles were centred but unscaled. The most likely number of distinct clusters K was inferred using the approach implemented in the software STRUCTURE (v.2.3.4; Pritchard, Stephens, & Donnelly, 2000). The parameter λ was inferred from a single initial run at $K = 1$, a burn-in of 5,000 Markov-Chain Monte-Carlo (MCMC) iterations, followed by 10,000 MCMC iterations. The final estimation was conducted allowing admixture and correlated allele frequencies, using sampling location as prior. An alternative ancestry prior of $\alpha = 1/K$ as starting value was employed following the recommendation by Wang (2017). Each estimation comprised an initial 150,000 iterations as burn-in, followed by an additional 300,000 iterations. Fifteen replicate estimations were conducted for values of K ranging from one to six. The most likely number of K was inferred from $Pr[X|K]$, where X denotes the data, as described by Pritchard et al. (2000) as well using the *ad hoc* statistic ΔK developed by Evanno, Regnaut, & Goudet (2005). Admixture proportions of each sample were plotted with CLUMPP

(v.1.1.2; Jakobsson & Rosenberg, 2007) and the *pophelper* R package (v.2.3.0; Francis, 2017). In order to uncover possible hierarchical structure, estimations were repeated within each initial cluster until the most likely value of K was equal to one.

Recent patterns of co-ancestry were further assessed using *fineRADstructure* (v.0.3; Malinsky, Trucchi, Lawson, & Falush, 2018), which applies a *fineSTRUCTURE* MCMC clustering algorithm (Lawson et al., 2012) to derive a matrix of coancestry coefficients based on the distribution of nearest neighbour haplotypes among samples. The matrix of between-individual co-ancestry coefficients provides a more intuitive representation of hierarchical structuring compared to *STRUCTURE*. Estimations were conducted with default parameter settings: 100,000 burn-in iterations, followed by 100,000 MCMC iterations and sampling occurring every 1,000th iteration. Results were visualised using the *fineradstructureplot.r* and *finestructurelibrary.r* scripts (available via <http://cichlid.gurdon.cam.ac.uk/fineRADstructure.html>). Convergence was assessed by visually comparing the results from three independent runs.

Pairwise Weir's θ was estimated using the *assigner* R package (v.0.5.6; Gosselin, 2019). Confidence intervals (95% CI) were estimated from 100 simulated data sets, each with the observed number of loci and samples and generated by random sampling of individual SNPs with replacement.

2.4.2 Population tree

To resolve the order of population divergences, a population tree was estimated using the Bayesian coalescent framework implemented in the software SNAPP (v.1.5; Bryant, Bouckaert, Felsenstein, Rosenberg, & Roychoudhury, 2012) implemented in BEAST2 (v.2.6.1; Bouckaert et al., 2014). SNAPP assumes zero migration after population divergence. All samples from the Mediterranean Sea were excluded in this estimation because previous studies (Bérubé et al., 1998; Palsbøll, Bérubé, Aguilar, Notarbartolo di Sciara, & Nielsen, 2004, chapter 4 in this thesis) suggested some gene flow between the Mediterranean Sea and the North Atlantic. Due to computational limitations, the final data set was limited to the four samples with the least amount of missing data from each sampling area, yielding a total sample size of 16.

The forward and backward mutation rates (u and v) were both fixed at one. The λ prior was set to a broad gamma distribution with a mean value of 1,000, set as $\alpha = 2$ and $\beta = 500$. The θ prior was also set as the default gamma distribution with a mean value of 0.067, defined as $\alpha = 2$ and $\beta = 30$. The average nucleotide diversity estimates were used to guide the choice of the θ prior. A mean $\theta = 0.067$ implies 6.7% variation between two

randomly sampled alleles in a population. Two independent estimations, each comprised of 2.5×10^6 iterations, sampling every 1,000th iteration and a burn-in of 10%. Trace files were inspected in TRACER (v.1.7.1; Rambaut, Drummond, Xie, Baele, & Suchard, 2018) for convergence. An effective sample size above 500 was taken as indication of adequate mixing and chain lengths. A maximum clade credibility tree (MCC) with median node heights was depicted with TreeAnnotator (v.2.6; Rambaut and Drummond).

2.4.3 Single population size changes

The null hypothesis of a constant N_e was tested with Tajima's D (Tajima, 1989) estimated in δadi (v.2.0.5; Gutenkunst et al. 2009).

Temporal changes in θ were inferred from the site frequency spectrum (SFS) using the multi-epoch model implemented in the Stairway Plot approach (v.2; Liu & Fu, 2015). A custom python script was employed to estimate the folded SFS for each sample partition. To obtain estimates of changes in θ over time, 200 sub-samples were generated by bootstrap sampling of two-thirds of the variant sites. The sub-samples were employed to estimate individual Stairway Plots with a random selection of four break points selected as $(nseq-2)/4$, $(nseq-2)/2$, $(nseq-2)*3/4$, $nseq-2$, respectively, where $nseq$ represents is the number of sampled gene copies. The Stairway Plot algorithm selects the optimal number of random break point to control overfitting based on the remaining one-third of variant sites.

Scaled time units were converted into years assuming three sets of annual, per-site mutation rates and generation times to assess the effects of low, mid, and high parameter estimate combinations; (1) $\mu = 1.07 \times 10^{-9}$ (estimated for the minke whale (*B. acutorostrata*) genome; Yim et al., 2014) and $g = 32.45$ (average of estimates provided by Taylor et al. 2007 and Pacifici et al. 2013), (2) $\mu = 1.76 \times 10^{-10}$ (lower boundary of mysticete estimate by Dornburg et al. (2012) and $g = 25.9$ (Taylor, Chivers, et al., 2007), and (3) $\mu = 1.07 \times 10^{-9}$ and $g = 39$ (Pacifici et al., 2013). The length parameter L , defined as the total number of observed nucleic polymorphic and monomorphic sites, was estimated as $\sum_{i=1}^n loci_i \times length_{RAD}/SNPs_i(1)$, where $loci_i$ denotes the number of RAD loci with i number of SNPs ($SNPs_i$) and $length_{RAD}$ denotes the RAD locus length in bps. The proposed estimation of L was deemed to more accurately reflect the total number of observed sites after thinning to one SNP per locus compared to the default estimation of L (total number of loci $\times length_{RAD}$).

2.4.4 Global population history model selection

Different models of the global population history were compared employing the diffusion approximation method based on two-dimensional joint-site frequency spectra (2D-JSFS) and three dimensional (3D) JSFS implemented in the software *δaδi* (v.2.0.5; Gutenkunst et al. 2009). We chose ten samples across a broad geographic range from the North Atlantic samples in comparisons with the North Pacific and Southern Ocean fin whales; the selection was extended to 20 North Atlantic samples for the 2D-JSFS with the Mediterranean Sea fin whales. The thinned VCF file was formatted to *δaδi*'s input file format using the custom perl script at https://github.com/wk8910/bio_tools/blob/master/01.dadi_fsc/00.convert_WithFSC/convert_vcf_to_dadi_input.pl. Due to uncertainty regarding the ancestral state the folded JSFS was employed. The SFS was projected down to (a) decrease the effect of different levels of missing data among SFS and (b) maximise the number of segregating sites.

Pairwise population (hereafter 2D) model selection was limited to four biologically meaningful fin whale population pairs: (1) North Pacific and Southern Ocean, (2) Southern Ocean and North Atlantic, (3) North Pacific and North Atlantic, and (4) North Atlantic and Mediterranean Sea. The demographic history of the Gulf of California was recently presented by Rivera-León et al. (2019) and hence not revisited here.

Models of alternative demographic histories were formulated based on hypothesised effects of past climatic oscillation on gene flow and N_e (Fig. 1). Gene flow was hypothesised to increase between Northern and Southern Hemisphere populations during glacial periods and between North Pacific and North Atlantic populations during interglacial periods. N_e was hypothesised to change in relation to habitat availability. Thirteen 2D models were fit using the workflow developed by Portik et al. (*dadi_pipeline*, 2017). The demographic models differed in terms of direction and timing of gene flow and change in population size (visually represented in Supplementary Fig. S1). The optimisation routine by Portik et al. (2017) was employed and comprised a number of user-defined optimisations, each consisting of multiple replicate estimations. An initial optimisation round was based upon randomly chosen parameter values. Subsequent optimisation rounds employed the parameter estimates from the preceding optimisation round as starting parameter values, presumably converging on the global maximum likelihood estimate during the final estimation (Portik et al., 2017). In this study, four such consecutive optimisation rounds were performed for the 2D models using the Nelder-Mead algorithm (Nelder & Mead, 1965). Each of the four optimisation rounds were based upon 20, 30, 40, and 50 replicates, respectively. The maximum number of iterations for each of the four optimisation rounds

was 5, 20, 50, and 100, respectively. Parameter perturbations decreased from three-fold during the first optimisation rounds, to two-fold during the second and third optimisation rounds, and one-fold during the last and final estimation. Extrapolation grid sizes were set at 40, 50, and 60. Model selection was conducted using the Akaike Information Criterion (AIC; Akaike, 1972) among the replicates from each model with the highest likelihood. We assumed that the likelihood scores represented the true, rather than composite, likelihood scores since the estimation was constrained to a single SNP per RAD locus. Ten independent estimations were conducted for each model to assess convergence. Model likelihoods that converged to within 10% of previous likelihoods were interpreted as convergence.

To assess whether the retained 2D demographic models represented plausible explanations of the observed JSFS, goodness of fit (GOF) tests were performed as described by Barratt et al. (2018). In short, the highest-ranking model was fitted with the optimised model parameters. The resulting model SFS was scaled by the inferred theta value and used to generate 100 Poisson-sampled SFS. For each of the simulated SFS, an optimisation was performed, consisting of 60 replicates over three optimisation rounds. The empirical model log-likelihood and Pearson's chi-squared test statistics were subsequently compared to the distribution obtained from the 100 replicates with highest likelihood scores (out of the 60 replicates from optimisation). The code for the GOF testing was provided by Portik and is available at https://github.com/dportik/dadi_pipeline/tree/master/Goodness_of_Fit.

Parameter estimates were transformed into years, N_e and number of migrants per generation (Nm) using three different sets of annual, per-site mutation rates and fin whale generation times; (1) $\mu = 1.07 \times 10^{-9}$ and $g = 32.45$, (2) $\mu = 1.79 \times 10^{-10}$ and $g = 25.9$, and (3) $\mu = 1.07 \times 10^{-9}$ and $g = 39$. The L parameter was estimated according to equation 1. The reference effective population size (N_{ref}) was estimated as $\theta/4\mu gL$ (where θ denotes the effective mutation rate of the reference population), which was used to derive the effective population sizes $N_e = nu_i \times N_{ref}$ (where nu_i specifies the size of population i relative to N_{ref}). Time (in years) was estimated as $2N_{ref}Tg$, where T denotes $\delta a \delta i$'s unscaled time parameter. Nm was estimated as $m_{ij}/2 \times nu_i$, where m_{ij} denotes the relative rate of migration from population j into population i . The 95% confidence interval (CI) of the parameter estimates were inferred using parametric bootstrapping, i.e. sampling from the simulated datasets employed in the GOF testing above.

The joint-demographic history of the global sample was explored employing 3D-JSFS in the North Pacific, Southern Ocean, and North Atlantic sample. The aim of the 3D model selection was to identify the changes and extent of gene flow among ocean basins. The

results of the model selection among the 2D models and the SNAPP estimation served as the basis for devising eight 3D models, differing by the nature of the split (i.e. simultaneous or consecutive split into three populations) and direction and timing of gene flow (visually represented in Supplementary Fig. S2). The optimisation procedure described above for the 2D models was also applied to the 3D models, except for the number of replicates, which was limited to 10, 20, 30, and 40 replicates in each optimisation, respectively, in order to maintain feasible computational times.

3. RESULTS

The total number of sequencing reads received was 1,661,253,516. Applying the *clone_filter* resulted in the removal of 5.9% of reads. The remaining 1,563,968,906 reads were processed with *precoss_radtags* resulting in the removal of an additional 9.0% low quality reads, for a total of 1,423,234,446 reads. The average number of reads per sample was at 6,683,917 (ranging from 1,089,489 - 20,037,357 reads), with a harmonic mean at 5,231,779 reads. Alignment rates for individual samples was on average 85.22%, ranging from 69.73 to 93.43%. Applying *gstacks* to the aligned data yielded 2,633,397 loci, with an effective per-sample coverage at an average of 27 (SD 13.0, ranging from 8.2 to 81.6).

One library, which was prepared using the quaddRAD protocol, showed clear evidence of a possible library batch effect (Supplementary Fig. S3). All individuals included in this library were fixed for one allele at six loci, and differed significantly from the allele frequency observed for the same sampling areas in the other libraries (per-locus Weir's $\theta = 1$). This "batch" effect disappeared after removing the six outlying loci (Fig. S3). Accordingly, all subsequent assessments excluded these six loci.

After selecting loci with *populations* and thinning with VCFTools (interval 10,000 bps), the final catalogue comprised 172 individuals genotyped at 13,336 RAD loci at a mean length of 118 bps (SD 0.01) containing a total of 22,785 SNPs. Missing data (2.32%) were randomly distributed among libraries ($F(3,168) = 0.46$, $P = 0.71$, Supplementary Fig. S4). The proportion of missing data was higher in the Gulf of California (on average 4.8%) and North Pacific (5.9%) sample, compared to the Mediterranean Sea (1.3%), North Atlantic (0.5%) and Southern Ocean (0.2%) sample (Supplementary Fig. S4). The thinned dataset with a single SNP per RAD locus was employed in all analyses, except fineRADstructure (Supplementary Table S1).

3.1 Population genetic structure

The Bayesian clustering analysis of 13,336 SNPs from 172 samples resulted in the detection of two main clusters based on Evanno's ΔK (Fig. 2B, Supplementary Fig. S5). The largest cluster comprised individuals from the North Atlantic and Mediterranean Sea, with no evidence of admixture. The second cluster included fin whales from the Gulf of California, North Pacific and Southern Ocean with some admixture in the North Pacific and Southern Ocean samples. The solution of $K = 3$ received support from $Pr[X|K]$ (Supplementary Fig. S5). Re-analysis of each main cluster separately partitioned the samples from Gulf of California and Southern Ocean into two distinct clusters with some degree of admixture among the North Pacific samples. No additional clusters were detected among North Atlantic and Mediterranean Sea fin whales when analysed separately.

The PCA clustered the samples into four distinct clusters (Fig. 2C). In agreement with the Bayesian clustering, the first principal component revealed a split between three groups, comprised of a combined North Atlantic and Mediterranean Sea cluster, a North Pacific and Southern Ocean cluster, and the Gulf of California cluster. North Pacific and Southern Ocean fin whales separated along the second principal component. Additional, weaker sub-structuring was apparent between the North Atlantic and Mediterranean Sea samples (Figure S6).

The co-ancestry matrix also supported a hierarchical clustering among fin whales, placing fin whales from the Gulf of California closest to animals from the North Pacific (Fig. 2A). The estimated degree of co-ancestry was higher among proximate samples compared to more distantly located samples.

Weir's θ estimates also reflected the highly divergent nature of the Gulf of California samples, even to the neighbouring fin whales in the North Pacific (Weir's $\theta = 0.22$; Table 1), which was in line with results from previous genetic assessments of this isolated population (Bérubé et al., 1998, 2002; Rivera-León et al., 2019). In comparison, the divergence between the North Atlantic and the Mediterranean Sea sample was much lower (Weir's θ 0.005, Table 1), but significantly different from zero. The level of divergence between the North Atlantic and North Pacific oceans was twice the (Weir's θ 0.21, Table 1) divergence between the North Pacific and Southern Ocean (Weir's θ 0.09, Table 1).

Figure 2. Results from contemporary global structuring analysis. (A) Clustered FINERADSTRUCTURE matrix of between-individual co-ancestry coefficients; colour gradient shows level of co-ancestry with yellow indicating low levels of co-ancestry, (B) Bar plot of admixture proportions for each individual fin whale as determined by STRUCTURE under the scenario of $K = 2-3$, (C) and Principal Component (PC) Analysis, with percentage of variation explained by PC1 and PC2. GC, Gulf of California; NP, North Pacific, SO, Southern Ocean; AT, North Atlantic; MED, Mediterranean Sea.

Table 1. Levels of divergence and deviations from mutation-drift equilibrium

	GC	NP	SO	AT	MED
Gulf of California (GC)	0.20				
North Pacific (NP)	0.22* (0.21-0.23)	-0.74			
Southern Ocean (SO)	0.28* (0.27-0.29)	0.09* (0.08-0.09)	-1.19		
North Atlantic (AT)	0.39* (0.37-0.41)	0.21* (0.20-0.22)	0.19* (0.18-0.20)	-1.61	
Mediterranean Sea (MED)	0.40* (0.38-0.41)	0.21* (0.20-0.22)	0.18* (0.17-0.19)	0.005* (0.004-0.006)	-1.48

Note. Below diagonal: Estimates of Weir and Cockerham's θ (95% confidence intervals in parentheses). * denotes statistical significance. Diagonal: Tajima's D estimates.

3.2 Population divergence order and Stairway Plots

The order of population divergence inferred from the SNAPP analysis suggested an initial split between fin whales from the Southern Ocean and the Northern Hemisphere populations, followed by a split between Pacific and North Atlantic fin whales (Fig. 6A). In comparison, the divergence between the Gulf of California and the North Pacific was relatively more recent, dated by Rivera-León et al. (2019) to approximately 2.3 kya (95% HPD: 0–62.5 kya).

The estimated Stairway Plots suggested differing trajectories and magnitudes of θ in all ocean basins and seas. The timing (in years) of these changes in θ depended heavily on which mutation rate and generation time were applied (Fig. 3, Supplementary Fig. S7). Assuming a $\mu = 1.07 \times 10^{-9}$ and $g = 32.45$, the Stairway Plot based upon the Southern Ocean sample suggested a steady and long-term increase in θ from 0.0004 to 0.006, starting 500 kya (Fig. 3, Supplementary Fig. S8). An increase in θ was also apparent in the Stairway Plot inferred from the North Pacific sample. However, the increasing trend in North Pacific sample plateaued at $\theta = 0.003$ approximately 150 kya. In the North Atlantic and Mediterranean Sea samples, θ increased from 150–100 kya, after which it plateaued at $\theta =$

0.003 followed by a sharp decline to $\theta = 0.001$ approximately 25-10 kya. The effective population size in the Gulf of California was comparatively stable during the above periods at $\theta = 0.0006$ but declined to $\theta = 0.0001$ approximately 2.5 kya. Different mutation rates, and (to a lesser extent) generation times, resulted in a significant change in the timing of these demographic changes. For example, assuming a lower mutation rate ($\mu = 1.76 \times 10^{-10}$) and shorter generation time ($g = 25.9$), placed the inferred increases in θ closer to the mid-Pleistocene transition (i.e. 1,250-700 kya; Elderfield et al. 2012).

The deviations from mutation-drift equilibrium inferred as expansions in the Stairway Plot analysis were also apparent as negative values of Tajima's D for all ocean samples except the Gulf of California (Table 1).

Figure 3. Population trajectories, in terms of median θ , inferred from Stairway Plot approach. The left side of the x-axis represent the present, looking back into the past. 95% confidence intervals for each trajectory are shown in Supplementary Fig. S8. LGM, Last Glacial Maximum 27-23 thousand years ago (kya); LIG, Last Interglacial 128-116 kya; MBE, Mid-Brunhes Event 400-300 kya; MPT, Mid-Pleistocene transition 1,250-700 kya.

3.3 Demographic model selection

The optimisation generally led to convergence of model likelihood estimates in the final round of replicates across estimations from models without population size changes (Supplementary Fig. S9). Models constraining inter-oceanic gene flow to zero resulted in the lowest likelihoods across all 2D-JSFS (Supplementary Fig. S9). The models in each 2D-JSFS model selection with highest likelihoods were refitted applying an additional size change step to explore patterns of population size expansion/contraction (as suggested by the Stairway Plots, see above). Models including such size change steps were more likely compared to models with constant population sizes but exhibited “runaway behaviour”, i.e. converging towards the boundary of the prior parameter range (Rosen et al., 2018).

Figure 4. Summary of ten independent $\delta a \delta i$ optimisation runs. The number of time a given model was scoring the highest (in terms of log-likelihood and AIC), are shown for each 2D JSFS analysis; SO-NP, Southern Ocean and North Pacific; AT-NP, North Atlantic and North Pacific; SO-AT, Southern Ocean and North Atlantic; AT-ME, North Atlantic and Mediterranean Sea. Full model specifications tabulated in Supplementary Fig. S1.

The demographic history of Southern Ocean and Northern Hemisphere fin whales was best captured by a two-epoch model with asymmetric gene flow and changes in effective population sizes, (Fig. 4, Tables 2 & 3, Supplementary Fig. S9). In the Southern Ocean and North Pacific comparison, the first epoch spanned the period from 318 kya (95% CI 21,200 - 68 kya) to 172 kya (95% CI 10,980 - 56 kya), which also represented the estimated time of divergence. In case of the North Atlantic and Southern Ocean, the first epoch among started at the estimated timing of divergence at 244 kya (95% CI 15,750 - 77 kya) and lasted until 94 kya (95% CI 9,560 - 51 kya). Timing of events depended on the assumed mutation rate and generation time (Table 3). In the first epoch, migration from the Northern to Southern Hemisphere was higher than in the opposite direction, estimated at 23 (95% CI 0.002-156) North Pacific Nm and 37 (95% CI 0.002-264) North Atlantic Nm into the Southern Ocean, compared to 0.02 (95% CI 0.001-109) and 0.03 (95% CI 0.001-128) Southern Ocean Nm to the North Pacific and North Atlantic, respectively (Table 3). During the second epoch, migration decreased to 0.8 (95% CI 0.1-14) North Pacific and 0.3 (95% CI 0.1-23) North Atlantic Nm to the Southern Ocean. Migration from the Southern to Northern Hemisphere increased slightly, estimated at 0.9 (95% CI 0.005-8) and 0.8 (95% CI 0.006-5) Southern Ocean Nm to the North Pacific and North Atlantic, respectively. Concurrently, the estimates of N_e decreased from 107,000 (95% CI 470 - 257,000) during the first epoch to 45,000 (95% CI 164 - 91,000) during the second epoch in the Southern Ocean. In the Northern Hemisphere, N_e increased from 421 (95% CI 174 - 69,000) to 6,130 (95% CI 1,350 - 13,700) in the North Pacific and from 406 (95% CI 164 - 91,000) to 6,520 (95% CI 1,740 - 13,100) in the North Atlantic. Estimates of N_e assuming alternative mutation rates and generation times are provided in Table 3.

In the Northern Hemisphere, the highest-ranking model was a model with secondary contact and symmetric gene flow between the North Pacific and the North Atlantic (Fig. 4, Tables 2&3, Supplementary Fig. S9). Assuming a value of μ at 1.07×10^{-9} and g at 32.45, the divergence time was estimated at 288 kya (95% CI 610 - 38 kya). The period of isolation was followed by a period of secondary contact from 217 kya (95% CI 387 - 28 kya) to 15 kya (95% CI 110 - 7 kya) during which Nm was estimated at 0.6 (95% CI 0.3 - 35) and 0.8 (95% CI 0.2 - 40) from the North Pacific into the North Atlantic, and vice versa, respectively.

Model residuals were low overall, but suggested that not all features of the empirical SFS were modelled adequately by the simplified demographic histories (Fig. 5). GOF tests revealed that the highest-ranking models were consistent with expectations of simulated data, both in terms of log-likelihood and Pearson's chi-square test statistics (Supplementary Fig. S10).

The maximum likelihood estimations for competing models describing the demographic history between the North Atlantic and Mediterranean Sea were very similar and consequently no single model was selected as the most probable (Fig. 4, Supplementary Fig. S9).

Table 2. Optimised parameters from highest-ranking models, in terms of AIC and log-likelihood, as inferred from 2D and 3D-JSFS analysis in $\delta a \delta i$.

	Model	θ	Optimised parameters
SO-NP	asym_mig_	768.41	$nu_{SOa} = 19.26, nu_{NPa} = 0.089, nu_{SOb} = 8.3, nu_{NPb} = 1.3, m_{12a} = 2.42, m_{21a}$
	twoepoch_size		$= 0.42, m_{12b} = 0.2, m_{21b} = 1.44, T_1 = 0.48, T_2 = 0.56$
AT-NP	sec_contact_sym_	257.4	$nu_{ATa} = 0.039, nu_{NPa} = 35.34, nu_{ATb} = 6.081, nu_{NPb} = 7.35, m = 0.21,$
	mig_size_3_epoch		$T_1 = 0.69, T_2 = 1.96, T_3 = 0.15$
SO-AT	asym_mig_	1528.72	$nu_{SOa} = 11.33, nu_{ATa} = 0.043, nu_{SOb} = 4.83, nu_{ATb} = 0.69, m_{12a} = 6.57, m_{21a}$
	twoepoch_size		$= 1.46, m_{12b} = 0.11, m_{21b} = 2.35, T_1 = 0.24, T_2 = 0.16$
SO-NP-AT	split_symmig_all	1369.36	$nu_{SO} = 3.87, nu_A = 0.022, nu_{NP} = 0.73, nu_{AT} = 0.66, m_A = 2.022,$ $m_{12} = 1.97, m_{23} = 0.20, m_{13} = 1.15, T_1 = 3.60, T_2 = 0.25$

Note. Parameter units are unconverted from $\delta a \delta i$. See model descriptions in Supporting Information Fig. S1 & Fig. S2 for parameter definitions.

Table 3. Conversion of model parameters inferred from the $\delta a \delta i$ 2D-JSFS analyses.

	$\mu = 1.07 \times 10^{-9}$ and $g = 32.45$			$\mu = 1.76 \times 10^{-10}$ and $g = 25.9$			$\mu = 1.07 \times 10^{-9}$ and $g = 39$		
Parameter	Estimate	Lower 95%	Upper 95%	Estimate	Lower 95%	Upper 95%	Estimate	Lower 95%	Upper 95%
Southern Ocean (SO) – North Pacific (NP)									
N_{SOa}	9.12E+04	3.59E+02	7.50E+04	6.96E+05	2.74E+03	5.72E+05	7.60E+04	2.99E+02	6.25E+04
$N_{NP a}$	4.21E+02	1.74E+02	6.93E+04	3.21E+03	1.33E+03	5.28E+05	3.51E+02	1.45E+02	5.77E+04
$N_{SO b}$	3.93E+04	2.00E+04	6.21E+04	3.00E+05	1.53E+05	4.74E+05	3.27E+04	1.67E+04	5.18E+04
$N_{NP b}$	6.13E+03	1.35E+03	1.37E+04	4.68E+04	1.03E+04	1.04E+05	5.11E+03	1.12E+03	1.14E+04
$Nm_{SO \leftarrow NP a}$	2.33E+01	1.97E-03	1.56E+02	2.33E+01	1.97E-03	1.56E+02	2.33E+01	1.97E-03	1.56E+02
$Nm_{NP \leftarrow SO a}$	1.85E-02	1.41E-03	1.09E+02	1.85E-02	1.41E-03	1.09E+02	1.85E-02	1.41E-03	1.09E+02
$Nm_{SO \leftarrow NP b}$	8.25E-01	1.08E-01	1.39E+01	8.25E-01	1.08E-01	1.39E+01	8.25E-01	1.08E-01	1.39E+01
$Nm_{NP \leftarrow SO b}$	9.32E-01	4.58E-03	8.31E+00	9.32E-01	4.58E-03	8.31E+00	9.32E-01	4.58E-03	8.31E+00
T_1	1.46E+05	1.21E+04	1.02E+07	8.90E+05	7.38E+04	6.21E+07	1.46E+05	1.21E+04	1.02E+07
T_2	1.72E+05	5.59E+04	1.10E+07	1.04E+06	3.40E+05	6.68E+07	1.72E+05	5.59E+04	1.10E+07
North Atlantic (AT) – North Pacific									
$N_{AT a}$	6.25E+01	9.45E+01	4.68E+04	4.77E+02	7.21E+02	3.57E+05	5.21E+01	7.87E+01	3.90E+04
$N_{NP a}$	5.60E+04	1.58E+02	4.24E+04	4.27E+05	1.20E+03	3.23E+05	4.67E+04	1.32E+02	3.53E+04
$N_{AT b}$	9.64E+03	5.96E+03	1.39E+04	7.36E+04	4.54E+04	1.06E+05	8.03E+03	4.96E+03	1.15E+04
$N_{NP b}$	1.16E+04	4.85E+03	1.59E+04	8.89E+04	3.70E+04	1.21E+05	9.71E+03	4.04E+03	1.33E+04
$Nm_{AT \leftarrow NP}$	6.47E-01	2.92E-01	3.54E+01	6.47E-01	2.92E-01	3.54E+01	6.47E-01	2.92E-01	3.54E+01
$Nm_{NP \leftarrow AT}$	7.82E-01	2.37E-01	4.06E+01	7.82E-01	2.37E-01	4.06E+01	7.82E-01	2.37E-01	4.06E+01
T_1	7.12E+04	9.65E+03	2.23E+05	4.33E+05	5.87E+04	1.35E+06	7.12E+04	9.65E+03	2.23E+05
T_2	2.02E+05	2.07E+04	2.77E+05	1.23E+06	1.26E+05	1.68E+06	2.02E+05	2.07E+04	2.77E+05
T_3	1.53E+04	7.10E+03	1.10E+05	9.30E+04	4.32E+04	6.66E+05	1.53E+04	7.10E+03	1.10E+05
Southern Ocean – North Atlantic									
$N_{SO a}$	1.07E+05	4.69E+02	2.57E+05	8.14E+05	2.37E+03	1.30E+06	8.89E+04	3.91E+02	2.14E+05
$N_{AT a}$	4.06E+02	1.64E+02	9.11E+04	3.10E+03	8.62E+02	4.62E+05	3.38E+02	1.37E+02	7.59E+04
$N_{SO b}$	4.55E+04	2.21E+04	1.11E+05	3.47E+05	1.12E+05	5.62E+05	3.79E+04	1.84E+04	9.25E+04
$N_{AT b}$	6.52E+03	1.74E+03	1.31E+04	4.97E+04	8.83E+03	6.62E+04	5.43E+03	1.45E+03	1.09E+04
$Nm_{SO \leftarrow AT a}$	3.72E+01	1.60E-03	2.64E+02	3.72E+01	1.60E-03	2.64E+02	3.72E+01	1.60E-03	2.64E+02
$Nm_{AT \leftarrow SO a}$	3.15E-02	4.81E-04	1.28E+02	3.15E-02	4.81E-04	1.28E+02	3.15E-02	4.81E-04	1.28E+02
$Nm_{SO \leftarrow AT b}$	2.68E-01	1.36E-01	2.27E+01	2.68E-01	1.36E-01	2.27E+01	2.68E-01	1.36E-01	2.27E+01
$Nm_{AT \leftarrow SO b}$	8.13E-01	5.69E-03	5.08E+00	8.13E-01	5.69E-03	5.08E+00	8.13E-01	5.69E-03	5.08E+00
T_1	1.50E+05	2.54E+04	6.19E+06	9.09E+05	1.55E+05	3.76E+07	1.50E+05	2.54E+04	6.19E+06
T_2	9.46E+04	5.11E+04	9.56E+06	5.75E+05	3.10E+05	5.81E+07	9.46E+04	5.11E+04	9.56E+06

Note. 95% upper and lower confidence intervals were generated using parametric bootstrap sampling. Three sets of conversions with differing annual, per-site mutation rates (μ) and generation times in years (g) are presented. N_i : effective population size in region i ; $Nm_{i \leftarrow j}$: number of migrants per generation received in region i from j ; T : time in units of years. Subscripts a and b refer to model epoch.

Figure 5. Final $\delta a \delta i$ model results of 2D JSFS analyses. First column shows a simplified schematic summary of the final demographic model retain for the given 2D JSFS. The empirical SFS (column 2) is compared to the modelled SFS fit under the highest-ranking demographic model (column 3). Model residuals are provided in column 4.

The 3D-JSFS-based assessment of the combined North Pacific, Southern Ocean and North Atlantic yielded an order of divergence times between oceanic basin fin whale populations similar to the topology inferred in the SNAPP analysis (Fig. 6). The support was highest for models with consecutive divergence of Southern Ocean fin whales, followed by divergence between North Pacific and North Atlantic fin whales; whereas likelihood was lower for models with simultaneous divergence. The model residuals were higher compared to the fit of the 2D demographic models, likely because of the 3D model was a simplified version of more detailed 2D demographic models. Estimates of Nm were higher from the Northern Hemisphere to the Southern Ocean, at 3.8 North Pacific and 2.2 North Atlantic Nm , compared to the opposite direction, estimated at 0.7 and 0.3 Southern Ocean Nm the North Pacific and North Atlantic, respectively. The lowest migration rates occurred among fin whales from the North Pacific and North Atlantic, estimated at 0.07 Nm .

Figure 6. (A) Maximum clade credibility tree from SNAPP analysis with 95% highest posterior density intervals on divergence time (given in coalescent units). (B) Log-likelihood for each demographic model summarised over ten independent runs. (C) Empirical and model joint site frequency spectra (JSFS) for each pairwise comparison of the 3D JSFS with model residuals.

4. DISCUSSION

Pleistocene climate forcing affected population dynamics in a wide range of terrestrial, freshwater, and marine taxa (Fraser et al., 2012; Hewitt, 2000, 2001; Lorenzen et al., 2011). Individual species' responses depended on a suite of extrinsic and intrinsic factors, influencing the rate at which species could adapt or shift along environmental gradients (Graham & Grimm, 1990). In the marine environment, coastal and polar species were particularly affected by changes in habitat availability due to fluctuations in global sea level, ocean circulation patterns, and the extent of ice caps (Ludt & Rocha, 2015; A. B. Wilson & Eigenmann Veraguth, 2010). This study adds to a growing body of literature highlighting that climate forcing not only affects shallow coastal habitats, but offshore, open ocean ecosystems as well (Cabrera, 2018; Fraser et al., 2012; J. X. Liu et al., 2011; Pastene et al., 2007). In accordance with our hypothesis, fin whale populations underwent marked fluctuations in effective population sizes and population connectivity, coinciding with the Pleistocene glacial-interglacial periods.

We hypothesised that the glacial cycles during the Pleistocene affected connectivity among fin whales in different ocean basins. In the present study, the genetic connectivity among

North Pacific and North Atlantic fin whales was approximated best with a model of secondary contact that occurred between 217 kya (95% CI 387 – 28 kya) to 15 kya (95% CI 110 – 7 kya). Trans-oceanic connectivity was likely only feasible during periods at low Arctic sea-ice cover, such as during the last interglacial period 125 kya (Stirling et al. 1998, Kopp et al. 2009), or earlier interglacial periods (i.e. if the mutation rate was lower than assumed in this assessment). During the last interglacial period (also known as the Eemian stage or Marine Isotope Stage 5e), polar temperatures were 3 - 5°C higher than at present. An influx of warm, salty Atlantic water into the Arctic Ocean reduced the sea-ice cover, at least in the marginal seas (Knies & Vogt, 2003; Otto-Bliesner et al., 2006; Spielhagen et al., 2004). The evidence of reduced sea-ice extent in the Arctic Ocean stems from the analysis of sediment cores leading to the detection of fossilised species that are now limited to subpolar habitats (Brigham-Grette & Hopkins, 1995; Polyak et al., 2010). Trans-oceanic dispersal via the Arctic Ocean during interglacial periods has been proposed for several marine taxa, including sea urchins (Palumbi & Kessing, 1991), gray whales (Alter et al., 2015) as well as bowhead whales (Foote, Kaschner, et al., 2013).

Between the oceanic fin populations in the Northern and Southern Hemisphere, we hypothesised an increase in connectivity during glacial periods, when fin whale habitat was contracted to glacial refugia at low and mid-latitude habitats, and decreased connectivity during interglacial periods, when fin whale habitat ranges shifted to higher latitudes. Instead of the hypothesised synchronous effect in both hemispheres, the two-epoch model with asymmetric gene flow suggested a temporal variation of the response of fin whales between hemispheres. High levels of connectivity (23 - 37 Nm) from the Northern Hemisphere to Southern Hemisphere prior to the last glacial period stood in contrast to reduced gene flow during the second epoch. Asynchronous changes in temperature in both hemispheres could explain the asymmetric gene flow. Although climate changes in the Northern and Southern Hemispheres are closely coupled, there is evidence for asynchronous climate change between hemispheres, related to the thermal bipolar 'see-saw', a signature of variations in ocean heat transport related to shifts in the Atlantic Ocean circulation (Blunier et al., 1998; Pedro et al., 2018; Stocker & Johnsen, 2003). Asymmetric gene flow from the Northern to Southern Hemisphere could also be indicative of expanding populations in the Northern Hemisphere that facilitated dispersal, as changes in N_e and Nm are inherently difficult to separate (Wang & Whitlock, 2003).

We hypothesised that the Pleistocene glacial-interglacial cycles also affected effective population sizes due to changes in habitat availability. We did not model changes in habitat availability (e.g. Varela et al. 2011), but estimated changes in fin whale effective population

sizes in all ocean basins and marginal seas consistent with our expectations of temporal variation of N_e in correlation to climatic oscillations. The Stairway Plot approach revealed population expansions in all oceans, except the Gulf of California, which were also reflected in the negative estimates of Tajima's D . Population expansions appeared to be sequential, starting in the Southern Ocean, followed by the North Pacific, and finally the North Atlantic and Mediterranean Sea. The Northern Hemisphere populations subsequently underwent population contractions, gradually in the North Pacific and abruptly in the North Atlantic and Mediterranean Sea. The specific timing of these demographic events varied greatly depending on the mutation rate. Based on $\mu = 1.76 \times 10^{-10}$ per site per year, the population expansions would have occurred during the mid-Pleistocene transition (1,250 - 700 kya). The mid-Pleistocene transition period was marked by a progressive increase in the amplitude of climate oscillations and was associated with severe cooling events, i.e. full glacial periods, and increased primary productivity on a global-scale (but dependent on regional hydrographic variability; Diester-Haass, Billups, & Lear, 2018; Elderfield et al., 2012; Head & Gibbard, 2015). Conversely, assuming $\mu = 1.07 \times 10^{-9}$ per site per year, the estimated population expansions would have occurred 400 - 150 kya; a period characterised by the mid-Brunhes climatic event, i.e. more glacial conditions (e.g. southward migration of the polar front) in the Northern Hemisphere and more interglacial conditions (e.g. higher sea surface temperatures) in the Southern Hemisphere (Jansen et al., 1986). Assuming a value of μ at 4.5×10^{-10} per site per year and g at 25.9 years, Árnason et al. (2018) found that the ancestral fin whale population increased 300 - 100 kya, followed by a gradual decline after 100 kya. Similarly, Yim et al. (2014) inferred a population increase 200 - 80 kya based on a North Pacific fin whale genome, followed by a gradual decline and a sharp increase ~12 kya, assuming $\mu = 1.07 \times 10^{-9}$ per site per year and g at 25.9 years.

Associating the inferred demographic events with major climatic events remains speculative due to the strong dependence on the assumed mutation rate and generation time to convert estimated temporal units to years (Palsbøll et al., 2013). However, the results of the three combinations of mutation rates and generation times pointed to a dominant expansion event, as inferred from the Stairway Plot approach, prior to the LGM. The population in the Gulf of California was the only population included in this study which did not seem to have undergone a population expansion (e.g. positive Tajima's D). We inferred a decline in genetic diversity ~2.5 kya, which coincides with the divergence time between the Gulf of California and North Pacific reported by Rivera et al. (2019); the part of the demographic history that precedes 2.5 kya may therefore represent the demographic changes of the shared ancestral population (likely the North Pacific). The trajectory of θ inferred among the North Atlantic and Mediterranean Sea fin whales differed from the population

trajectories inferred from coalescent analyses of mitochondrial control region DNA sequences, which reported an exponential increase in the North Atlantic and a constant effective population size followed by a recent decline in the Mediterranean Sea (Chapter 4 in this thesis). Mito-nuclear discordances in demographic inferences have been previously observed and attributed to differences in the evolutionary history of the markers (Hinojosa et al., 2019). However, one important caveat of the Stairway Plot approach is that it does not account for gene flow among populations. When the level of gene flow is high, θ reflects the genetic diversity of the global (as opposed to local) population. Low levels of gene flow among highly differentiated populations increases local θ (from which N_e is inferred). Temporal variations in θ may therefore not directly translate to changes in N_e (Palsbøll et al., 2013). The Stairway Plot approach is known to have limitations on inferring ancient histories and generally performs better in the inference of recent demographic histories (< 30 generations before present; Liu & Fu 2015, Patton et al. 2019). Given these limitations and other potential issues of noise overfitting (Lapierre et al., 2017; Patton et al., 2019), the presented trajectories of θ should be interpreted with caution.

The demographic modelling framework were unable to discern among competing models for the history of the North Atlantic and Mediterranean Sea. The diffusion approximation of $\delta a \delta i$ may not be well suited to resolve demographic histories of populations with moderate gene flow (2-20 females per generation) and generally performs best when migration rates are at the order of $1/N_e$ (Gutenkunst et al., 2009). This problem highlights the importance of multiple independent optimisation runs to assess whether replicates converge on the global optimum or get stuck at local optima (Portik et al., 2017). In our case, complex models with population size changes often struggled to converge on a single log-likelihood. The problem was exacerbated by parameter runaway behaviour, where inferred population sizes degenerated to zero or diverged to infinity, which Rosen et al. (2018) described as pathological behaviour of several demographic inference methods. The behaviour may be failure to include a model close to the “true” population model or by fitting a model to the noise in the data. Considering that equivalent models without the size change step converged well among estimations, the interpretation of results should focus on the common demographic trends among top-scoring models rather than the parameter estimates *per se*.

The study of demographic histories allowed us to contextualise the contemporary global population genetic structure of fin whales. Several lines of evidence point towards the Southern Ocean as origin of Northern Hemisphere populations with the split of Southern Ocean fin whales estimated to precede the population split of Northern Hemisphere

populations. Among ocean basins, the lowest degree of genetic differentiation was estimated among fin whales from the Southern Ocean and North Pacific (Weir's $\theta \sim 0.09$), which coincided with estimated migration rates that were nearly twice as high as migration rates estimated among Southern Ocean and North Atlantic fin whales, where Weir's $\theta \sim 0.19$. The low levels of gene flow, likely limited to the Eemian interglacial, resulted in relatively high levels of differentiation among North Pacific and North Atlantic fin whales (Weir's $\theta \sim 0.21$). These results are congruent with previous estimates of genetic population differentiation among North Pacific, North Atlantic and Southern Hemisphere fin whales using 23 SNPs (Archer et al., 2019). Our topology of population divergence times from SNAPP was in agreement with the recent divergence among North Pacific and Gulf of California fin whales as described by Rivera-León et al. (2019). Similarly, our estimate of Weir's $\theta \sim 0.22$ was comparable to the estimated population differentiation at $F_{ST} \sim 0.2$ between the North Pacific and Gulf of California (employing 18 microsatellite loci; Rivera-León et al. 2019). Overall, the inclusion of Gulf of California samples highlighted the high degree of isolation of this population within the context of the global genetic population structure of fin whales (Bérubé et al., 1998, 2002; Rivera-León et al., 2019). In contrast, the degree of genetic differentiation among North Atlantic and Mediterranean Sea fin whales was low (Weir's $\theta \sim 0.005$), in accordance with previous studies (Bérubé et al. 1998; chapter 4 in this thesis).

Although past Pleistocene climate changes may not serve as perfect analogy to the contemporary global warming (A. J. Davis et al., 1998), it appears likely that ice-free waters in the Arctic Ocean once again may facilitate trans-oceanic connectivity between the North Pacific and North Atlantic. Fin whales are commonly observed at the ice edge. The northernmost fin whale observations reported were at $\sim 70^\circ\text{N}$ and $\sim 80^\circ\text{N}$ in the North Pacific and North Atlantic, respectively (Edwards et al., 2015; Lydersen et al., 2020). McKeon et al. (2016) proposed the fin whale as a species likely to undertake trans-oceanic movements based on its current range in the event of melting sea ice barriers. There is already evidence of poleward expansion of the distribution of fin whales in the North Atlantic (G. E. Davis et al., 2020; Vacqu-Garca et al., 2017).

In summary, the results in the present study suggested that Pleistocene climate forcing led to changes in population connectivity and effective population sizes in a highly dispersive pelagic species, the fin whale. Asynchronous demographic responses among fin whale populations from different ocean basins and marginal seas were likely the result differing climatic and oceanographic contexts between hemispheres. The precise timing of demographic events, and hence the association with specific Pleistocene climatic events, was

subject to uncertainties in assumed nuisance parameters (e.g. mutation rates and generation times), but appear to have occurred prior to the LGM.

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SUPPLEMENTARY MATERIAL

2D demographic inference models

Simple Models

Models with secondary contact or ancient migration

Models with migration occurring at different epochs

Models with a population size change and variable migration

Figure S1. Schematic representation of 2D demographic models (modified from Portik et al., 2017). Abbreviations are as follows: nu1, nu2, effective population sizes under the constant population size model; nu1a, nu2a, effective population sizes before instantaneous size change; nu1b, nu2b, effective population sizes after instantaneous size change; m,

symmetric migration rate between population one and two; m_1 , symmetric migration rate during first epoch; m_2 , symmetric migration rate during second epoch; m_{12} , migration rate from population two to population one; m_{21} , migration rate from population one to population two; m_{12a} and m_{21a} , migrations rates before population size change; m_{12b} and m_{21b} , migration rates after population size change; T_1 , unscaled time between population split and the present or end of first epoch; T_2 , unscaled time of second epoch.

3D Demographic Inference Models

Models with consecutive splitting

Models with simultaneous splitting

Figure S2. Schematic representation of 3D demographic models. Modified from Portik et al., 2017. Abbreviations are as follows: m_A , symmetric ancient migration rate between population one and the ancestral population of 2 and 3; m_{ij} , symmetric migration rate between two populations as indicated by arrows; m_{ij} , migration rate from population j to population i ; $m_{ij,a}$, migrations rates during first epoch; $m_{ij,b}$, migrations rates during second epoch; T_1 -3, unscaled time interval.

Figure S3. Principal Component (PC) Analysis of North Atlantic fin whale samples coloured by library. The plot on the left shows a clear batch effect affecting library ddrad018. Removal of six problem loci removed the batch effect as shown in the right plot. The two red outliers were two samples from the Gulf of St. Lawrence that formed a father-son dyad. The close relatedness likely caused the samples to appear as outliers. Because the samples were collected independently from each other both samples were retained in the analyses.

Figure S4. Comparison of percentage of missing data by ddrad library and sampling region. AT, North Atlantic; GC, Gulf of California; MED, Mediterranean Sea; NP, North Pacific; SO, Southern Ocean.

Figure S5. STRUCTURE analysis log likelihood summaries for cluster solutions one to six.

Figure S6. Principal Component (PC) analysis of North Atlantic (AT) and Mediterranean Sea (MED) fin whale samples, coloured by sample origin.

Figure S7. Stairway Plot trajectories of median θ assuming an annual, per site mutation rate and generation time in years at (A) $\mu = 1.76 \times 10^{-10}$ and $g = 25.9$ and (B) $\mu = 1.07 \times 10^{-9}$ and $g = 39$. LGM, Last Glacial Maximum 27-23 thousand years ago (kya); LIG, Last Interglacial 128-116 kya; MBE, Mid-Brunhes Event 400-300 kya; MPT, Mid-Pleistocene transition 1,250-700 kya.

Figure S8. Stairway Plot trajectories of median θ with 95% confidence intervals. Time units in thousand years ago (kya).

Figure S9. Model summary results of log-likelihood from ten independent runs. Colours correspond to those in Fig 4. Model description given in Fig S1.

Figure S10. Results of Goodness-of-fit (GOF) tests of final models. Empirical log-likelihood and log chi-squared test statistics (blue lines) are compared to a distribution of simulated values to assess GOF.

Table S1. Summary of datasets used in each type of analysis, in terms of sample sizes (N), filtering of 1 SNP per RAD locus, and sampling regions. GC, Gulf of California; NP, North Pacific, SO, Southern Ocean; AT, North Atlantic; MED, Mediterranean Sea.

Analysis	N	1 SNP/RAD locus	Region	Comment
STRUCTURE	172	Yes	all	
fineRADstructure	172	No	all	Additional plot with 10 AT & MED samples for better visualisation (total N = 62)
PCA	172	Yes	all	
FST	172	Yes	all	
SNAPP	16	Yes	GC, NP, SO, AT	
STAIRWAY PLOT	172	Yes	all	
$\delta a \delta i$	22	Yes	NP, SO, AT, MED

CHAPTER

06

6

Synthesis

1. POPULATION BIOLOGY OF FIN WHALES

This thesis aims to provide novel insight into the population biology of fin whales (*Balaenoptera physalus*) by employing a range of different approaches from the fields of population and molecular ecology. Chapter 2 applies mark-recapture models to photo-identification data from the northern Gulf of St. Lawrence, Québec, Canada. In Chapter 3, generalised additive models (GAMs) are employed to quantify the importance of bathymetric, oceanographic and simulated variables in explaining the spatio-temporal distribution of fin whales in the northern Gulf of St. Lawrence. Chapter 4 describes a multi-faceted approach to studying the population genetic structure of North Atlantic and Mediterranean Sea fin whales, using complementary analyses of fixation indices, kinship, and coalescent-based approaches. In Chapter 5, alternative hypotheses of demographic histories are tested to resolve the global genomic diversification process in fin whales. Key results from this thesis include:

- A decline in abundance in the northern Gulf of St. Lawrence from an estimated 335 (95% confidence interval (CI) 321-348) fin whales in 2004-2010 to 291 (95% CI 270-312) in 2010-2016, mirrored by a decline in apparent survival rates (1990-2015) (Chapter 2);
- The identification of two areas with recurrently high relative fin whale abundance in the Jacques-Cartier Passage, with significant overlap with shipping corridors (Chapter 3);
- The description of the population genetic structure of North Atlantic fin whales, characterised by a stepping-stone model with recurrent gene flow among adjacent areas (Chapter 4); and
- The quantification of gene flow and changes in effective population sizes in the context of the Pleistocene glacial cycles as driver of the global genomic diversification process in fin whales (Chapter 5).

A recurrent theme across all chapters is the demographic effects of changing environmental conditions. The demographic histories of fin whale populations, as inferred from coalescent-based (Chapter 4) and diffusion approximation (Chapter 5) approaches, are marked by significant changes in effective population sizes and/or gene flow. There is evidence of secondary contact among fin whales from the North Pacific and North Atlantic and periods of effective population size expansion in the North Pacific, North Atlantic, and

Southern Ocean. Those demographic changes are hypothesised to be a response to altered environmental conditions, e.g. related to the Pleistocene glaciation cycle.

Support for the hypothesis that environmental conditions drive large-scale demographic processes in fin whales can be found in the current response of fin whales to climate change. Over the course of three decades, fin whales shifted their arrival date to the Gulf of St. Lawrence at a rate of one day earlier per year, which correlated with earlier winter sea ice break up and higher sea surface temperatures (Ramp et al., 2015). In the Irminger Sea, one of the North Atlantic feeding grounds with the highest density of fin whales, a significant increase in fin whale numbers after 1995 was linked to bottom-up effects of changing hydrographic conditions mediated by changes in prey availability (Vikingsson et al., 2015). A clear northward shift in fin whale occurrence was also reported in a study on the acoustic occurrence of baleen whales in the western North Atlantic from 2004-2014, with a concomitant decline on the Scotian Shelf and southern New England waters after 2010 (G. E. Davis et al., 2020).

The reported northward shift in distribution of western North Atlantic fin whales coincided temporally with the decline in abundance and apparent survival rates observed in the Gulf of St. Lawrence after 2010 (Chapters 2 & 3). In Chapter 3, I test the hypothesis that the decline in abundance was the result of changing environmental conditions in the Gulf of St. Lawrence from 2007-2013. Previous studies reported major ecosystem shifts over the past decades due to climate change and anthropogenic pressures (Bui et al., 2010; Savenkoff et al., 2007; Simard et al., 2019; Thibodeau et al., 2010). While the results of the species distribution models (SDMs) support the findings of a gradual annual decline in relative fin whale abundance of Chapter 2, the decline cannot be attributed to the proxy oceanographic variables included in the models, i.e. sea surface temperature, chlorophyll *a*, modelled krill biomass, and the North Atlantic Oscillation indices. The small spatial scale of the study site in the northern Gulf of St. Lawrence (ca. 8000 km²) and the limited number of available dynamic proxy and prey variables could be the reason why the model fails to capture the large-scale ecosystem changes responsible for the northward shifts in multiple baleen whale species in the western North Atlantic (G. E. Davis et al., 2020; Simard et al., 2019).

The decline in fin whale abundance in the northern Gulf of St. Lawrence bears similarities with the population trends reported from the Pelagos Sanctuary in the northwestern Mediterranean Sea. In the Pelagos Sanctuary, fin whale abundance was reported to have decline from nearly 1,100 (CV 30%) to around 330 (CV 34%) individuals over two decades (Forcada et al., 1995; Panigada et al., 2017). As was the case in Chapter 2, the reduction in estimated fin whale abundance could be the result of either changes in the patterns of

distribution, possibly driven by a shift in prey availability, or a true decline caused by increased mortality rates (Panigada et al., 2017). Given the relatively small study areas, ca. 8000 km² in the Gulf of St. Lawrence and 87,500 km² in the Pelagos Sanctuary, compared to seasonal fin whale ranging patterns, it is important to gain knowledge on inter-annual variability in distribution patterns in relation to environmental conditions to be able to distinguish between shifts in distribution and true declines.

While there are multiple indications of large-scale ecosystem shifts in the Gulf of St. Lawrence, increased rates of mortality cannot be ruled out as the cause of the observed decline in abundance. From 1994 to 2008, ship collisions were the most common anthropogenic trauma in fin whales in the Gulf of St. Lawrence, accounting for 22% of all strandings (Truchon et al., 2018). In the Jacques Cartier Passage, more than one fifth of all fin whale sightings from 2007-2013 occurred inside the shipping corridor. The risk of mortality due to entanglement in fishing gear has been suggested to be of low levels of concern in fin whales (DFO, 2016). However, a recent study that employed unmanned aerial systems, i.e. drones, to study the scarring rates in fin whales in the Gulf of St. Lawrence estimated that 44-54% of fin whales had previously been entangled in fishing gear, highlighting that this threat had been vastly underestimated in fin whales thus far (Ramp et al., 2021). It is therefore conceivable that anthropogenic mortality contributed, at least partially, to the observed local decline in the northern Gulf of St. Lawrence.

Another consideration when assessing the nature of local declines in abundance is the mode of recruitment into the population and, hence, the demographic connectivity among adjacent populations. Small populations face a higher risk of extinction due to demographic stochasticity, genetic deterioration, social dysfunction, and extrinsic forces (Shaffer, 1981; Simberloff, 1986). When dispersal among populations is limited, i.e. most recruitment is local, reduced birth rates or survivorship cannot be compensated by an influx of individuals from adjacent populations. Previous studies reported evidence in favour of a small, distinct population in the Gulf of St. Lawrence based on rates of whaling stock depletion, acoustic song signatures and heavy metal load (Delarue et al., 2009; Hobbs et al., 2001; Mitchell, 1974; Sergeant, 1977). In terms of population genetic structuring, statistically significant levels of divergence among fin whales from the Gulf of St. Lawrence and Gulf of Maine were reported in Chapter 4 (based on genotypes at 20 microsatellite loci). However, statistically significant differences based on molecular markers do not preclude demographic connectivity among fin whales from adjacent areas.

Demographic connectivity is not assessed explicitly in this thesis and inferences are limited to a few simple observations. Of 41 photographically identified calves in the Gulf of St.

Lawrence, nine individuals were subsequently sighted again on the same feeding ground, in accordance with previous reports of maternally directed feeding site fidelity in fin whales in the Gulf of Maine (Agler et al., 1993). Despite numerous (ca. 180) genetic recaptures of Gulf of St. Lawrence fin whales, no direct recaptures occurred between the Gulf of St. Lawrence and the Gulf of Maine. In Chapter 4, I note that fewer parent-offspring pairs were observed between the Gulf of St. Lawrence and the Gulf of Maine than expected by chance. Overall the population genetic analysis of North Atlantic fin whales suggests a stepping-stone gene flow model with recurrent gene flow among neighbouring regions and increased differentiation with oceanic distance. Such a model would explain the perceived stratification among western North Atlantic whaling stocks (Mitchell, 1974).

2. IMPLICATIONS FOR CONSERVATION BIOLOGY AND FUTURE WORK

The results of this thesis can be employed to inform conservation strategies of fin whales in the North Atlantic and Mediterranean Sea in the context of ongoing anthropogenic pressures and climate change.

The results from Chapter 4 support the notion that the Mediterranean Sea fin whales would benefit from a separate conservation management plan given the limited amount of gene flow between North Atlantic and Mediterranean Sea fin whales (< 1 female per year) and differing demographic histories. There is some evidence indicative of a population decline in the northwestern Mediterranean Sea (Panigada et al., 2011, 2017). The kinship-based analysis and direct recaptures of individuals (Chapter 4) suggests that the range of Mediterranean Sea fin whales includes the Strait of Gibraltar, where previous sightings of fin whales were generally attributed to northeastern North Atlantic fin whales entering or leaving the Mediterranean Sea (Notarbartolo di Sciara et al., 2003). The conclusion that Mediterranean Sea fin whales can range beyond the Strait of Gibraltar is also supported by the detection of Mediterranean acoustic patterns in the seas to the southwest of Portugal (Pereira et al., 2020). As one of the world's busiest waterways, the Strait of Gibraltar should be included as high-risk area for ship strikes in future assessments of collision rates concerning the Mediterranean Sea fin whale subpopulation (Panigada et al., 2006).

The population genetic structure of North Atlantic fin whales, which is consistent with a stepping-stone gene flow model, provides useful information for the definition of stock structure hypotheses as employed in the Revised Management Procedure developed by the Scientific Committee of the International Whaling Commission (IWC) to estimate sustainable catch limits for commercial whaling of baleen whales (IWC, 2017). For instance, the Scientific Committee of the IWC currently only considers the hypothesis of a

single breeding stock in the western North Atlantic (East Canada and West Greenland), whereas the kinship-based analysis from Chapter 4 suggests deviations from a null hypothesis of a single panmictic population in the western North Atlantic, based on samples from the Gulf of Maine and the Gulf of St. Lawrence. Defining management units in populations characterised by isolation-by-distance is inherently difficult; however, establishing multiple management units has been suggested to improve conservation outcomes compared to managing the entire area as single unit for stocks subject to isolation-by-distance (Spies et al., 2015; Taylor & Dizon, 1999).

The estimated decline in local abundance and survival rates in the Gulf of St. Lawrence warrants further investigations into the causes and extent of the population trend. Future mark-recapture and habitat modelling studies in the Gulf of St. Lawrence would benefit from an extended survey coverage to assess the cumulative effects of changing environmental conditions and anthropogenic pressures on the abundance and distribution of cetaceans throughout the Gulf of St. Lawrence. A multi-site approach would also allow the application of alternative mark-recapture models, e.g. using a Bayesian framework (Durban et al., 2005; Nykänen et al., 2020) or other spatially explicit approaches (Borchers & Efford, 2008). Ideally, line transect surveys specifically designed to ensure equal coverage probability in combination with distance sampling would be employed to conduct regular monitoring of cetacean abundance and distribution, as were conducted under the SCANS projects in the European Atlantic shelf waters, for example (Hammond et al., 2013).

To further test to what extent past changes in effective population sizes, as inferred from demographic history modelling, are directly linked to changes in habitat availability, a habitat niche analysis should be conducted (Varela et al., 2011). Changes in suitable habitat under various climate scenarios can serve as a useful factor to explain demographic changes (Foote, Kaschner, et al., 2013; Knowles et al., 2007; Louis et al., 2020); however, predictions based on habitat niche modelling alone may be misleading if inter-specific interactions, e.g. predator-prey relationship or competition, are also altered by future climate change or anthropogenic pressures (A. J. Davis et al., 1998). Assessments should therefore be conducted within a framework that considers the cumulative effect of ecological and anthropogenic factors. As highlighted in Chapter 5, the correlation of past demographic changes with the timing of climatic events is strongly dependent on the assumed nucleotide substitution rate. However, with published mutation rates that differ by an order of magnitude (Dornburg et al., 2012; Yim et al., 2014), it can be difficult to judge which estimate is the best approximation of the true mutation rate. The uncertainty linked to mutation rates is a considerable limitation that should be addressed either by improving the

precision/accuracy of mutation rate estimates or by explicitly accounting for parameter uncertainty in models that currently assume a single point value mutation rate.

Data used in this thesis are biased towards summer feeding aggregations. The winter distribution and location of breeding grounds remain largely unknown for North Atlantic fin whales, although recent studies employing year-round acoustic arrays, satellite tagging, or stable isotope analysis have provided insight into fin whale distribution and movement patterns during winter months (G. E. Davis et al., 2020; Muirhead et al., 2018; Pérez-Jorge et al., 2020; Romagosa et al., 2020; Silva et al., 2019). The distribution of parent-offspring dyads with members sampled at different feeding aggregations in the North Atlantic and Mediterranean Sea suggests that either there is an overlap on breeding grounds of fin whales from different summer feeding aggregations or they represent instances of individuals dispersing to adjacent feeding grounds. Inferences made about the distribution of related individuals would therefore benefit from a better understanding of the winter distribution of fin whales.

3. CONCLUDING COMMENTS

SDMs aim to elucidate habitat relationships based on a set of pre-selected environmental variables (Becker et al., 2020; Redfern et al., 2006). The true factors driving cetacean distributions generally relate to spatio-temporal heterogeneity in prey availability, a variable that is rarely quantified directly *in situ* (Torres et al., 2008). Prey availability is therefore often approximated by alternative variables e.g. available from remote sensing (Becker et al., 2010). Remote sensing data have had a major influence on the development of SDMs, opening new venues to explore habitat use in relation to sea surface temperature, salinity, and chlorophyll *a*. With the advent of powerful ecosystem models, e.g. SEAPODYM, prey data can now be derived for different depth layers while accounting for daily vertical migration patterns of prey species (Lambert et al., 2014). The integration of oceanographic models in cetacean SDMs is a promising step towards a better understanding of geographical differences in habitat relationships of cetaceans (Mannocci et al., 2020). These new datasets will bring about novel challenges, e.g. how to account for uncertainty in modelled prey variables in the final cetacean SDM. In Chapter 3, the SDM with modelled prey data has a lower explanatory performance than the SDM with traditional proxy data, likely because the GAM used to model krill biomass failed to capture the fine-scale dynamic heterogeneity in prey availability required to explain fin whale distribution patterns on a feeding ground. However, as proxies for prey availability become increasingly closer approximations to the “true” value, SDMs for cetaceans and other marine top predators are likely going to improve in their predictive power (Laidre et al., 2010; Lambert et al., 2014).

The spatial structuring of fin whales in the North Atlantic and Mediterranean Sea has previously been described based on differences in stable isotope signatures (Borrell et al., 2012; Das et al., 2017; Gauffier et al., 2020; Giménez et al., 2013; Silva et al., 2019; Vighi et al., 2016), acoustic song patterns (Castellote et al., 2012; Delarue et al., 2009; Pereira et al., 2020), contaminant levels (Fossi et al., 2016; Hobbs et al., 2001; Sanpera et al., 1996), and other non-genetic markers (Vikingsson & Gunnlaugsson, 2006). Often these methods are employed towards the same goal as genetic markers, namely to inform population structure or the delineation of conservation units. However, the inferences drawn from these differing methodologies may not be directly comparable. Ecological markers, such as stable isotope signatures, are influenced by external factors such as the individual's diet or geographical location, whereas genetic markers are fixed at birth independent of the environment. Consequently, it is possible to find a single panmictic genetic breeding population with spatial structuring of stable isotope signatures on distinct feeding grounds. As such, genetic and non-genetic markers are generally used to infer different units of conservation, e.g. evolutionary significant units or ecological management units (Clapham et al., 2008; Giménez et al., 2018; Moritz, 1994; Palsbøll et al., 2007; Waples & Gaggiotti, 2006). The different concepts relate to the ecological and evolutionary paradigms proposed to define 'populations' (Waples & Gaggiotti, 2006), as discussed in Chapter 1.

Clapham et al. (2008) proposed that evidence from non-genetic techniques should be integrated with genetic analyses to inform the delineation of ecologically meaningful management units. The population genetic structuring in the North Atlantic and Mediterranean Sea fin whales (Chapter 4) is largely concordant with previous inferences drawn from ecological markers. Despite overall low levels of genetic divergence in the eastern North Atlantic based on fixation indices, genetic relatedness (from kinship-based analysis) was significantly higher within regions, indicative of demographic discontinuities. In comparison, Gauffier et al. (2020) found limited isotopic niche overlap among fin whales from Iceland, northwest Spain, the Azores archipelago, and the Strait of Gibraltar. Similarly, isotopic profiles indicated an ecological differentiation of fin whales from Irish/UK waters compared to those sampled in the Bay of Biscay and the Mediterranean Sea (Das et al., 2017; C. Ryan et al., 2013). Estimates of Weir's θ based on mitochondrial control region DNA sequences suggested larger-than-zero degrees of divergence among fin whales from Ireland and adjacent areas, except for northwest Spain (Chapter 4). Niche variation owing to individual differences in foraging ecology has been proposed as driver of evolutionary divergence in cetaceans (Foote, Newton, et al., 2013; Louis et al., 2014). A full integration of genetic and non-genetic inferences on fin whale population structuring could therefore

provide a more complete picture on the link between genetic clustering and ecological niches.

CHAPTER

07

A

References

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Authors and affiliations

About the author

Acknowledgements

References

- Agapow, P.-M., & Burt, A. (2001). Indices of multilocus linkage disequilibrium. *Molecular Ecology Notes*, 1, 101–102. <https://doi.org/10.1046/j.1471-8278.2000.00014.x>
- Agler, B. A., Beard, J., Bowman, R., Corbett, H., Frohock, S. E., Hawvermale, M., Katona, S. K., Sadove, S., & Seipt, I. E. (1990). Fin Whale (*Balaenoptera physalus*) Photographic Identification: Methodology and Preliminary Results from the Western North Atlantic. *Reports of the International Whaling Commission (Special Issue)*, 12, 349–356. <https://doi.org/10.1098/rsbl.2010.0638>
- Agler, B. A., Schooley, R. L., Frohock, S. E., Katona, S. K., & Seipt, I. E. (1993). Reproduction of photographically identified fin whales, *Balaenoptera physalus*, from the Gulf of Maine. *Journal of Mammalogy*, 74(3), 577–587. <https://doi.org/10.2307/1382276>
- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (Eds) *Proc 2nd Int Symp Information Theory*. Akademiai Kiado, Budapest, 267–281.
- Alter, S. E., Meyer, M., Post, K., Czechowski, P., Gravlund, P., Gaines, C., Rosenbaum, H. C., Kaschner, K., Turvey, S. T., Van Der Plicht, J., Shapiro, B., & Hofreiter, M. (2015). Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100. *Molecular Ecology*, 24(7), 1510–1522. <https://doi.org/10.1111/mec.13121>
- Alter, S. E., & Palumbi, S. R. (2009). Comparing evolutionary patterns and variability in the mitochondrial control region and cytochrome b in three species of baleen whales. *Journal of Molecular Evolution*, 68(1), 97–111. <https://doi.org/10.1007/s00239-008-9193-2>
- Altukhov, A. V., Andrews, R. D., Calkins, D. G., Gelatt, T. S., Gurarie, E. D., Loughlin, T. R., Mamaev, E. G., Nikulin, V. S., Permyakov, P. A., Ryazanov, S. D., Vertyankin, V. V., & Burkanov, V. N. (2015). Age specific survival rates of steller sea lions at rookeries with divergent population trends in the Russian far east. *PLoS ONE*, 10(5), e0127292. <https://doi.org/10.1371/journal.pone.0127292>
- Anderson, D., Burnham, K., & White, G. (1994). AIC model selection in overdispersed capture-recapture data. *Ecology*, 75(6), 1780–1793. <http://www.esajournals.org/doi/abs/10.2307/1939637>
- Anderson, J. B., Shipp, S. S., Lowe, A. L., Wellner, J. S., & Mosola, A. B. (2002). The Antarctic Ice Sheet during the Last Glacial Maximum and its subsequent retreat history: A review. *Quaternary Science Reviews*, 21(1–3), 49–70. [https://doi.org/10.1016/S0277-3791\(01\)00083-X](https://doi.org/10.1016/S0277-3791(01)00083-X)
- Archer, F. I., Adams, P. E., & Schneiders, B. B. (2017). STRATAG: An R package for manipulating, summarizing and analysing population genetic data. *Molecular Ecology Resources*, 17(1), 5–11. <https://doi.org/10.1111/1755-0998.12559>
- Archer, F. I., Brownell, R. L., Hancock-Hanser, B. L., Morin, P. A., Robertson, K. M., Sherman, K. K., Calambokidis, J., Urbán R, J., Rosel, P. E., Mizroch, S. A., Panigada, S., & Taylor, B. L. (2019).

- Revision of fin whale *Balaenoptera physalus* (Linnaeus, 1758) subspecies using genetics. *Journal of Mammalogy*, 100(5), 1653–1670. <https://doi.org/10.1093/jmammal/gyz121>
- Árnason, Ú., Gullberg, A., & Widegren, B. (1993). Cetacean mitochondrial DNA control region: Sequences of all extant baleen whales and two sperm whale species. *Molecular Biology and Evolution*, 10(5), 960–970.
- Árnason, Ú., Lammers, F., Kumar, V., Nilsson, M. A., & Janke, A. (2018). Whole-genome sequencing of the blue whale and other rorquals finds signatures for introgressive gene flow. *Science Advances*, 4, eaap9873. <https://doi.org/10.1126/sciadv.aap9873>
- Arso Civil, M., Cheney, B., Quick, N. J., Thompson, P. M., & Hammond, P. S. (2017). A new approach to estimate fecundity rate from inter-birth intervals. *Ecosphere*, 8(4), e01796. <https://doi.org/10.1002/ecs2.1796>
- Avice, J. C. (2000). *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.
- Azzellino, A., Panigada, S., Lanfredi, C., Zanardelli, M., Airoidi, S., & Notarbartolo di Sciara, G. (2012). Predictive habitat models for managing marine areas: Spatial and temporal distribution of marine mammals within the Pelagos Sanctuary (Northwestern Mediterranean Sea). *Ocean and Coastal Management*, 67, 63–74. <https://doi.org/10.1016/j.ocecoaman.2012.05.024>
- Baines, M., Reichelt, M., & Griffin, D. (2017). An autumn aggregation of fin (*Balaenoptera physalus*) and blue whales (*B. musculus*) in the Porcupine Seabight, southwest of Ireland. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141, 168–177. <https://doi.org/10.1016/j.dsr2.2017.03.007>
- Baker, C. S., Perry, A., Bannister, J. L., Weinrich, M. T., Abernethy, R. B., Calambokidis, J., Lien, J., Lambertsen, R. H., Urbán Ramírez, J., Vasquez, O., Clapham, P. J., Alling, A., O'Brien, S. J., & Palumbi, S. R. (1993). Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proceedings of the National Academy of Sciences of the United States of America*, 90(17), 8239–8243. <https://doi.org/10.1073/pnas.90.17.8239>
- Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the “predator pit” topographies. *Progress in Oceanography*, 68(2–4), 271–288. <https://doi.org/10.1016/j.pocean.2006.02.004>
- Bargelloni, L., Alarcon, J. A., Alvarez, M. C., Penzo, E., Magoulas, A., Reis, C., & Patarnello, T. (2003). Discord in the family Sparidae (Teleostei): Divergent phylogeographical patterns across the Atlantic-Mediterranean divide. *Journal of Evolutionary Biology*, 16(6), 1149–1158. <https://doi.org/10.1046/j.1420-9101.2003.00620.x>
- Barker, R. J. (1997). Joint Modeling of Live-Recapture, Tag-Resight, and Tag-Recovery Data. *Biometrics*, 53(2), 666–677.
- Barratt, C. D., Bwong, B. A., Jehle, R., Liedtke, H. C., Nagel, P., Onstein, R. E., Portik, D. M., Streicher, J. W., & Loader, S. P. (2018). Vanishing refuge? Testing the forest refuge hypothesis in coastal East Africa using genome-wide sequence data for seven amphibians. *Molecular Ecology*, 27(21),

- 4289–4308. <https://doi.org/10.1111/mec.14862>
- Becker, E. A., Carretta, J. V., Forney, K. A., Barlow, J., Brodie, S., Hoopes, R., Jacox, M. G., Maxwell, S. M., Redfern, J. V., Sisson, N. B., Welch, H., & Hazen, E. L. (2020). Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. *Ecology and Evolution*, 10(12), 5759–5784. <https://doi.org/10.1002/ece3.6316>
- Becker, E. A., Foley, D. G., Forney, K. A., Barlow, J., Redfern, J. V., & Gentemann, C. L. (2012). Forecasting cetacean abundance patterns to enhance management decisions. *Endangered Species Research*, 16(2), 97–112. <https://doi.org/10.3354/esr00390>
- Becker, E. A., Forney, K. A., Ferguson, M. C., Foley, D. G., Smith, R. C., Barlow, J., & Redfern, J. V. (2010). Comparing California current cetacean-habitat models developed using in situ and remotely sensed sea surface temperature data. *Marine Ecology Progress Series*, 413, 163–183. <https://doi.org/10.3354/meps08696>
- Becker, E. A., Forney, K. A., Fiedler, P. C., Barlow, J., Chivers, S. J., Edwards, C. A., Moore, A. M., & Redfern, J. V. (2016). Moving towards dynamic ocean management: How well do modeled ocean products predict species distributions? *Remote Sensing*, 8(2), 1–26. <https://doi.org/10.3390/rs8020149>
- Beerli, P. (2004). Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. *Molecular Ecology*, 13(4), 827–836. <https://doi.org/10.1111/j.1365-294X.2004.02101.x>
- Beerli, P., & Felsenstein, J. (2001). Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences of the United States of America*, 98(8), 4563–4568. <https://doi.org/10.1073/pnas.081068098>
- Beichman, A. C., Huerta-Sanchez, E., & Lohmueller, K. E. (2018). Using genomic data to infer historic population dynamics of nonmodel organisms. *Annual Review of Ecology, Evolution, and Systematics*, 49, 433–456. <https://doi.org/10.1146/annurev-ecolsys-110617-062431>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate : a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300.
- Bentaleb, I., Martin, C., Vrac, M., Mate, B., Mayzaud, P., Siret, D., De Stephanis, R., & Guinet, C. (2011). Foraging ecology of Mediterranean fin whales in a changing environment elucidated by satellite tracking and baleen plate stable isotopes. *Marine Ecology Progress Series*, 438, 285–302. <https://doi.org/10.3354/meps09269>
- Benton, T. G., & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *TREE*, 14(12), 467–471.
- Bérubé, M., Aguilar, A., Dendanto, D., Larsen, F., Notarbartolo di Sciara, G., Sears, R., Sigurjónsson, J., Urban-R, J., & Palsbøll, P. J. (1998). Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* (Linnaeus 1758):

- analysis of mitochondrial and nuclear loci. *Molecular Ecology*, 7(5), 585–599. <http://www.ncbi.nlm.nih.gov/pubmed/9633102>
- Bérubé, M., Berchok, C., & Sears, R. (2001). Observation of a male-biased sex ratio in the Gulf of St. Lawrence fin whales (*Balaenoptera physalus*): Temporal, geographical, or group structure segregation? *Marine Mammal Science*, 17(2), 371–381. <https://doi.org/10.1111/j.1748-7692.2001.tb01279.x>
- Bérubé, M., Daniélsdóttir, A. K., Aguilar, A., Árnason, Ú., Bloch, D., Dendanto, D., Larsen, F., Lien, J., Notarbartolo di Sciarra, G., Sears, R., Sigurjónsson, J., Urban-R., J., Witting, L., Øien, N., Víkingsson, G. A., & Palsbøll, P. J. (2006). High rates of gene flow among geographic locations in North Atlantic fin whales (*Balaenoptera physalus*). *Paper Presented to the IWC Scientific Committee, May 2006, St. Kitts and Nevis, West Indies (Unpublished)*, SC/58/PFI6, 17pp.
- Bérubé, M., Jørgensen, H., McEwing, R., & Palsbøll, P. J. (2000). Polymorphic di-nucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. *Molecular Ecology*, 9(12), 2181–2183. <https://doi.org/10.1046/j.1365-294X.2000.01053.x>
- Bérubé, M., & Palsbøll, P. J. (1996a). Erratum of identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology*, 5, 602.
- Bérubé, M., & Palsbøll, P. J. (1996b). Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology*, 5, 283–287. <https://doi.org/10.1046/j.1365-294X.1996.00072.x>
- Bérubé, M., Rew, M. B., Skaug, H., Jørgensen, H., Robbins, J., Best, P., Sears, R., & Palsbøll, P. J. (2005). Polymorphic microsatellite loci isolated from humpback whale, *Megaptera novaeangliae* and fin whale, *Balaenoptera physalus*. *Conservation Genetics*, 6(4), 631–636. <https://doi.org/10.1007/s10592-005-9017-5>
- Bérubé, M., Urbán, J., Dizon, A. E., Brownell, R. L., & Palsbøll, P. J. (2002). Genetic identification of a small and highly isolated population of fin whales (*Balaenoptera physalus*) in the Sea of Cortez, Mexico. *Conservation Genetics*, 3(2), 183–190. <https://doi.org/10.1023/a:1015224730394>
- Blunier, T., Chappellaz, J., Schwander, J., Dällenbach, A., Stauffer, B., Stocker, T., Raynaud, D., Jouzel, J., Clausen, H., Hammer, C., & Johnsen, S. J. (1998). Asynchrony of Antarctic and Greenland climate change during the last glacial period. *Nature*, 394, 739–743.
- Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64(2), 377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>
- Borregaard, M. K., & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *Quarterly Review of Biology*, 85(1), 3–25. <https://doi.org/10.1086/650265>
- Borrell, A., Abad-Oliva, N., Gómez-Campos, E., Giménez, J., & Aguilar, A. (2012). Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Communications in Mass Spectrometry: RCM*, 26(14), 1596–1602.

<https://doi.org/10.1002/rcm.6267>

- Borrell, A., Saiz, L., Víkingsson, G. A., Gauffier, P., López Fernández, A., & Aguilar, A. (2018). Fin whales as bioindicators of multi-decadal change in carbon and oxygen stable isotope shifts in the North Atlantic. *Marine Environmental Research*, 138, 129–134. <https://doi.org/10.1016/j.marenvres.2018.04.014>
- Bossart, J. L., & Prowell, D. P. (1998). Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends in Ecology and Evolution*, 13(5), 202–206.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., Suchard, M. A., Rambaut, A., & Drummond, A. J. (2014). BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Computational Biology*, 10(4), 1–6. <https://doi.org/10.1371/journal.pcbi.1003537>
- Bourque, M. C., Kelley, D. E., Bourque, M., & Kelley, D. E. (1995). Evidence of wind-driven upwelling in Jacques-Cartier Strait. *Atmosphere-Ocean*, 33(4), 621–637. <https://doi.org/10.1080/07055900.1995.9649548>
- Box, G. E. P. (1979). Robustness in the Strategy of Scientific Model Building. In *In Robustness in Statistics* (Launer, R.L. and Wilkinson, G.N., eds), Academic Press. ACADEMIC PRESS, INC. <https://doi.org/10.1016/b978-0-12-438150-6.50018-2>
- Boyce, M. S. (1992). Population Viability Analysis. *Annual Review of Ecology and Systematics*, 23, 481–506.
- Bradshaw, C. J. A., Barker, R. J., Harcourt, R. G., & Davis, L. S. (2003). Estimating Survival and Capture Probability of Fur Seal Pups Using Multistate Mark–Recapture Models. *Journal of Mammalogy*, 84(1), 65–80. [https://doi.org/10.1644/1545-1542\(2003\)084<0065:ESACPO>2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084<0065:ESACPO>2.0.CO;2)
- Branch, T. (2007). Abundance of Antarctic blue whales south of 60°S from three completed circumpolar sets of surveys. *Journal of Cetacean Research and Management*, 9(3), 253–262.
- Brassel, K. E., & Reif, D. (1979). Procedure to Generate Thiessen Polygons. *Geographical Analysis*, 11(3), 289–303.
- Briggs, J. C. (1970). A faunal history of the North Atlantic Ocean. *Systematic Biology*, 19(1), 9–34. <https://doi.org/10.1093/sysbio/19.1.19>
- Brigham-Grette, J., & Hopkins, D. M. (1995). Emergent marine record and paleoclimate of the last interglaciation along the northwest Alaskan coast. *Quaternary Research*, 43, 159–173.
- Brosset, P., Doniol-Valcroze, T., Swain, D. P., Lehoux, C., Van Beveren, E., Mbaye, B. C., Emond, K., & Plourde, S. (2018). Environmental variability controls recruitment but with different drivers among spawning components in Gulf of St. Lawrence herring stocks. *Fisheries Oceanography*, 28(1), 1–17. <https://doi.org/10.1111/fog.12272>
- Bryant, D., Bouckaert, R., Felsenstein, J., Rosenberg, N. A., & Roychoudhury, A. (2012). Inferring species trees directly from biallelic genetic markers: Bypassing gene trees in a full coalescent analysis. *Molecular Biology and Evolution*, 29(8), 1917–1932.

- <https://doi.org/10.1093/molbev/mss086>
- Bui, A. O. V., Ouellet, P., Castonguay, M., & Brêthes, J. C. (2010). Ichthyoplankton community structure in the northwest Gulf of St. Lawrence (Canada): Past and present. *Marine Ecology Progress Series*, 412, 189–205. <https://doi.org/10.3354/meps08687>
- Burger, R., & Lynch, M. (1995). Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution*, 49(1), 151–163.
- Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodal inference: a practical information-theoretic approach. *New York: Springer-Verlag*.
- Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., Brown, C., Bruno, J. F., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F. B., Sydeman, W. J., & Richardson, A. J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334(6056), 652–655. <https://doi.org/10.1126/science.1210288>
- Cabrera, A. A. (2018). *Evolutionary Ecology of Marine Mammals. PhD Thesis, University of Groningen, Groningen, The Netherlands*.
- Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., & Hammond, P. S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15(5), 495–521. <https://doi.org/10.1002/aqc.689>
- Cao, Y., Bark, A., & Williams, W. (1997). A comparison of clustering methods for river benthic community analysis. *Hydrobiologica*, 347, 25–40. <https://doi.org/10.1023/A:1002938721135>
- Carroll, E. L., Alderman, R., Bannister, J. L., Bérubé, M., Best, P. B., Boren, L., Baker, C. S., Constantine, R., Findlay, K., Harcourt, R., Lemaire, L., Palsbøll, P. J., Patenaude, N. J., Rowntree, V. J., Seger, J., Steel, D., Valenzuela, L. O., Watson, M., & Gaggiotti, O. E. (2018). Incorporating non-equilibrium dynamics into demographic history inferences of a migratory marine species. *Heredity*, 122, 53–68. <https://doi.org/10.1038/s41437-018-0077-y>
- Castellote, M., Clark, C. W., & Lammers, M. O. (2012). Fin whale (*Balaenoptera physalus*) population identity in the western Mediterranean Sea. *Marine Mammal Science*, 28(2), 325–344. <https://doi.org/10.1111/j.1748-7692.2011.00491.x>
- Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: Building and genotyping loci de novo from short-read sequences. *G3: Genes, Genomes, Genetics*, 1(3), 171–182. <https://doi.org/10.1534/g3.111.000240>
- Charlesworth, B. (2015). What use is population genetics? *Genetics*, 200(3), 667–669. <https://doi.org/10.1534/genetics.115.178426>
- Charlesworth, B., & Charlesworth, D. (2017). Population genetics from 1966 to 2016. *Heredity*, 118(1), 2–9. <https://doi.org/10.1038/hdy.2016.55>

- Cheney, B., Corkrey, R., Durban, J. W., Grellier, K., Hammond, P. S., Islas-Villanueva, V., Janik, V. M., Lusseau, S. M., Parsons, K. M., Quick, N. J., Wilson, B., & Thompson, P. M. (2014). Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status. *Global Ecology and Conservation*, 2, 118–128. <https://doi.org/10.1016/j.gecco.2014.08.010>
- Cheney, B., Thompson, P. M., Ingram, S. N., Hammond, P. S., Stevick, P. T., Durban, J. W., Culloch, R. M., Elwen, S. H., Mandleberg, L., Janik, V. M., Quick, N. J., Islas-Villanueva, V., Robinson, K. P., Costa, M., Eisefeld, S. M., Walters, A., Phillips, C., Weir, C. R., Evans, P. G. H., ... Wilson, B. (2013). Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. *Mammal Review*, 43(1), 71–88. <https://doi.org/10.1111/j.1365-2907.2011.00208.x>
- Choquet, R., Lebreton, A., Gimenez, J., & Pradel, R. (2005). U-CARE 2.2 User's Manual. *CEFE, Montpellier, France (Http://Ftp.Cefe.Cnrs.Fr/Biom/Soft-CR/)*, 53pp.
- Clapham, P. J., Aguilar, A., & Hatch, L. T. (2008). Determining spatial and temporal scales for management: lessons from whaling. *Marine Mammal Science*, 24(1), 183–201. <https://doi.org/10.1111/j.1748-7692.2007.00175.x>
- Clapham, P. J., & Seipt, I. E. (1991). Resightings of independent fin whales, *Balaenoptera physalus*, on maternal summer ranges. *Journal of Mammalogy*, 72(4), 788–790. <https://doi.org/10.1126/science.95.2469.427-b>
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., & McCabe, A. M. (2009). The Last Glacial Maximum. *Science (New York, N.Y.)*, 325(5941), 710–714. <https://doi.org/10.1126/science.1172873>
- Clarke, R. (2004). Pygmy fin whales. *Marine Mammal Science*, 20(2), 329–334. <https://doi.org/10.1111/j.1748-7692.2004.tb01161.x>
- Coakes, A., Gowans, S., Simard, P., Giard, J., Vashro, C., & Sears, R. (2005). Photographic identification of fin whales (*Balaenoptera physalus*) off the Atlantic coast of Nova Scotia, Canada. *Marine Mammal Science*, 21(2), 323–326. <https://doi.org/10.1111/j.1748-7692.2005.tb01232.x>
- Cole, L. C. (1957). Sketches of general and comparative demography. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 1–15. <https://doi.org/10.1101/SQB.1957.022.01.004>
- Cole, T. L., Dutoit, L., Dussex, N., Hart, T., Alexander, A., Younger, J. L., Clucas, G. V., Frugone, M. J., Cherel, Y., Cuthbert, R., Ellenberg, U., Fiddaman, S. R., Hiscock, J., Houston, D., Jouventin, P., Mattern, T., Miller, G., Miskelly, C., Nolan, P., ... Waters, J. M. (2019). Receding ice drove parallel expansions in Southern Ocean penguins. *Proceedings of the National Academy of Sciences of the United States of America*, 116(52), 26690–26696. <https://doi.org/10.1073/pnas.1904048116>
- Committee on Taxonomy. (2020). *List of marine mammal species and subspecies*. Society for Marine Mammalogy. Available at: [Www.Marinemammalscience.Org](http://www.Marinemammalscience.Org). (Accessed: 27 June 2020).

- Cooke, J. G. (2018). *Balaenoptera physalus* (Fin whale). *The IUCN Red List of Threatened Species 2018: E.T2478A50349982*. https://doi.org/10.1007/978-1-4612-9824-3_33
- Costa, K. M., McManus, J. F., & Anderson, R. F. (2018). Paleoproductivity and Stratification Across the Subarctic Pacific Over Glacial-Interglacial Cycles. *Paleoceanography and Paleoclimatology*, 33(9), 914–933. <https://doi.org/10.1029/2018PA003363>
- Cotté, C., Guinet, C., Taupier-Letage, I., Mate, B., & Petiau, E. (2009). Scale-dependent habitat use by a large free-ranging predator, the Mediterranean fin whale. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(5), 801–811. <https://doi.org/10.1016/j.dsr.2008.12.008>
- Cotté, C., & Simard, Y. (2005). Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. *Marine Ecology Progress Series*, 288, 199–210. <https://doi.org/10.3354/meps288199>
- Crandall, E. D., Toonen, R. J., & Selkoe, K. A. (2019). A coalescent sampler successfully detects biologically meaningful population structure overlooked by F-statistics. *Evolutionary Applications*, 12(2), 255–265. <https://doi.org/10.1111/eva.12712>
- Croll, D., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R., & Tershy, B. (2005). From wind to whales: trophic links in a coastal upwelling system. *Marine Ecology Progress Series*, 289, 117–130. <https://doi.org/10.3354/meps289117>
- Crowder, L., & Crouse, D. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications*, 4(3), 437–445. <http://www.esajournals.org/doi/abs/10.2307/1941948>
- Curtis, C., Stewart, B. S., & Karl, S. A. (2009). Pleistocene population expansions of Antarctic seals. *Molecular Ecology*, 18(10), 2112–2121. <https://doi.org/10.1111/j.1365-294X.2009.04166.x>
- Cury, P., Boyd, I., Bonhommeau, S., Anker-Nilssen, T., Crawford, R., Furness, R. W., Mills, J., Murphy, E., Österblom, H., Paleczny, M., Piatt, J., Roux, J., Shannon, L., & Sydeman, W. J. (2011). Global seabird response to forage fish depletion - One third for the birds. *Science*, 334(6063), 1703–1706. <https://doi.org/10.1126/science.202625>
- Daly, R., Smale, M. J., Cowley, P. D., & Froneman, P. W. (2014). Residency patterns and migration dynamics of adult bull sharks (*Carcharhinus leucas*) on the east coast of Southern Africa. *PLoS ONE*, 9(10), e109357. <https://doi.org/10.1371/journal.pone.0109357>
- Das, K., Holleville, O., Ryan, C., Berrow, S., Gilles, A., Ody, D., & Michel, L. N. (2017). Isotopic niches of fin whales from the Mediterranean Sea and the Celtic Sea (North Atlantic). *Marine Environmental Research*, 127, 75–83. <https://doi.org/10.1016/j.marenvres.2017.03.009>
- Davis, A. J., Jenkinson, L., Lawton, J. H., Shorrocks, B., & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.
- Davis, G. E., Baumgartner, M. F., Corkeron, P. J., Bell, J., Berchok, C., Bonnell, J. M., Thornton, J. B., Brault, S., Buchanan, G. A., Cholewiak, D., Clark, C. W., Delarue, J., Hatch, L. T., Klinck, H., Kraus, S. D., Martin, B., Mellinger, D. K., Moors-Murphy, H., Nieukirk, S. L., ... Van Pa. (2020).

- Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. *Global Change Biology*. <https://doi.org/10.1111/GCB.15191>
- Dawson, M. N., & Hamner, W. M. (2008). A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *Journal of the Royal Society Interface*, 5(19), 135–150. <https://doi.org/10.1098/rsif.2007.1089>
- De Bruyn, M., Hall, B. L., Chauke, L. F., Baroni, C., Koch, P. L., & Hoelzel, A. R. (2009). Rapid response of a marine mammal species to holocene climate and habitat change. *PLoS Genetics*, 5(7), e1000554. <https://doi.org/10.1371/journal.pgen.1000554>
- de Vernal, A., Rosell-Melé, A., Kucera, M., Hillaire-Marcel, C., Eynaud, F., Weinelt, M., Dokken, T., & Kageyama, M. (2006). Comparing proxies for the reconstruction of LGM sea-surface conditions in the northern North Atlantic. *Quaternary Science Reviews*, 25(21–22), 2820–2834. <https://doi.org/10.1016/j.quascirev.2006.06.006>
- Delarue, J., Todd, S. K., Van Parijs, S. M., & Di Iorio, L. (2009). Geographic variation in Northwest Atlantic fin whale (*Balaenoptera physalus*) song: implications for stock structure assessment. *The Journal of the Acoustical Society of America*, 125(3), 1774–1782. <https://doi.org/10.1121/1.3068454>
- DFO. (2016). Management Plan for the fin whale (*Balaenoptera physalus*), Atlantic population in Canada [proposed]. *Species at Risk Act Management Plan Series*, DFO, Ottawa, iv, 37pp.
- Diester-Haass, L., Billups, K., & Lear, C. (2018). Productivity changes across the mid-Pleistocene climate transition. *Earth-Science Reviews*, 179, 372–391. <https://doi.org/10.1016/j.earscirev.2018.02.016>
- Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillett, B. J., & Ovenden, J. R. (2014). NeEstimator v2: Re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. *Molecular Ecology Resources*, 14(1), 209–214. <https://doi.org/10.1111/1755-0998.12157>
- Doniol-Valcroze, T., Berteaux, D., Larouche, P., & Sears, R. (2007). Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series*, 335, 207–216. <https://doi.org/10.3354/meps335207>
- Dornburg, A., Brandley, M. C., McGowen, M. R., & Near, T. J. (2012). Relaxed clocks and inferences of heterogeneous patterns of nucleotide substitution and divergence time estimates across whales and dolphins (Mammalia: Cetacea). *Molecular Biology and Evolution*, 29(2), 721–736. <https://doi.org/10.1093/molbev/msr228>
- Douglas, A. B., Calambokidis, J., Raverty, S., Jeffries, S. J., Lambourn, D. M., & Norman, S. A. (2008). Incidence of ship strikes of large whales in Washington State. *Journal of the Marine Biological Association of the United Kingdom*, 88(06), 1121–1132. <https://doi.org/10.1017/S0025315408000295>
- Drouot, V., Bérubé, M., Gannier, A., Goold, J. C., Reid, R. J., & Palsbøll, P. J. (2004). A note on genetic

- isolation of Mediterranean sperm whales (*Physeter macrocephalus*) suggested by mitochondrial DNA. *Journal of Cetacean Research and Management*, 6(1), 29–32.
- Durban, J. W., Elston, D. A., Ellifrit, D. K., Dickson, E., Hammond, P. S., & Thompson, P. M. (2005). Multisite mark-recapture for cetaceans: Population estimates with Bayesian model averaging. *Marine Mammal Science*, 21(1), 80–92. <https://doi.org/10.1111/j.1748-7692.2005.tb01209.x>
- Edwards, E. F., Hall, C., Moore, T. J., Sheredy, C., & Redfern, J. V. (2015). Global distribution of fin whales *Balaenoptera physalus* in the post-whaling era (1980–2012). *Mammal Review*, 45(4), 197–214. <https://doi.org/10.1111/mam.12048>
- El-Sabh, M. (1976). Surface Circulation Pattern in the Gulf of St. Lawrence. *Journal of Fishery Research Board of Canada*, 33(1971), 124–138.
- Elderfield, H., Ferretti, P., Greaves, M., Crowhurst, S. J., McCave, I. N., Hodell, D. a, & Piotrowski, A. M. (2012). Evolution of ocean temperature and ice volume through the mid-Pleistocene climate transition. *Science*, 337, 704–709. <https://doi.org/10.1594/PANGAEA.786205>
- Escoda, L., Fernández-González, Á., & Castresana, J. (2019). Quantitative analysis of connectivity in populations of a semi-aquatic mammal using kinship categories and network assortativity. *Molecular Ecology Resources*, 19(2), 310–326. <https://doi.org/10.1111/1755-0998.12967>
- Escoda, L., González-Esteban, J., Gómez, A., & Castresana, J. (2017). Using relatedness networks to infer contemporary dispersal: Application to the endangered mammal *Galemys pyrenaicus*. *Molecular Ecology*, 26(13), 3343–3357. <https://doi.org/10.1111/mec.14133>
- Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, 14(8), 2611–2620. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Excoffier, L., Foll, M., & Petit, R. J. (2009). Genetic Consequences of Range Expansions. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 481–501. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173414>
- Excoffier, L., Smouse, P. E., & Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics*, 131(2), 479–491. <https://doi.org/10.1007/s00424-009-0730-7>
- Félix, F., Castro, C., Laake, J. L., Haase, B. E. N., & Scheidat, M. (2011). Abundance and survival estimates of the southeastern pacific humpback whale stock from 1991–2006 photo-identification surveys in Ecuador. *Journal of Cetacean Research and Management (Special Issue)*, 3, 301–307.
- Felsenstein, J. (1985). Confidence Limits on Phylogenies: An Approach Using the Bootstrap. *Evolution*, 39(4), 783. <https://doi.org/10.2307/2408678>
- Florko, K. R. N., Bernhardt, W., Breiter, C. J. C., Ferguson, S. H., Hainstock, M., Young, B. G., & Petersen, S. D. (2018). Decreasing sea ice conditions in western Hudson Bay and an increase in abundance of harbour seals (*Phoca vitulina*) in the Churchill River. *Polar Biology*, 41(6), 1187–

1195. <https://doi.org/10.1007/s00300-018-2277-6>
- Foltz, D. W., Nguyen, A. T., Kiger, J. R., & Mah, C. L. (2008). Pleistocene speciation of sister taxa in a North Pacific clade of brooding sea stars (Leptasterias). *Marine Biology*, 154(3), 593–602. <https://doi.org/10.1007/s00227-008-0952-9>
- Fontaine, M. C., Roland, K., Calves, I., Austerlitz, F., Palstra, F. P., Tolley, K. A., Ryan, S., Ferreira, M., Jauniaux, T., Llavona, A., Öztürk, B., Öztürk, A. A., Ridoux, V., Rogan, E., Sequeira, M., Siebert, U., Vikingsson, G. A., Borrell, A., Michaux, J. R., & Aguilar, A. (2014). Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. *Molecular Ecology*, 23(13), 3306–3321. <https://doi.org/10.1111/mec.12817>
- Foote, A. D., Kaschner, K., Schultze, S. E., Garilao, C., Ho, S. Y. W., Post, K., Higham, T. F. G., Stokowska, C., van der Es, H., Embling, C. B., Gregersen, K., Johansson, F., Willerslev, E., & Gilbert, M. T. P. (2013). Ancient DNA reveals that bowhead whale lineages survived Late Pleistocene climate change and habitat shifts. *Nature Communications*, 4, 1677. <https://doi.org/10.1038/ncomms2714>
- Foote, A. D., Newton, J., Ávila-Arcos, M. C., Kampmann, M. L., Samaniego, J. A., Post, K., Rosing-Asvid, A., Sinding, M. H. S., & Gilbert, M. T. P. (2013). Tracking niche variation over millennial timescales in sympatric killer whale lineages. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768). <https://doi.org/10.1098/rspb.2013.1481>
- Forcada, J., Di Sciara, G. N., & Fabbri, F. (1995). Abundance of fin whales and striped dolphins summering in the Corso-Ligurian Basin. *Mammalia*, 59(1), 127–140. <https://doi.org/10.1515/mamm.1995.59.1.127>
- Forney, K. A. (2000). Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. *Conservation Biology*, 14(5), 1271–1286. <https://doi.org/10.1046/j.1523-1739.2000.99412.x>
- Forney, K. A., Ferguson, M., Becker, E., Fiedler, P., Redfern, J. V., Barlow, J., Vilchis, I., & Ballance, L. (2012). Habitat-based spatial models of cetacean density in the eastern Pacific Ocean. *Endangered Species Research*, 16(2), 113–133. <https://doi.org/10.3354/esr00393>
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5(7), 673–677. <https://doi.org/10.1038/nclimate2647>
- Fossi, M. C., Marsili, L., Baini, M., Giannetti, M., Coppola, D., Guerranti, C., Caliani, I., Minutoli, R., Lauriano, G., Finoia, M. G., Rubegni, F., Panigada, S., Bérubé, M., Urban-R., J., & Panti, C. (2016). Fin whales and microplastics: The Mediterranean Sea and the Sea of Cortez scenarios. *Environmental Pollution*, 209, 68–78. <https://doi.org/10.1016/j.envpol.2015.11.022>
- Fossi, M. C., Urban, J., Casini, S., Maltese, S., Spinsanti, G., Panti, C., Porcelloni, S., Panigada, S., Lauriano, G., Niño-Torres, C., Rojas-Bracho, L., Jimenez, B., Muñoz-Arnanz, J., & Marsili, L. (2010). A multi-trial diagnostic tool in fin whale (*Balaenoptera physalus*) skin biopsies of the Pelagos Sanctuary (Mediterranean Sea) and the Gulf of California (Mexico). *Marine*

- Environmental Research*, 69(SUPPL. 1), 10–13.
<https://doi.org/10.1016/j.marenvres.2009.10.006>
- Foster, G. L., & Sexton, P. F. (2014). Enhanced carbon dioxide outgassing from the eastern equatorial Atlantic during the last glacial. *Geology*, 42(11), 1003–1006. <https://doi.org/10.1130/G35806.1>
- Fountain, T., Husby, A., Nonaka, E., DiLeo, M. F., Korhonen, J. H., Rastas, P., Schulz, T., Saastamoinen, M., & Hanski, I. (2018). Inferring dispersal across a fragmented landscape using reconstructed families in the Glanville fritillary butterfly. *Evolutionary Applications*, 11(3), 287–297. <https://doi.org/10.1111/eva.12552>
- Franchini, P., Monné Parera, D., Kautt, A. F., & Meyer, A. (2017). quaddRAD: a new high-multiplexing and PCR duplicate removal ddRAD protocol produces novel evolutionary insights in a nonradiating cichlid lineage. *Molecular Ecology*, 26(10), 2783–2795. <https://doi.org/10.1111/mec.14077>
- Francis, R. M. (2017). pophelter: an R package and web app to analyse and visualize population structure. *Molecular Ecology Resources*, 17(1), 27–32. <https://doi.org/10.1111/1755-0998.12509>
- Frantz, A. C., Cellina, S., Krier, A., Schley, L., & Burke, T. (2009). Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: Clusters or isolation by distance? *Journal of Applied Ecology*, 46(2), 493–505.
- Frantz, A. C., Pope, L. C., Etherington, T. R., Wilson, G. J., & Burke, T. (2010). Using isolation-by-distance-based approaches to assess the barrier effect of linear landscape elements on badger (*Meles meles*) dispersal. *Molecular Ecology*, 19(8), 1663–1674. <https://doi.org/10.1111/j.1365-294X.2010.04605.x>
- Fraser, C. I., Nikula, R., Ruzzante, D. E., & Waters, J. M. (2012). Poleward bound: Biological impacts of Southern Hemisphere glaciation. *Trends in Ecology and Evolution*, 27(8), 462–471. <https://doi.org/10.1016/j.tree.2012.04.011>
- Fraser, C. I., Nikula, R., Spencer, H. G., & Waters, J. M. (2009). Kelp genes reveal effects of subantarctic sea ice during the Last Glacial Maximum. *Proceedings of the National Academy of Sciences of the United States of America*, 106(9), 3249–3253. <https://doi.org/10.1073/pnas.0810635106>
- Friesinger, S., & Bernatchez, P. (2010). Perceptions of Gulf of St. Lawrence coastal communities confronting environmental change: Hazards and adaptation, Québec, Canada. *Ocean and Coastal Management*, 53(11), 669–678. <https://doi.org/10.1016/j.ocecoaman.2010.09.001>
- Gaggiotti, O. E., Bekkevold, D., Jørgensen, H. B. H., Foll, M., Carvalho, G. R., Andre, C., & Ruzzante, D. E. (2009). Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: Atlantic herring as a case study. *Evolution*, 63(11), 2939–2951. <https://doi.org/10.1111/j.1558-5646.2009.00779.x>
- Galbraith, P. S., Larouche, P., Chassé, J., & Petrie, B. (2012). Sea-surface temperature in relation to air temperature in the Gulf of St. Lawrence: Interdecadal variability and long term trends. *Deep-Sea Research Part II*, 77–80, 10–20. <https://doi.org/10.1016/j.dsr2.2012.04.001>

- Galindo, H. M., Olson, D. B., & Palumbi, S. R. (2006). Seascape Genetics: A Coupled Oceanographic-Genetic Model Predicts Population Structure of Caribbean Corals. *Current Biology*, 16(16), 1622–1626. <https://doi.org/10.1016/j.cub.2006.06.052>
- Gauffier, P., Borrell, A., Silva, M. A., Víkingsson, G., López, A., Giménez, J., Colaço, A., Halldórsson, S. D., Vighi, M., Prieto, R., de Stephanis, R., & Aguilar, A. (2020). Wait your turn, North Atlantic fin whales share a common feeding ground sequentially. *Marine Environmental Research*, 155, 104884. <https://doi.org/10.1016/J.MARENRES.2020.104884>
- Gauffier, P., Verborgh, P., Gauffier, P., Verborgh, P., Giménez, J., Esteban, R., Manuel, J., Sierra, S., & Stephanis, R. De. (2018). Contemporary migration of fin whales through the Strait of Gibraltar. *Marine Ecology Progress Series*, 588, 215–228. <https://doi.org/10.3354/meps12449>
- Gavrilchuk, K., Lesage, V., Ramp, C., Sears, R., Bérubé, M., Bearhop, S., & Beuplet, G. (2014). Trophic niche partitioning among sympatric baleen whale species following the collapse of groundfish stocks in the Northwest Atlantic. *Marine Ecology Progress Series*, 497, 285–301. <https://doi.org/10.3354/meps10578>
- Geijer, C. K. A., Notarbartolo di Sciara, G., & Panigada, S. (2016). Mysticete migration revisited: are Mediterranean fin whales an anomaly? *Mammal Review*, 46(4), 284–296. <https://doi.org/10.1111/mam.12069>
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7(4), 457–511. <https://doi.org/10.1214/ss/1177013604>
- Gerrodette, T. (1987). A power analysis for detecting trends. In *Ecology* (Vol. 68, Issue 5, pp. 1364–1372). <https://doi.org/10.2307/1939220>
- Gerrodette, T., & Forcada, J. (2005). Non-recovery of two spotted and spinner dolphin population in the eastern Tropical Pacific. *Marine Ecology Progress Series*, 291, 1–21. <https://doi.org/10.3354/meps291001>
- Gersonde, R., Crosta, X., Abelman, A., & Armand, L. (2005). Sea-surface temperature and sea ice distribution of the Southern Ocean at the EPILOG Last Glacial Maximum - A circum-Antarctic view based on siliceous microfossil records. *Quaternary Science Reviews*, 24(7-9 SPEC. ISS.), 869–896. <https://doi.org/10.1016/j.quascirev.2004.07.015>
- Gilmore, R. (1957). Whales Aground in Cortés' Sea: Tragic Strandings in the Gulf of California. *Pacific Discovery*, 10, 22–27.
- Giménez, J., Gómez-Campos, E., Borrell, A., Cardona, L., & Aguilar, A. (2013). Isotopic evidence of limited exchange between Mediterranean and eastern North Atlantic fin whales. *Rapid Communications in Mass Spectrometry*, 27(15), 1801–1806. <https://doi.org/10.1002/rcm.6633>
- Giménez, J., Gómez-Campos, E., Borrell, A., Cardona, L., & Aguilar, A. (2014). The uncertain status of the Mediterranean and northeastern North Atlantic fin whale subpopulations: Reply to Castellote et al., Rapid Commun. Mass Spectrom. 2014, 28, 665–667. *Rapid Communications in Mass Spectrometry*, 28(6), 668–670. <https://doi.org/10.1002/rcm.6817>

- Giménez, J., Louis, M., Barón, E., Ramírez, F., Verborgh, P., Gauffier, P., Esteban, R., Eljarrat, E., Barceló, D., G. Forero, M., & de Stephanis, R. (2018). Towards the identification of ecological management units: A multidisciplinary approach for the effective management of bottlenose dolphins in the southern Iberian Peninsula. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(1), 205–215. <https://doi.org/10.1002/aqc.2814>
- Gosselin, T. (2019). *assigner: Assignment Analysis with GBS/RAD Data using R*. <https://doi.org/10.5281/zenodo.592677>
- Graham, R. W., & Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution*, 5(9), 289–292. [https://doi.org/10.1016/0169-5347\(90\)90083-P](https://doi.org/10.1016/0169-5347(90)90083-P)
- Graham, R. W., Lundelius, E. L., Graham, M. A., Schroeder, E. K., Toomey, R. S., Anderson, E., Barnosky, A. D., Burns, J. A., Churcher, C. S., Grayson, D. K., Guthrie, R. D., Harington, C. R., Jefferson, G. T., Martin, L. D., McDonald, H. G., Morlan, R. E., Semken, H. A., Webb, S. D., Werdelin, L., & Wilson, M. C. (1996). Spatial Response of Mammals to Late Quaternary Environmental Fluctuations. *Science*, 272(5268), 1601–1606. <https://doi.org/10.1126/science.272.5268.1601>
- Greene, C. H., & Pershing, A. J. (2000). The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. *ICES Journal of Marine Science*, 57, 1536–1544. <https://doi.org/10.1006/jmsc.2000.0966>
- Guillot, G., Leblois, R., Coulon, A., & Frantz, A. C. (2009). Statistical methods in spatial genetics. *Molecular Ecology*, 18(23), 4734–4756. <https://doi.org/10.1111/j.1365-294X.2009.04410.x>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Gutenkunst, R. N., Hernandez, R. D., Williamson, S. H., & Bustamante, C. D. (2009). Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. *PLoS Genetics*, 5(10). <https://doi.org/10.1371/journal.pgen.1000695>
- Hall, L. A., Palsbøll, P. J., Beissinger, S. R., Harvey, J. T., Bérubé, M., Raphael, M. G., Nelson, S. K., Golightly, R. T., McFarlane-Tranquilla, L., Newman, S. H., & Peery, M. Z. (2009). Characterizing dispersal patterns in a threatened seabird with limited genetic structure. *Molecular Ecology*, 18(24), 5074–5085. <https://doi.org/10.1111/j.1365-294X.2009.04416.x>
- Hammond, P. S. (1990a). Capturing whales on film—estimating cetacean population parameters from individual recognition data. *Mammal Review*, 20(1), 17–22. <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2907.1990.tb00099.x/abstract>
- Hammond, P. S. (1990b). Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. *Reports of the International Whaling Commission (Special Issue)*, 12, 135–139.
- Hammond, P. S. (2017). Mark-recapture. In B. Würsig, J. G. M. Thewissen, & K. Kovacs (Eds.),

Encyclopedia of Marine Mammals, 3rd Ed. (Pp. 580– 584). San Diego, CA: Elsevier.

- Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., MacLeod, K., Ridoux, V., Santos, M., Scheidat, M., Teilmann, J., Vingada, J., & Øien, N. (2017). Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys. *Sea Mammal Research Unit, University of St Andrews, UK*, Pp. 40.
- Hammond, P. S., Macleod, K., Berggren, P., Borchers, D. L., Burt, L., Cañadas, A., Desportes, G., Donovan, G. P., Gilles, A., Gillespie, D., Gordon, J., Hiby, L., Kuklik, I., Leaper, R., Lehnert, K., Leopold, M., Lovell, P., Øien, N., Paxton, C. G. M., ... Vázquez, J. A. (2013). Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation*, 164, 107–122. <https://doi.org/10.1016/j.biocon.2013.04.010>
- Hammond, P. S., Macleod, K., Burt, L., Cañadas, A., Lens, S., Mikkelsen, B., Rogan, E., Santos, B., Uriarte, A., Van Canneyt, O., & Vázquez, J. A. (2011). Abundance of baleen whales in the European Atlantic. *Paper SC/63/RMP24 Presented to the IWC Scientific Committee*, 1–22.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41–49. <https://doi.org/10.1038/23876>
- Hardy, O. J., & Vekemans, X. (1999). Isolation by distance in a continuous population: reconciliation between spatial autocorrelation analysis and population genetics models. *Heredity*, 83(145–154), 145–154.
- Harpending, H. C., Batzer, M., Gurven, M., Jorde, L. B., Rogers, A. R., & Sherry, S. T. (1998). Genetic traces of ancient demography. *Proceedings of the National Academy of Sciences of the United States of America*, 95(4), 1961–1967. <https://doi.org/10.1073/pnas.95.4.1961>
- Hartl, D. L., & Clark, A. G. (1988). *Principles of Population Genetics*. Sinauer Associates, Sunderland, Massachusetts.
- Hastie, T., & Tibshirani, R. (1990). Generalized additive models. *Chapman & Hall, London*.
- Hatch, L. T. (2004). Structure and diversity among fin whales, *Balaenoptera physalus*, from the North Pacific and North Atlantic Oceans: A comparison of maternally, paternally and biparentally inherited genetic markers. *PhD Thesis, Cornell University*, 32–112.
- Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S. A., Dunne, J. P., Costa, D. P., Crowder, L. B., & Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, 3(3), 234–238. <https://doi.org/10.1038/nclimate1686>
- Hazen, E. L., Palacios, D. M., Forney, K. A., Howell, E. A., Becker, E., Hoover, A. L., Irvine, L., DeAngelis, M., Bograd, S. J., Mate, B. R., & Bailey, H. (2017). WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. *Journal of Applied Ecology*, 54(5), 1415–1428. <https://doi.org/10.1111/1365-2664.12820>
- Head, M. J., & Gibbard, P. L. (2015). Early-Middle Pleistocene transitions: Linking terrestrial and

- marine realms. *Quaternary International*, 389, 7–46.
<https://doi.org/10.1016/j.quaint.2015.09.042>
- Hedrick, P. W. (2005). A standardised genetic differentiation measure. *Evolution*, 59(8), 1633–1638.
- Hernández-Almeida, I., Ausín, B., Saavedra-Pellitero, M., Baumann, K. H., & Stoll, H. M. (2019). Quantitative reconstruction of primary productivity in low latitudes during the last glacial maximum and the mid-to-late Holocene from a global *Florisphaera profunda* calibration dataset. *Quaternary Science Reviews*, 205, 166–181.
<https://doi.org/10.1016/j.quascirev.2018.12.016>
- Hewitt, G. M. (2000). The genetic legacy of the quaternary ice ages. *Nature*, 405(6789), 907–913.
<https://doi.org/10.1038/35016000>
- Hewitt, G. M. (2001). Speciation, hybrid zones and phylogeography - Or seeing genes in space and time. *Molecular Ecology*, 10(3), 537–549. <https://doi.org/10.1046/j.1365-294X.2001.01202.x>
- Hinojosa, J. C., Koubínová, D., Szenteczki, M. A., Pitteloud, C., Dincă, V., Alvarez, N., & Vila, R. (2019). A mirage of cryptic species: Genomics uncover striking mitonuclear discordance in the butterfly *Thymelicus sylvestris*. *Molecular Ecology*, 28(17), 3857–3868.
<https://doi.org/10.1111/mec.15153>
- Hixon, M. A., & Jones, G. P. (2005). Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, 86(11), 2847–2859. <https://doi.org/10.1890/04-1455>
- Hobbs, K. E., Muir, D. C. G., & Mitchell, E. (2001). Temporal and biogeographic comparisons of PCBs and persistent organochlorine pollutants in the blubber of fin whales from eastern Canada in 1971–1991. *Environmental Pollution*, 114(2), 243–254. [https://doi.org/10.1016/S0269-7491\(00\)00211-6](https://doi.org/10.1016/S0269-7491(00)00211-6)
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., & Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science (New York, N.Y.)*, 318(5857), 1737–1742.
<https://doi.org/10.1126/science.1152509>
- Huggins, R. (1989). On the statistical analysis of capture experiments. *Biometrika*, 76(1), 133–140.
- Hughes, P. D., & Gibbard, P. L. (2015). A stratigraphical basis for the Last Glacial Maximum (LGM). *Quaternary International*, 383, 174–185. <https://doi.org/10.1016/j.quaint.2014.06.006>
- Huijser, L. A. E., Bérubé, M., Cabrera, A. A., Prieto, R., Silva, M. A., Robbins, J., Kanda, N., Pastene, L. A., Goto, M., Yoshida, H., Víkingsson, G. A., & Palsbøll, P. J. (2018). Population structure of North Atlantic and North Pacific sei whales (*Balaenoptera borealis*) inferred from mitochondrial control region DNA sequences and microsatellite genotypes. *Conservation Genetics*, 19(4), 1007–1024. <https://doi.org/10.1007/s10592-018-1076-5>
- Hurrell, J. W., Kushnir, Y., & Ottersen, G. (2003). An overview of the North Atlantic Oscillation. *Climatic Significance and Environmental Impact. Geophysical Monograph*, 134, 1–35.

<https://doi.org/10.1029/134GM01>

- Iacchei, M., Ben-Horin, T., Selkoe, K. A., Bird, C. E., García-Rodríguez, F. J., & Toonen, R. J. (2013). Combined analyses of kinship and F_{ST} suggest potential drivers of chaotic genetic patchiness in high gene-flow populations. *Molecular Ecology*, 22(13), 3476–3494. <https://doi.org/10.1111/mec.12341>
- Ibrahim, K. M., Nichols, R. A., & Hewitt, G. M. (1996). Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity*, 77(3), 282–291. <https://doi.org/10.1038/hdy.1994.41>
- Ingebrigsten, A. (1929). Whales caught in the North Atlantic and other seas. *Conseil International Pour l'Exploration Scientifique Du Mer*, 56, 1-26 (fin whale only, 12-17).
- Ingram, S. N., Walshe, L., Johnston, D., & Rogan, E. (2007). Habitat partitioning and the influence of benthic topography and oceanography on the distribution of fin and minke whales in the Bay of Fundy, Canada. *Journal of the Marine Biological Association of the UK*, 87, 149–152. <https://doi.org/10.1017/S0025315407054884>
- International Whaling Commission. (2017a). Report of the Scientific Committee. Annex D. Report of the Sub-Committee on the Revised Management Procedure. *Journal of Cetacean Research and Management*, 18(SUPPL.), 123–173.
- International Whaling Commission. (2017b). Report of the Sub-Committee on the Revised Management Procedure. *Journal of Cetacean Research and Management*, 18(Suppl.), 123–173.
- Isojunno, S., Matthiopoulos, J., & Evans, P. G. H. (2012). Harbour porpoise habitat preferences: Robust spatio-temporal inferences from opportunistic data. *Marine Ecology Progress Series*, 448, 155–170. <https://doi.org/10.3354/meps09415>
- Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, 23(14), 1801–1806. <https://doi.org/10.1093/bioinformatics/btm233>
- Jansen, J. H. F., Kuijpers, A., & Troelstra, S. R. (1986). A Mid-Brunhes Climatic Event : Long-Term changes in global atmosphere and ocean circulation. *Science*, 232(4750), 619–622.
- Johnston, D. W., Bowers, M. T., Friedlaender, A. S., & Lavigne, D. M. (2012). The effects of climate change on harp seals (*Pagophilus Groenlandicus*). *PLoS ONE*, 7(1), 1–8. <https://doi.org/10.1371/journal.pone.0029158>
- Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24, 1403–1405.
- Jonckers, L. H. M. (1973). The concept of population in biology - A logical analysis with a suggestion to diminish the confusion of thought. *Acta Biotheoretica*, 22(2), 78–108. <https://doi.org/10.1007/BF01601984>
- Jones, A. T., Ovenden, J. R., & Wang, Y. G. (2016). Improved confidence intervals for the linkage

- disequilibrium method for estimating effective population size. *Heredity*, 117(4), 217–223. <https://doi.org/10.1038/hdy.2016.19>
- Jost, L. (2008). GST and its relatives do not measure differentiation. *Molecular Ecology*, 17(18), 4015–4026. <https://doi.org/10.1111/j.1365-294X.2008.03887.x>
- Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16(5), 1099–1106. <https://doi.org/10.1111/j.1365-294X.2007.03089.x>
- Kalinowski, S. T., Wagner, A. P., & Taper, M. L. (2006). ML-RELATE: A computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, 6(2), 576–579. <https://doi.org/10.1111/j.1471-8286.2006.01256.x>
- Kamvar, Z., Tabima, J., & Grünwald, N. (2014). Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ*, 2, e281.
- Keenan, K., McGinnity, P., Cross, T. F., Crozier, W. W., & Prodöhl, P. A. (2013). DiveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, 4(8), 782–788. <https://doi.org/10.1111/2041-210X.12067>
- Kellogg, R. (1928). What is known of the migrations of some of the whalebone whales. *Annual Report Smithsonian Institution*, 467–494.
- Kendall, W. L. (1999). Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*, 80(8), 2517–2525. [https://doi.org/https://doi.org/10.1890/0012-9658\(1999\)080\[2517:ROCCRM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2517:ROCCRM]2.0.CO;2)
- Kendall, W. L., Nichols, J. D., Hines, J. E., & Mar, N. (1997). Estimating Temporary Emigration Using Capture-Recapture Data with Pollock's Robust Design. *Ecology*, 78(2), 563–578.
- Kim, Y. J., & Gu, C. (2004). Smoothing spline Gaussian regression: More scalable computation via efficient approximation. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, 66(2), 337–356. <https://doi.org/10.1046/j.1369-7412.2003.05316.x>
- Kingman, J. F. C. (1982). The coalescent. *Stochastic Processes and Their Applications*, 13(3), 235–248. [https://doi.org/10.1016/0304-4149\(82\)90011-4](https://doi.org/10.1016/0304-4149(82)90011-4)
- Knies, J., & Vogt, C. (2003). Freshwater pulses in the eastern Arctic Ocean during Saalian and Early Weichselian ice-sheet collapse. *Quaternary Research*, 60(3), 243–251. <https://doi.org/10.1016/j.yqres.2003.07.008>
- Knowles, L. L., Carstens, B. C., & Keat, M. L. L. (2007). Coupling Genetic and Ecological-Niche Models to Examine How Past Population Distributions Contribute to Divergence. *Current Biology*, 17(11), 940–946. <https://doi.org/10.1016/j.cub.2007.04.033>
- Kopp, R. E., Simons, F. J., Mitrovica, J. X., Maloof, A. C., & Oppenheimer, M. (2009). Probabilistic assessment of sea level during the last interglacial stage. *Nature*, 462(7275), 863–867.

<https://doi.org/10.1038/nature08686>

- Krebs, C. J. (1972). *Ecology: The experimental analysis of distribution and abundance*. Harper & Row, New York.
- Kriebel, D., Tickner, J., Epstein, P., Lemons, J., Levins, R., Loechler, E. L., Quinn, M., Rudel, R., Schettler, T., & Stoto, M. (2001). The precautionary principle in environmental science. *Environmental Health Perspectives*, 109(9), 871–876. <https://doi.org/10.2307/3454986>
- Kuhlemann, J., Rohling, E. J., Krumrei, I., Kubik, P., Ivy-Ochs, S., & Kucera, M. (2008). Regional Synthesis of Mediterranean Atmospheric Circulation During the Last Glacial Maximum. *Science*, 321(5894), 1338–1340. <https://doi.org/10.1126/science.1157638>
- Kuhner, M. K. (2009). Coalescent genealogy samplers: windows into population history. *Trends in Ecology and Evolution*, 24(2), 86–93. <https://doi.org/10.1016/j.tree.2008.09.007>
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33(7), 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Laake, J., & Rexstad, E. (2008). RMark -an alternative approach to building linear models in MARK. In: Cooch, E. and White, G.C. (Eds). *Program MARK: A Gentle Introduction*, 111pp. http://www.phidot.org/software/mark/docs/book/pdf/app_3.pdf
- Laidre, K., Heide-Jørgensen, M., Heagerty, P., Cossio, A., Bergström, B., & Simon, M. (2010). Spatial associations between large baleen whales and their prey in West Greenland. *Marine Ecology Progress Series*, 402, 269–284. <https://doi.org/10.3354/meps08423>
- Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., & Podesta, M. (2001). Collisions Between Ships and Whales. *Marine Mammal Science*, 17(1), 35–75. <https://doi.org/10.1111/j.1748-7692.2001.tb00980.x>
- Laist, D. W., Knowlton, A. R., & Pendleton, D. (2014). Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. *Endangered Species Research*, 23(2), 133–147. <https://doi.org/10.3354/esr00586>
- Lambert, C., Mannocci, L., Lehodey, P., & Ridoux, V. (2014). Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. *PLoS ONE*, 9(8). <https://doi.org/10.1371/journal.pone.0105958>
- Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, 9(4), 357–359. <https://doi.org/10.1038/nmeth.1923>
- Langtimm, C. A. (2009). Modeling Demographic Processes In Marked Populations. *Environmental and Ecological Statistics*, 3, 579–591. <https://doi.org/10.1007/978-0-387-78151-8>
- Lapierre, M., Lambert, A., & Achaz, G. (2017). Accuracy of demographic inferences from the site frequency spectrum: The case of the yoruba population. *Genetics*, 206(1), 139–449. <https://doi.org/10.1534/genetics.116.192708>

- Larouche, P., & Galbraith, P. S. (2016). Canadian Coastal Seas and Great Lakes Sea Surface Temperature Climatology and Recent Trends. *Canadian Journal of Remote Sensing*, 42(3), 243–258. <https://doi.org/10.1080/07038992.2016.1166041>
- Lawson, D. J., Hellenthal, G., Myers, S., & Falush, D. (2012). Inference of population structure using dense haplotype data. *PLoS Genetics*, 8(1), 11–17. <https://doi.org/10.1371/journal.pgen.1002453>
- Lawton, J. H. (1993). Range, population abundance and conservation. *Trends in Ecology and Evolution*, 8(11), 409–413. [https://doi.org/10.1016/0169-5347\(93\)90043-O](https://doi.org/10.1016/0169-5347(93)90043-O)
- Lebreton, A. J., Burnham, K. P., Clobert, J., David, R., Monographs, S. E., & Mar, N. (1992). Modeling survival and testing biological hypotheses using marked animals : a unified approach with case studies. *Ecological Monographs*, 62(1), 67–118. <https://doi.org/10.2307/2937171>
- Lewontin, R. C. (2004). Building a science of population biology. In *The Evolution of Population Biology*, ed. R. S. Singh and M. K. Uyenoyama. Cambridge University Press, New York.
- Lipcius, R., & Hines, A. (1986). Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology*, 67(5), 1361–1371.
- Liu, J. X., Tatarenkov, A., Beacham, T. D., Gorbachev, V., Wildes, S., & Avise, J. C. (2011). Effects of Pleistocene climatic fluctuations on the phylogeographic and demographic histories of Pacific herring (*Clupea pallasii*). *Molecular Ecology*, 20(18), 3879–3893. <https://doi.org/10.1111/j.1365-294X.2011.05213.x>
- Liu, X., & Fu, Y.-X. (2015). Exploring population size changes using SNP frequency spectra. *Nature Genetics*, 47(5), 555–559. <https://doi.org/10.1038/ng.3254>
- Lockyer, C., & Pike, D. G. (2009). Volume 7: North Atlantic Sightings Surveys: Counting whales in the North Atlantic 1987–2001. *NAMMCO Scientific Publications*, Tromsø, Norway, pp244.
- López, M. E. J., Palacios, D. M., Legorreta, A. J., Urbán, J. R., & Mate, B. R. (2019). Fin whale movements in the Gulf of California, Mexico, from satellite telemetry. *PLoS ONE*, 14(1), e0209324. <https://doi.org/10.1371/journal.pone.0209324>
- Lorenzen, E. D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K. A., Ugan, A., Borregaard, M. K., Gilbert, M. T. P., Nielsen, R., Ho, S. Y. W., Goebel, T., Graf, K. E., Byers, D., Stenderup, J. T., Rasmussen, M., Campos, P. F., Leonard, J. A., Koepfli, K. P., ... Willerslev, E. (2011). Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature*, 479(7373), 359–364. <https://doi.org/10.1038/nature10574>
- Louis, M., Fontaine, M. C., Spitz, J., Schlund, E., Dabin, W., Deaville, R., Caurant, F., Cherel, Y., Guinet, C., & Simon-Bouhet, B. (2014). Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141558. <https://doi.org/10.1098/rspb.2014.1558>
- Louis, M., Skovrind, M., Samaniego Castruita, J. A., Garilao, C., Kaschner, K., Gopalakrishnan, S., Haile, J. S., Lydersen, C., Kovacs, K. M., Garde, E., Heide-Jørgensen, M. P., Postma, L.,

- Ferguson, S. H., Willerslev, E., & Lorenzen, E. D. (2020). Influence of past climate change on phylogeography and demographic history of narwhals, *Monodon monoceros*. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20192964. <https://doi.org/10.1098/rspb.2019.2964>
- Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, 19(15), 3038–3051. <https://doi.org/10.1111/j.1365-294X.2010.04688.x>
- Ludt, W. B., & Rocha, L. A. (2015). Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. *Journal of Biogeography*, 42(1), 25–38. <https://doi.org/10.1111/jbi.12416>
- Lydersen, C., Vacquié-Garcia, J., Heide-Jørgensen, M. P., Øien, N., Guinet, C., & Kovacs, K. M. (2020). Autumn movements of fin whales (*Balaenoptera physalus*) from Svalbard, Norway, revealed by satellite tracking. *Scientific Reports*, 10, 16966. <https://doi.org/10.1038/s41598-020-73996-z>
- Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers. *Genetics*, 152(4), 1753–1766.
- Maggs, C. A., Castilho, R., Foltz, D., Henzler, C., Jolly, M. T., Kelly, J., Olsen, J., Perez, K. E., Stam, W., Väinölä, R., Viard, F., & Wares, J. (2008). Evaluating signatures of glacial refugia for north atlantic benthic marine taxa. *Ecology*, 89(11 SUPPL.), 108–122. <https://doi.org/10.1890/08-0257.1>
- Malinsky, M., Trucchi, E., Lawson, D. J., & Falush, D. (2018). RADpainter and fineRADstructure: Population Inference from RADseq Data. *Molecular Biology and Evolution*, 35(5), 1284–1290. <https://doi.org/10.1093/molbev/msy023>
- Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, 11(2), 210–219. <https://doi.org/10.1093/beheco/11.2.210>
- Manni, F., Guerard, E., & Heyer, E. (2004). Geographic Patterns of (Genetic, Morphologic, Linguistic) Variation: How Barriers Can Be Detected by Using Monmonier's Algorithm. *Human Biology*, 76(2), 173–190. <https://doi.org/10.1353/hub.2004.0034>
- Mannocci, L., Roberts, J. J., Pedersen, E. J., & Halpin, P. N. (2020). Geographical differences in habitat relationships of cetaceans across an ocean basin. *Ecography*, 43, 1250–1259. <https://doi.org/10.1111/ecog.04979>
- Mantel, N. (1967). The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research*, 27(2), 209–220.
- Marko, P. B., & Hart, M. W. (2011). The complex analytical landscape of gene flow inference. *Trends in Ecology and Evolution*, 26(9), 448–456. <https://doi.org/10.1016/j.tree.2011.05.007>
- Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models. *Computational Statistics and Data Analysis*, 55(7), 2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>

- Matul, A. G. (2017). Probable limits of sea ice extent in the northwestern Subarctic Pacific during the last glacial maximum. *Oceanology*, 57(5), 700–706. <https://doi.org/10.1134/S0001437017050113>
- May, R., & McLean, A. (2007). *Theoretical Ecology. Principles and Applications* (3rd edition). Oxford University Press Inc., New York. <https://doi.org/10.2307/4085526>
- Mckeon, C. S., Weber, M. X., Alter, S. E., Seavy, N. E., Crandall, E. D., Barshis, D. J., Fechter-Leggett, E. D., & Oleson, K. L. L. (2016). Melting barriers to faunal exchange across ocean basins. *Global Change Biology*, 22(2), 465–473. <https://doi.org/10.1111/gcb.13116>
- McQuinn, I. H., Plourde, S., St. Pierre, J. F., & Dion, M. (2015). Spatial and temporal variations in the abundance, distribution, and aggregation of krill (*Thysanoessa raschii* and *Meganyctiphanes norvegica*) in the lower estuary and Gulf of St. Lawrence. *Progress in Oceanography*, 131, 159–176. <https://doi.org/10.1016/j.pocean.2014.12.014>
- Meirmans, P. G. (2012). The trouble with isolation by distance. *Molecular Ecology*, 21, 2839–2846. <https://doi.org/doi:10.1111/j.1365-294X.2012.05578.x>
- Mikkelsen, B. (2007). A note on movements of two fin whales (*Balaenoptera physalus*) tracked by satellite telemetry from the Faroe Islands in 2001. *Journal of Cetacean Research and Management*, 9(2), 115–120.
- Miller, D. L., Burt, M. L., Rexstad, E. A., & Thomas, L. (2013). Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution*, 4(11), 1001–1010. <https://doi.org/10.1111/2041-210X.12105>
- Milligan, B. G. (2003). Maximum-likelihood estimation of relatedness. *Genetics*, 163(3), 1153–1167. <https://doi.org/10.1086/302112>
- Mitchell, E. (1974). Present status of northwest Atlantic fin and other whale stocks. In *The whale problem, a status report*. Edited by W.E. Schevill. Harvard University Press, Cambridge, Massachusetts (pp. 108–169).
- Mizroch, S. A., Rice, D. W., & Breiwick, J. M. (1984). The fin whale (*Balaenoptera physalus*). *Marine Fisheries Review*, 46(4), 20–24.
- Mizroch, S. A., Rice, D. W., Zwiefelhofer, D., Waite, J., & Perryman, W. L. (2009). Distribution and movements of fin whales in the North Pacific Ocean. *Mammal Review*, 39(3), 193–227. <https://doi.org/10.1111/j.1365-2907.2009.00147.x>
- Monmonier, M. S. (1973). Maximum-difference barriers: An alternative numerical regionalization method. *Geographical Analysis*, 3, 245–261.
- Moore, M., Steiner, L., & Jann, B. (2003). Cetacean surveys in the Cape Verde Islands and the use of cookiecutter shark bite lesions as a population marker for fin whales. *Aquatic Mammals*, 29(3), 383–389. <https://doi.org/10.1578/01675420360736569>
- Moore, S. E., Urbán, J. R., Perryman, W. L., Gulland, F., Perez-Cortes, H. M., Wade, P. R., Rojas-

- Bracho, L., & Rowles, T. (2001). Are gray whales hitting “K” hard? *Marine Mammal Science*, 17(4), 954–958.
- Moritz, C. (1994). Defining ‘Evolutionarily Significant Units.’ *Trends in Ecology and Evolution*, 9(10), 373–375. <https://doi.org/10.1016/j.jembe.2009.04.004>
- MPO. (2003). Capelan de l’estuaire et du golfe du Saint-Laurent (4RST) en 2002. *MPO - Sciences, Rapport Sur l’état Des Stocks 2003/009*, 1–14.
- Muirhead, C. A., Warde, A. M., Biedron, I. S., Nicole Mihnovets, A., Clark, C. W., & Rice, A. N. (2018). Seasonal acoustic occurrence of blue, fin, and North Atlantic right whales in the New York Bight. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(3), 744–753. <https://doi.org/10.1002/aqc.2874>
- Murtagh, F., & Legendre, P. (2014). Ward’s Hierarchical Agglomerative Clustering Method: Which Algorithms Implement Ward’s Criterion? *Journal of Classification*, 31, 274–295. <https://doi.org/10.1007/s00357>
- Myers, N. (1993). Biodiversity and the precautionary principle. *Ambio*, 22(2–3), 74–79. <https://doi.org/10.4324/9781849770583>
- NAMMCO-North Atlantic Marine Mammal Commission. (2018). Report of the NAMMCO Scientific Working Group on Abundance Estimates. Available at <https://Nammco.No/Topics/Sc-Working-Group-Reports/>, 1–38.
- Nei, M. (1972). Genetic distance between populations. *The American Naturalist*, 106(949), 283–292. <https://doi.org/10.1086/285153>
- Nelder, J., & Mead, R. (1965). A simplex method for function minimization. *The Computer Journal*, 7, 308–313.
- Nichols, J. D., Kendall, W. L., Hines, J. E., & Spendelow, J. A. (2004). Estimation of sex-specific survival from capture-recapture data when sex is not always known. *Ecology*, 85(12), 3192–3201. <https://doi.org/10.1890/03-0578>
- Nielsen, R., & Wakeley, J. (2001). Distinguishing Migration From Isolation: A Markov Chain Monte Carlo Approach. *Genetics*, 158, 885–896.
- Notarbartolo di Sciara, G., Castellote, M., Druon, J.-N., & Panigada, S. (2016). Fin Whales, *Balaenoptera physalus*: At Home in a Changing Mediterranean Sea? In *Advances in Marine Biology* (1st ed., Vol. 75). Elsevier Ltd. <https://doi.org/10.1016/bs.amb.2016.08.002>
- Notarbartolo di Sciara, G., Zanardelli, M., Jahoda, M., Panigada, S., & Airoidi, S. (2003). The fin whale *Balaenoptera physalus* (L. 1758) in the Mediterranean Sea. *Mammal Review*, 33(2), 105–150. <https://doi.org/10.1046/j.1365-2907.2003.00005.x>
- Nykänen, M., Oudejans, M. G., Rogan, E., Durban, J. W., & Ingram, S. N. (2020). Challenges in monitoring mobile populations : Applying bayesian multi-site mark – recapture abundance estimation to the monitoring of a highly mobile coastal population of bottlenose dolphins.

- Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–15. <https://doi.org/10.1002/aqc.3355>
- O’Corry-Crowe, G. (2008). Climate change and the molecular ecology of arctic marine mammals. *Ecological Applications*, 18(SUPPL.2), 56–76. <https://doi.org/10.1890/06-0795.1>
- Økland, J.-M., Haaland, Ø. A., & Skaug, H. J. (2010). A method for defining management units based on genetically determined close relatives. *ICES Journal of Marine Science*, 67(3), 551–558. <https://doi.org/10.1093/icesjms/fsp260>
- Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H., Hu, A., & CAPE Last Interglacial Project members. (2006). Simulating Arctic Climate Warmth and Icefield Retreat in the Last Interglaciation. *Science*, 311, 1751–1753.
- Pace, R. M., Corkeron, P. J., & Kraus, S. D. (2017). State-space mark-recapture estimates reveal a recent decline in abundance of North Atlantic right whales. *Ecology and Evolution*, May, 8730–8741. <https://doi.org/10.1002/ece3.3406>
- Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5, 89–94. <https://doi.org/10.3897/natureconservation.5.5734>
- Palsbøll, P. J. (1999). Genetic tagging: contemporary molecular ecology. *Biological Journal of the Linnean Society*, 68, 3–22. <https://doi.org/10.1006/bijl.1999.0327>
- Palsbøll, P. J., Bérubé, M., Aguilar, A., Notarbartolo di Sciara, G., & Nielsen, R. (2004). Discerning between recurrent gene flow and recent divergence under a finite-site mutation model applied to North Atlantic and Mediterranean Sea fin whales (*Balaenoptera physalus*) populations. *Evolution*, 58(3), 670–675.
- Palsbøll, P. J., Bérubé, M., & Allendorf, F. (2007). Identification of management units using population genetic data. *Trends in Ecology & Evolution*, 22(1), 11–16. <https://doi.org/10.1016/j.tree.2006.09.003>
- Palsbøll, P. J., Bérubé, M., Larsen, A. H., & Jørgensen, H. (1997). Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. *Molecular Ecology*, 6(9), 893–895. <https://doi.org/10.1111/j.1365-294X.1997.tb00146.x>
- Palsbøll, P. J., Heide-Jørgensen, M. P., & Dietz, R. (1997). Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from mtDNA analysis. *Heredity*, 78(3), 284–292. <https://doi.org/10.1038/hdy.1997.43>
- Palsbøll, P. J., Larsen, F., & Sigurd Hansen, E. (1991). Sampling of Skin Biopsies from Free-Ranging Large Cetaceans in West Greenland: Development of new Biopsy Tips and Bolt Designs. *Report of the International Whaling Commission (Special Issue)*, 13, 71–79.
- Palsbøll, P. J., Peery, M. Z., & Bérubé, M. (2010). Detecting populations in the “ambiguous” zone: Kinship-based estimation of population structure at low genetic divergence. *Molecular Ecology Resources*, 10(5), 797–805. <https://doi.org/10.1111/j.1755-0998.2010.02887.x>

- Palsbøll, P. J., Zachariah Peery, M., Olsen, M. T., Beissinger, S. R., & Bérubé, M. (2013). Inferring recent historic abundance from current genetic diversity. *Molecular Ecology*, 22(1), 22–40. <https://doi.org/10.1111/mec.12094>
- Palumbi, S. R. (2003). Population Genetics, Demographic Connectivity, and the Design of Marine Reserves. *Ecological Applications*, 13(1), 146–158.
- Palumbi, S. R. (2004). Marine reserves and ocean neighborhoods: the spatial scale of marine populations and their management. *Annual Review of Environment and Resources*, 29(1), 31–68. <https://doi.org/10.1146/annurev.energy.29.062403.102254>
- Palumbi, S. R., & Kessing, B. D. (1991). Population biology of the trans-arctic exchange: mtDNA sequence similarity between Pacific and Atlantic sea urchins. *Evolution*, 45(8), 1790–1805.
- Panigada, S., Lauriano, G., Burt, L., Pierantonio, N., & Donovan, G. (2011). Monitoring winter and summer abundance of cetaceans in the Pelagos Sanctuary (Northwestern Mediterranean Sea) through aerial surveys. *PLoS ONE*, 6(7), e22878. <https://doi.org/10.1371/journal.pone.0022878>
- Panigada, S., Lauriano, G., Donovan, G., Pierantonio, N., Cañadas, A., Vázquez, J. A., & Burt, L. (2017). Estimating cetacean density and abundance in the Central and Western Mediterranean Sea through aerial surveys: Implications for management. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141(April 2017), 41–58. <https://doi.org/10.1016/j.dsr2.2017.04.018>
- Panigada, S., Notarbartolo di Sciara, G., Zanardelli Panigada, M., Airolidi, S., Borsani, J. F., & Jahoda, M. (2005). Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: distribution, encounter rate, mean group size and relation to physiographic variables. *Journal of Cetacean Research and Management*, 7(2), 137–145.
- Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A., & Weinrich, M. T. (2006). Mediterranean fin whales at risk from fatal ship strikes. *Marine Pollution Bulletin*, 52(10), 1287–1298. <https://doi.org/10.1016/j.marpolbul.2006.03.014>
- Paradis, E. (2010). Pegas: An R package for population genetics with an integrated-modular approach. *Bioinformatics*, 26(3), 419–420. <https://doi.org/10.1093/bioinformatics/btp696>
- Pastene, L. A., Goto, M., Kanda, N., Zerbini, A. N., Kerem, D., Watanabe, K., Bessho, Y., Hasegawa, M., Nielsen, R., Larsen, F., & Palsbøll, P. J. (2007). Radiation and speciation of pelagic organisms during periods of global warming: The case of the common minke whale, *Balaenoptera acutorostrata*. *Molecular Ecology*, 16(7), 1481–1495. <https://doi.org/10.1111/j.1365-294X.2007.03244.x>
- Patton, A. H., Margres, M. J., Stahlke, A. R., Hendricks, S., Lewallen, K., Hamede, R. K., Ruiz-Aravena, M., Ryder, O., McCallum, H. I., Jones, M. E., Hohenlohe, P. A., & Storfer, A. (2019). Contemporary Demographic Reconstruction Methods Are Robust to Genome Assembly Quality: A Case Study in Tasmanian Devils. *Molecular Biology and Evolution*, 36(12), 2906–2921. <https://doi.org/10.1093/molbev/msz191>
- Pearse, D. E., & Crandall, K. A. (2004). Beyond FST: Analysis of population genetic data for conservation. *Conservation Genetics*, 5, 585–602.

- Pease, C., Lande, R., & Bull, J. (1989). A Model of Population Growth, Dispersal and Evolution in a Changing Environment. *Ecology*, 70(6), 1657–1664.
- Pedro, J. B., Jochum, M., Buizert, C., He, F., Barker, S., & Rasmussen, S. O. (2018). Beyond the bipolar seesaw: Toward a process understanding of interhemispheric coupling. *Quaternary Science Reviews*, 192, 27–46. <https://doi.org/10.1016/j.quascirev.2018.05.005>
- Peery, M. Z., Beissinger, S. R., House, R. F., Bérubé, M., Hall, L. A., Sellas, A., & Palsbøll, P. J. (2008). Characterizing source sink dynamics with genetic parentage assignments. *Ecology*, 89(10), 2746–2759. <https://doi.org/10.1890/07-2026.1>
- Peñaloza, C. L., Kendall, W. L., & Langtimm, C. A. (2014). Reducing bias in survival under nonrandom temporary emigration. *Ecological Applications*, 24(5), 1155–1166. <https://doi.org/10.1890/13-0558.1>
- Pendleton, G. W., Pitcher, K. W., Fritz, L. W., York, A. E., Raum-Suryan, K. L., Loughlin, T. R., Calkins, D. G., Hastings, K. K., Gelatt, T. S., Pendleton, G. W., Pitcher, K. W., Raum-Suryan, K. L., Calkins, D. G., Hastings, K. K., Gelatt, T. S., Fritz, L. W., York, A. E., & Loughlin, T. R. (2006). Survival of Steller sea lions in Alaska: a comparison of increasing and decreasing populations. *Canadian Journal of Zoology*, 84(8), 1163–1172. <https://doi.org/10.1139/Z06-103>
- Pennino, M. G., Mérigot, B., Fonseca, V. P., Monni, V., & Rotta, A. (2016). Habitat modeling for cetacean management: Spatial distribution in the southern Pelagos Sanctuary (Mediterranean Sea). *Deep-Sea Research Part II: Topical Studies in Oceanography*, 141, 203–211. <https://doi.org/10.1016/j.dsr2.2016.07.006>
- Pereira, A., Harris, D., Tyack, P., & Matias, L. (2020). Fin whale acoustic presence and song characteristics in seas to the southwest of Portugal. *The Journal of the Acoustical Society of America*, 147(4), 2235–2249. <https://doi.org/10.1121/10.0001066>
- Pérez-Jorge, S., Tobeña, M., Prieto, R., Vandepierre, F., Calmettes, B., Lehodey, P., & Silva, M. A. (2020). Environmental drivers of large-scale movements of baleen whales in the mid-North Atlantic Ocean. *Diversity and Distributions*, 26, 683–698. <https://doi.org/10.1111/ddi.13038>
- Perryman, W., Donahue, M., Perkins, P., & Reilly, S. (2002). Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Marine Mammal Science*, 18(1), 121–144. <http://onlinelibrary.wiley.com/doi/10.1111/j.1748-7692.2002.tb01023.x/abstract>
- Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One*, 7(5), e37135. <https://doi.org/10.1371/journal.pone.0037135>
- Pew, J., Muir, P. H., Wang, J., & Frasier, T. R. (2015). related: An R package for analysing pairwise relatedness from codominant molecular markers. *Molecular Ecology Resources*, 15(3), 557–561. <https://doi.org/10.1111/1755-0998.12323>
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and

- pseudo-absence data. *Ecological Applications*, 19(1), 181–197. <https://doi.org/10.1890/07-2153.1>
- Piatt, J. F., Methven, D. a., Burger, A. E., McLagan, R. L., Mercer, V., & Creelman, E. (1989). Baleen whales and their prey in a coastal environment. *Canadian Journal of Zoology*, 67(177), 1523–1530. <https://doi.org/10.1139/z89-217>
- Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Halldórsson, S. D., & Víkingsson, G. A. (2019). Estimates of the Abundance of Cetaceans in the Central North Atlantic Based on the NASS Icelandic and Faroese Shipboard Surveys Conducted in 2015. *NAMMCO Scientific Publications*, 11. <https://doi.org/10.7557/3.5269>
- Pike, D. G., Gunnlaugsson, T., Mikkelsen, B., Halldórsson, S. D., Víkingsson, G. A., Acquarone, M., & Desportes, G. (2020). Estimates of the Abundance of Cetaceans in the Central North Atlantic from the T-NASS Icelandic and Faroese Ship Surveys Conducted in 2007. *NAMMCO Scientific Publications*, 11. <https://doi.org/10.7557/3.5269>
- Pike, D. G., Gunnlaugsson, T., Víkingsson, G. A., & Mikkelsen, B. (2008). Estimates of the abundance of fin whales (*Balaenoptera physalus*) from the T-NASS Icelandic and Faroese ship surveys conducted in 2007. *Report of the International Whaling Commission SC/60/PFI13- Revised*, 1–16.
- Pizzolato, L., Howell, S. E. L., Dawson, J., Laliberté, F., & Copland, L. (2016). The influence of declining sea ice on shipping activity in the Canadian Arctic. *Geophysical Research Letters*, 43, 12,146–12,154. <https://doi.org/10.1002/2016GL071489>
- Planes, S., Jones, G. P., & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences*, 106(14), 5693–5697. <https://doi.org/10.1073/pnas.0808007106>
- Plourde, S., Galbraith, P. S., Lesage, V., Grégoire, F., Bourdages, H., Gosselin, J.-F., McQuinn, I., & Scarratt, M. (2014). Ecosystem perspective on changes and anomalies in the Gulf of St. Lawrence: a context in support of the management of the St. Lawrence beluga whale population. *DFO Can. Sci. Advis. Sec. Res. Doc. 2013/129*, v + 29p.
- Plourde, S., Grégoire, F., Lehoux, C., Galbraith, P. S., Castonguay, M., & Ringuette, M. (2015). Effect of environmental variability on body condition and recruitment success of Atlantic Mackerel (*Scomber scombrus* L.) in the Gulf of St. Lawrence. *Fisheries Oceanography*, 24(4), 347–363. <https://doi.org/10.1111/fog.12113>
- Plourde, S., Lehoux, C., McQuinn, I. H., & Lesage, V. (2016). Describing krill distribution in the western North Atlantic using statistical habitat models. *Fisheries and Oceans Canada Canadian Science Advisory Secretariat Research Document 2016/111*, 111, v + 34 p.
- Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: convergence diagnosis and output analysis for MCMC. *R News*, 6, 7–11. <https://doi.org/10.1159/000323281>
- Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107, 1–97.

- Polyak, L., Alley, R. B., Andrews, J. T., Brigham-Grette, J., Cronin, T. M., Darby, D. A., Dyke, A. S., Fitzpatrick, J. J., Funder, S., Holland, M., Jennings, A. E., Miller, G. H., O'Regan, M., Savelle, J., Serreze, M., St. John, K., White, J. W. C., & Wolff, E. (2010). History of sea ice in the Arctic. *Quaternary Science Reviews*, 29(15–16), 1757–1778. <https://doi.org/10.1016/j.quascirev.2010.02.010>
- Pomeroy, P. P., Fedak, M. A., Rothery, P., & Anderson, S. (1999). Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, 68, 235–253. <https://doi.org/10.1046/j.1365-2656.1999.00281.x>
- Portik, D. M., Leaché, A. D., Rivera, D., Barej, M. F., Burger, M., Hirschfeld, M., Rödel, M. O., Blackburn, D. C., & Fujita, M. K. (2017). Evaluating mechanisms of diversification in a Guineo-Congolian tropical forest frog using demographic model selection. *Molecular Ecology*, 26(19), 5245–5263. <https://doi.org/10.1111/mec.14266>
- Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, 25(7), 1253–1256. <https://doi.org/10.1093/molbev/msn083>
- Pradel, R. (1993). Flexibility in Survival Analysis from Recapture Data: Handling Trap-Dependence. In *In Marked Individuals in the Study of Bird Populations* (J.-D. Lebreton and P. M. North, eds.) 29–38. Birkhauser, Basel.
- Pradel, R., Hines, J. E., Lebreton, J.-D., & Nichols, J. D. (1997). Capture-Recapture Survival Models Taking Account of Transients. *Biometrics*, 53, 60–72. <https://doi.org/10.2307/2533097>
- Pradel, R., & Sanz-Aguilar, A. (2012). Modeling trap-awareness and related phenomena in capture-recapture studies. *PLoS ONE*, 7(3), e32666. <https://doi.org/10.1371/journal.pone.0032666>
- Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155(2), 945–959. <https://doi.org/10.1111/j.1471-8286.2007.01758.x>
- Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B: Biological Sciences*, 267, 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>
- QGIS Development Team. (2016). QGIS geographic information system. *Open Source Geospatial Foundation Project* <https://Qgis.Org/En/Site>.
- Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution*, 43(2), 258–275. <https://doi.org/10.1111/j.1558-5646.1989.tb04226.x>
- R Core Team. (2015). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL <http://Www.R-Project.Org/>.
- R Core Team. (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL <http://Www.R-Project.Org/>.
- Radi, T., & De Vernal, A. (2008). Last glacial maximum (LGM) primary productivity in the northern

- North Atlantic Ocean. *Canadian Journal of Earth Sciences*, 45(11), 1299–1316.
<https://doi.org/10.1139/E08-059>
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67(5), 901–904.
<https://doi.org/10.1093/sysbio/syy032>
- Ramp, C., Delarue, J., Bérubé, M., Hammond, P. S., & Sears, R. (2014). Fin whale survival and abundance in the Gulf of St. Lawrence, Canada. *Endangered Species Research*, 23(2), 125–132.
<https://doi.org/10.3354/esr00571>
- Ramp, C., Delarue, J., Palsbøll, P. J., Sears, R., & Hammond, P. S. (2015). Adapting to a warmer ocean - Seasonal shift of baleen whale movements over three decades. *PLoS ONE*, 10(3), e0121374.
<https://doi.org/10.1371/journal.pone.0121374>
- Ramp, C., Gaspard, D., Gavrilchuk, K., Unger, M., Schleimer, A., Delarue, J., Landry, S., & Sears, R. (2021). Up in the air: drone images reveal underestimation of entanglement rates in large rorqual whales. *Endangered Species Research*, 33, 33–44.
- Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M. F., Forney, K. A., Ballance, L. T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A. J., Qian, S. S., Read, A., Reilly, S., Torres, L., & Werner, F. (2006). Techniques for cetacean – habitat modeling. *Marine Ecology Progress Series*, 310, 271–295.
- Redfern, J. V., McKenna, M. F., Moore, T. J., Calambokidis, J., Deangelis, M. L., Becker, E. A., Barlow, J., Forney, K. A., Fiedler, P. C., & Chivers, S. J. (2013). Assessing the Risk of Ships Striking Large Whales in Marine Spatial Planning. *Conservation Biology*, 27(2), 292–302.
<https://doi.org/10.1111/cobi.12029>
- Redfern, J. V., Moore, T. J., Fiedler, P. C., de Vos, A., Brownell, R. L., Forney, K. A., Becker, E. A., & Ballance, L. T. (2017). Predicting cetacean distributions in data-poor marine ecosystems. *Diversity and Distributions*, 23, 394–408. <https://doi.org/10.1111/ddi.12537>
- Reed, J. M., Mills, L. S., Dunning, J. B., Menges, E. S., McKelvey, K. S., Frye, R., Beissinger, S. R., Anstett, M. C., & Miller, P. (2002). Emerging issues in population viability analysis. *Conservation Biology*, 16(1), 7–19. <https://doi.org/10.1046/j.1523-1739.2002.99419.x>
- Reeves, R. R., & Smith, T. D. (2006). A Taxonomy of World Whaling: Operations and Eras. *Whales, Whaling, and Ocean Ecosystems (JA Estes, DP DeMaster, DF Doak, TM Williams, and RL Brownell, Jr., Eds.)*. University of California Press, Berkeley, 82–101.
- Ressler, P. H., Dalpadado, P., Macaulay, G. J., & Handegard, N. (2015). Acoustic surveys of euphausiids and models of baleen whale distribution in the Barents Sea. *Marine Ecology Progress Series*, 527, 13–29. <https://doi.org/10.3354/meps11257>
- Rivera-León, V. E., Urbán, J., Mizroch, S., Brownell, R. L., Oosting, T., Hao, W., Palsbøll, P. J., & Bérubé, M. (2019). Long-term isolation at a low effective population size greatly reduced genetic diversity in Gulf of California fin whales. *Scientific Reports*, 9(1), 12391.
<https://doi.org/10.1038/s41598-019-48700-5>

- Robbins, J., Dendanto, D., Giard, J., Panigada, S., Sears, R., & Zanardelli, M. (2007). Photo-ID studies of fin whales in the North Atlantic Ocean and the Mediterranean Sea. *Rep Sci Comm Int Whal Comm SC/59/PF11*, 1–4.
- Rolland, R., Schick, R., Pettis, H., Knowlton, A., Hamilton, P., Clark, J., & Kraus, S. (2016). Health of North Atlantic right whales *Eubalaena glacialis* over three decades: from individual health to demographic and population health trends. *Marine Ecology Progress Series*, 542, 265–282. <https://doi.org/10.3354/meps11547>
- Romagosa, M., Baumgartner, M., Cascão, I., Lammers, M. O., Marques, T. A., Santos, R. S., & Silva, M. A. (2020). Baleen whale acoustic presence and behaviour at a Mid-Atlantic migratory habitat, the Azores Archipelago. *Scientific Reports*, 10(1), 1–11. <https://doi.org/10.1038/s41598-020-61849-8>
- Roman, J., & Palumbi, S. R. (2003). Whales before whaling in the North Atlantic. *Science (New York, N.Y.)*, 301(5632), 508–510. <https://doi.org/10.1126/science.1084524>
- Rosen, Z., Bhaskar, A., Roch, S., & Song, Y. S. (2018). Geometry of the Sample Frequency Spectrum and the Perils of Demographic Inference. *Genetics*, 210(October), 665–682.
- Rousset, F. (1997). Genetic Differentiation and Estimation of Gene Flow from F-Statistics Under Isolation by Distance. *Genetics*, 145, 1219–1228. <https://doi.org/10.1002/ajmg.c.30221>
- Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J. C., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. E., & Sánchez-Gracia, A. (2017). DnaSP 6: DNA Sequence Polymorphism Analysis of Large Data Sets. *Molecular Biology and Evolution*, 34(12), 3299–3302. <https://doi.org/10.1093/molbev/msx248>
- Ryan, C., McHugh, B., Trueman, C. N., Sabin, R., Deaville, R., Harrod, C., Berrow, S. D., & O'Connor, I. (2013). Stable isotope analysis of baleen reveals resource partitioning among sympatric rorquals and population structure in fin whales. *Marine Ecology Progress Series*, 479, 251–261. <https://doi.org/10.3354/meps10231>
- Ryan, W. B. F., Carbotte, S. M., Coplan, J. O., O'Hara, S., Melkonian, A., Arko, R., Weissel, R. A., Ferrini, V., Goodwillie, A., Nitsche, F., Bonczkowski, J., & Zemsky, R. (2009). Global multi-resolution topography synthesis. *Geochemistry, Geophysics, Geosystems*, 10(3), Q03014. <https://doi.org/10.1029/2008GC002332>
- Sahade, R., Lager, C., Torre, L., Momo, F., Monien, P., Schloss, I., Barnes, D. K. A., Servetto, N., Tarantelli, S., Tatián, M., Zamboni, N., & Abele, D. (2015). Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. *Science Advances*, 1(10), e1500050. <https://doi.org/10.1126/sciadv.1500050>
- Sambrook, J., Fritsch, E., & Maniatis, T. (1989). Molecular cloning. A laboratory manual. In *Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY*.
- Sanpera, C., González, M., & Jover, L. (1996). Heavy metals in two populations of North Atlantic fin whales (*Balaenoptera physalus*). *Environmental Pollution*, 91(3), 299–307.

- Santora, J., Reiss, C., Loeb, V., & Veit, R. (2010). Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Marine Ecology Progress Series*, 405, 255–269. <https://doi.org/10.3354/meps08513>
- Sanz-Aguilar, A., Tavecchia, G., Minguez, E., Massa, B., Valvo, F. Lo, Ballesteros, G. A., Barberá, G. G., Amengual, J. F., Rodriguez, A., McMinn, M., & Oro, D. (2010). Recapture processes and biological inference in monitoring burrow-nesting seabirds. *Journal of Ornithology*, 151(1), 133–146. <https://doi.org/10.1007/s10336-009-0435-x>
- Savenkoff, C., Castonguay, M., Chabot, D., Hammill, M. O., Bourdages, H., & Morissette, L. (2007). Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? *Estuarine, Coastal and Shelf Science*, 73(3–4), 711–724. <https://doi.org/10.1016/j.ecss.2007.03.011>
- Scales, K. L., Schorr, G. S., Hazen, E. L., Bograd, S. J., Miller, P. I., Andrews, R. D., Zerbini, A. N., & Falcone, E. A. (2017). Should I stay or should I go? Modelling year-round habitat suitability and drivers of residency for fin whales in the California Current. *Diversity and Distributions*, 23(10), 1204–1215. <https://doi.org/10.1111/ddi.12611>
- Schaub, M., Gimenez, O., Schmidt, B. R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology*, 85(8), 2107–2113. <https://doi.org/10.1890/03-3110>
- Schleimer, A., Ramp, C., Delarue, J., Carpentier, A., Bérubé, M., Palsbøll, P. J., Sears, R., & Hammond, P. S. (2019). Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence. *Ecology and Evolution*, 9(7), 4231–4244. <https://doi.org/10.1002/ece3.5055>
- Schneider, V., & Pearce, D. (2004). What saved the whales? An economic analysis of 20th century whaling. *Biodiversity and Conservation*, 13(3), 543–562. <https://doi.org/10.1023/B:BIOC.0000009489.08502.1a>
- Schwarz, C., & Arnason, A. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, 52(3), 860–873. <http://www.jstor.org/stable/10.2307/2533048>
- Selkoe, K. A., Henzler, C. M., & Gaines, S. D. (2008). Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries*, 9(4), 363–377. <https://doi.org/10.1111/j.1467-2979.2008.00300.x>
- Sergeant, D. E. (1977). Stocks of fin whales *Balaenoptera physalus* L. in the North Atlantic Ocean. *Report of the International Whaling Commission*, 27, 460–473.
- Shaffer, M. L. (1981). Minimum Population Sizes for Species Conservation. *BioScience*, 31(2), 131–134. <https://doi.org/10.2307/1308256>
- Sigurjónsson, J. (1988). Operational factors of the Icelandic large whale fishery. *Report of the International Whaling Commission*, 38, 327–333.

- Sigurjónsson, J., & Gunnlaugsson, T. (2006). Revised catch series and cpue for fin whales taken from the early modern whaling land stations in Iceland. *International Whaling Commission SC/58/PFI4*, 1–22.
- Sigurjónsson, J., Mitchell, E., & Gunnlaugsson, T. (1991). Fin whale markings in the North Atlantic with special reference to the stock identity question. *Report of the International Whaling Commission SC/F91/F20*, 17pp.
- Silva, M. A., Borrell, A., Prieto, R., Gauffier, P., Bérubé, M., Palsbøl, P. J., & Colaço, A. (2019). Stable isotopes reveal winter feeding in different habitats in blue, fin and sei whales migrating through the Azores. *Royal Society Open Science*, 6(8), 181800. <https://doi.org/10.1098/rsos.181800>
- Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? *PloS One*, 8(10), e76507. <https://doi.org/10.1371/journal.pone.0076507>
- Simard, Y., Lavoie, D., & Saucier, F. J. (2002). Channel head dynamics: capelin (*Mallotus villosus*) aggregation in the tidally driven upwelling system of the Saguenay - St. Lawrence Marine Park's whale feeding ground. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(2), 197–210. <https://doi.org/10.1139/f01-210>
- Simard, Y., Roy, N., Giard, S., & Aulancier, F. (2019). North Atlantic right whale shift to the Gulf of St. Lawrence in 2015, revealed by long-term passive acoustics. *Endangered Species Research*, 40, 271–284. <https://doi.org/10.3354/ESR01005>
- Simberloff, D. (1986). The Proximate Causes of Extinction. In: Raup D.M., Jablonski D. (Eds) *Patterns and Processes in the History of Life. Dahlem Workshop Reports (Life Sciences Research Reports)*, Vol 36. Springer, Berlin, Heidelberg, 259–276. https://doi.org/10.1007/978-3-642-70831-2_14
- Simon, M., Stafford, K. M., Beedholm, K., Lee, C. M., & Madsen, P. T. (2010). Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. *The Journal of the Acoustical Society of America*, 128(5), 3200–3210. <https://doi.org/10.1121/1.3495946>
- Skaug, H. J., Bérubé, M., & Palsbøl, P. J. (2010). Detecting dyads of related individuals in large collections of DNA-profiles by controlling the false discovery rate. *Molecular Ecology Resources*, 10(4), 693–700. <https://doi.org/10.1111/j.1755-0998.2010.02833.x>
- Slatkin, M. (1993). Isolation by Distance in Equilibrium and Non-Equilibrium Populations. *Evolution*, 47(1), 264–279.
- Slatkin, M. (2005). Seeing ghosts: The effect of unsampled populations on migration rates estimated for sampled populations. *Molecular Ecology*, 14(1), 67–73. <https://doi.org/10.1111/j.1365-294X.2004.02393.x>
- Soulé, M. E. (1985). What is conservation biology? *BioScience*, 35(11), 727–734.
- Spielhagen, R. F., Baumann, K. H., Erlenkeuser, H., Nowaczyk, N. R., Nørgaard-Pedersen, N., Vogt, C., & Weiel, D. (2004). Arctic Ocean deep-sea record of northern Eurasian ice sheet history.

- Quaternary Science Reviews*, 23(11–13), 1455–1483.
<https://doi.org/10.1016/j.quascirev.2003.12.015>
- Spies, I., Spencer, P. D., & Punt, A. E. (2015). Where do we draw the line? A simulation approach for evaluating management of marine fish stocks with isolation-by-distance stock structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(7), 968–982.
<https://doi.org/10.1139/cjfas-2014-0366>
- Stange, M., Sánchez-Villagra, M. R., Salzburger, W., & Matschiner, M. (2018). Bayesian divergence-time estimation with genome-wide single-nucleotide polymorphism data of sea catfishes (Ariidae) supports miocene closure of the Panamanian Isthmus. *Systematic Biology*, 67(4), 681–699. <https://doi.org/10.1093/sysbio/syy006>
- Stefánsson, G., Sigurjónsson, J., & Víkingsson, G. A. (1997). On dynamic interactions between some fish resources and cetaceans off Iceland based on a simulation model. *Journal of Northwest Atlantic Fishery Science*, 22, 357–370.
http://www.hafro.is/~gisli/greinar/Stefansson_et.al_NAFO_1997.pdf
- Stevick, P. T., Allen, J., Clapham, P. J., Katona, S. K., Larsen, F., Lien, J., Mattila, D. K., Palsbøll, P. J., Sears, R., Sigurjónsson, J., Smith, T. D., Víkingsson, G., Øien, N., & Hammond, P. S. (2006). Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, 270(2), 244–255. <https://doi.org/10.1111/j.1469-7998.2006.00128.x>
- Stirling, C. H., Esat, T. M., Lambeck, K., & McCulloch, M. T. (1998). Timing and duration of the Last Interglacial: Evidence for a restricted interval of widespread coral reef growth. *Earth and Planetary Science Letters*, 160(3–4), 745–762. [https://doi.org/10.1016/S0012-821X\(98\)00125-3](https://doi.org/10.1016/S0012-821X(98)00125-3)
- Stocker, T. F., & Johnsen, S. J. (2003). A minimum thermodynamic model for the bipolar seesaw. *Paleoceanography*, 18(4), 1–9. <https://doi.org/10.1029/2003PA000920>
- Sullivan-Lord, R., Ramp, C., Uggadan, E., Schleimer, A., Delarue, J., Sears, R., Bérubé, M., & Palsbøll, P. J. (in prep). Declining reproductive success of humpback and fin whales in the Gulf of St. Lawrence. *In Preparation*.
- Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, 123, 585–595.
- Tamura, K., & Nei, M. (1993). Estimation of the Number of Nucleotide Substitutions in the Control Region of Mitochondrial DNA in Humans and. *Molecular Biology and Evolution*, 10(3), 512–526.
- Taylor, B. L., Chivers, S. J., Larese, J., & Perrin, W. F. (2007). Generation and percent mature estimates for IUCN assessments of cetaceans. *Administrative Report LJ-07-01, Southwest Fisheries Science Center, 8604 La Jolla Shores Blvd., La Jolla, CA 92038, USA. 24 Pp.*
- Taylor, B. L., & Dizon, A. E. (1996). The Need to Estimate Power to Link Genetics and Demography for Conservation. *Conservation Biology*, 10(2), 661–664.

- Taylor, B. L., & Dizon, A. E. (1999). First policy then science: why a management unit based solely on genetic criteria cannot work. *Molecular Ecology*, 8(s1), S11–S16. <https://doi.org/10.1046/j.1365-294x.1999.00797.x>
- Taylor, B. L., & Gerrodette, T. (1993). The Uses of Statistical Power in Conservation Biology: The Vaquita and Northern Spotted Owl. *Conservation Biology*, 7(3), 489–500. <https://doi.org/10.1046/j.1523-1739.1993.07030489.x>
- Taylor, B. L., Martinez, M., Gerrodette, T., Barlow, J., & Hrovat, Y. N. (2007). Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science*, 23(1), 157–175. <https://doi.org/10.1111/j.1748-7692.2006.00092.x>
- Templeton, A. R. (1981). Mechanisms of Speciation - A Population Genetic Approach. *Annual Review of Ecology and Systematics*, 12(1), 23–48. <https://doi.org/10.1146/annurev.es.12.110181.000323>
- Tereshy, B. R., Urbán-Ramírez, J., Breese, D., Rojas-Bracho, L., & Findley, L. T. (1993). Are fin whales resident to the Gulf of California? *Revista de Investigación Científica*, 1, 69–72.
- Thibodeau, B., De Vernal, A., Hillaire-Marcel, C., & Mucci, A. (2010). Twentieth century warming in deep waters of the Gulf of St. Lawrence: A unique feature of the last millennium. *Geophysical Research Letters*, 37(17), 1–5. <https://doi.org/10.1029/2010GL044771>
- Thomas, E., Booth, L., Maslin, M., & Shackleton, N. J. (1995). Northeastern Atlantic benthic foraminifera during the last 45,000 years: Changes in productivity seen from the bottom up. *Paleoceanography*, 10(3), 545–562. <https://doi.org/10.1029/94PA03056>
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R., Marques, T. A., & Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *The Journal of Applied Ecology*, 47(1), 5–14. <https://doi.org/10.1111/j.1365-2664.2009.01737.x>
- Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22(22), 4673–4680. <https://doi.org/10.1093/nar/22.22.4673>
- Thompson, P. M., Wilson, B., Grellier, K., & Hammond, P. S. (2000). Combining Power Analysis and Population Viability Analysis to Compare Traditional and Precautionary Approaches to Conservation of Coastal Cetaceans. *Conservation Biology*, 14(5), 1253–1263.
- Thomson, J. A., Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Fraser, M. W., Statton, J., & Kendrick, G. A. (2015). Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Global Change Biology*, 21(4), 1463–1474. <https://doi.org/10.1111/gcb.12694>
- Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD - A platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>

- Tollis, M., Robbins, J., Webb, A. E., Kuderna, L. F. K., Caulin, A. F., Garcia, J. D., Bérubé, M., Pourmand, N., Marques-Bonet, T., O'Connell, M. J., Palsbøll, P. J., Maley, C. C., & Shapiro, B. (2019). Return to the Sea, Get Huge, Beat Cancer: An Analysis of Cetacean Genomes Including an Assembly for the Humpback Whale (*Megaptera novaeangliae*). *Molecular Biology and Evolution*, 36(8), 1746–1763. <https://doi.org/10.1093/molbev/msz099>
- Torres, L. G., Read, A. J., & Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? *Ecological Applications : A Publication of the Ecological Society of America*, 18(7), 1702–1717. <http://www.ncbi.nlm.nih.gov/pubmed/18839765>
- Troëng, S., & Rankin, E. (2005). Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation*, 121, 111–116. <https://doi.org/10.1016/j.biocon.2004.04.014>
- Truchon, M.-H., Measures, L., Brêthes, J.-C., Albert, É., & Michaud, R. (2018). Influence of anthropogenic activities on marine mammal strandings in the estuary and northwestern Gulf of St. Lawrence, Quebec, Canada, 1994-2008. *J. Cetacean Res. Manage*, 18, 11–21. <http://www.sararegistry.gc.ca>.
- Tulloch, V. J. D., Plagányi, É. E., Brown, C., Richardson, A. J., & Matear, R. (2019). Future recovery of baleen whales is imperiled by climate change. *Global Change Biology*, 25(4), 1263–1281. <https://doi.org/10.1111/GCB.14573>
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Tyne, J. A., Loneragan, N. R., Johnston, D. W., Pollock, K. H., Williams, R., & Bejder, L. (2016). Evaluating monitoring methods for cetaceans. *Biological Conservation*, 201, 252–260. <https://doi.org/10.1016/j.biocon.2016.07.024>
- Urbán, J. R., Rojas-Bracho, L., Guerrero-Ruíz, M., Jaramillo-Legorreta, A., & Findley, L. T. (2005). Cetacean diversity and conservation in the Gulf of California. In: *Biodiversity, Ecosystems, and Conservation in Northern Mexico*. Edited by. J. E. Cartron, G.Ceballos, and R.S. Felger. Oxford University Press, New York, 276–297.
- Vacquié-Garcia, J., Lydersen, C., Marques, T. A., Aars, J., Ahonen, H., Skern-Mauritzen, M., Øien, N., & Kovacs, K. M. (2017). Late summer distribution and abundance of ice-associated whales in the Norwegian High Arctic. *Endangered Species Research*, 32(1), 59–70. <https://doi.org/10.3354/esr00791>
- Valenzuela, L. O., Sironi, M., Rowntree, V. J., & Seger, J. (2009). Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology*, 18(5), 782–791. <https://doi.org/10.1111/j.1365-294X.2008.04069.x>
- Valsecchi, E., & Amos, W. (1996). Microsatellite markers for the study of cetacean populations.

- Molecular Ecology*, 5(1), 151–156. <https://doi.org/10.1111/j.1365-294X.1996.tb00301.x>
- Van Der Hoop, J. M., Moore, M. J., Barco, S. G., Cole, T. V. N., Daoust, P. Y., Henry, A. G., Mcalpine, D. F., Mclellan, W. A., Wimmer, T., & Solow, A. R. (2013). Assessment of Management to Mitigate Anthropogenic Effects on Large Whales. *Conservation Biology*, 27(1), 121–133. <https://doi.org/10.1111/j.1523-1739.2012.01934.x>
- Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). MICRO - CHECKER : software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, 4, 535–538. <https://doi.org/10.1111/j.1471-8286.2004.00684.x>
- Van Waerebeek, K., & Leaper, R. (2008). Second Report of the IWC Vessel Strike Data Standardisation Working Group. *International Whaling Commission, Scientific Committee Document SC/60/BC5, Santiago, Chile*, 8p. <https://doi.org/10.13140/RG.2.1.2020.2001>
- Vandermeer, J. H., & Goldberg, D. E. (2013). *Population ecology: first principle (2nd edition)* Princeton University Press, Princeton, New Jersey.
- Varela, S., Lobo, J. M., & Hortal, J. (2011). Using species distribution models in paleobiogeography: A matter of data, predictors and concepts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 310(3–4), 451–463. <https://doi.org/10.1016/j.palaeo.2011.07.021>
- Venables, W., & Ripley, B. (2002). Modern applied statistics with S, 4th edn. Springer, New York, NY.
- Ver Hoef, J., & Boveng, P. (2007). Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, 88(11), 2766–2772. <http://www.esajournals.org/doi/abs/10.1890/07-0043.1>
- Vighi, M., Borrell, A., & Aguilar, A. (2016). Stable isotope analysis and fin whale subpopulation structure in the eastern North Atlantic. *Marine Mammal Science*, 32(2), 535–551. <https://doi.org/10.1111/mms.12283>
- Vighi, M., Borrell, A., Víkingsson, G. A., Gunnlaugsson, T., & Aguilar, A. (2019). Strontium in fin whale baleen: A potential tracer of mysticete movements across the oceans? *Science of the Total Environment*, 650, 1224–1230. <https://doi.org/10.1016/j.scitotenv.2018.09.103>
- Víkingsson, G. A. (1997). Feeding of fin whales (*Balaenoptera physalus*) off Iceland—diurnal and seasonal variation and possible rates. *Journal of the Northwest Atlantic Fisheries Science*, 22, 77–89.
- Víkingsson, G. A., & Gunnlaugsson, T. (2006). Stock structure of fin whales (*Balaenoptera physalus*) in the North Atlantic – Indications from non-genetic data. *Paper Presented at the Joint North Atlantic Marine Mammal Commission (NAMMCO) and International Whaling Commission (IWC) Scientific Workshop on the Catch History, Stock Structure and Abundance of North Atlantic Fin Whales, 23rd March – 26th March 2006, Re.*
- Víkingsson, G. A., Pike, D. G., Desportes, G., Øien, N., Gunnlaugsson, T., & Bloch, D. (2009). Distribution and abundance of fin whales (*Balaenoptera physalus*) in the Northeast and Central Atlantic as inferred from the North Atlantic Sightings Surveys 1987–2001. *NAMMCO Scientific*

- Publications*, 7, 49–72. <https://doi.org/10.7557/3.2705>
- Víkingsson, G. A., Pike, D. G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B. Á., Mikkelsen, B., Øien, N., Desportes, G., Bogason, V., & Hammond, P. S. (2015). Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology and Evolution*, 3, 1–18. <https://doi.org/10.3389/fevo.2015.00006>
- Virgili, A., Racine, M., Authier, M., Monestiez, P., & Ridoux, V. (2017). Comparison of habitat models for scarcely detected species. *Ecological Modelling*, 346, 88–98. <https://doi.org/10.1016/j.ecolmodel.2016.12.013>
- Visser, F., Hartman, K., Pierce, G., Valavanis, V., & Huisman, J. (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Marine Ecology Progress Series*, 440, 267–279. <https://doi.org/10.3354/meps09349>
- Waelbroeck, C., Paul, A., Kucera, M., Rosell-Melé, A., Weinelt, M., Schneider, R., Mix, A. C., Abelmann, A., Armand, L., Bard, E., Barker, S., Barrows, T. T., Benway, H., Cacho, I., Chen, M. T., Cortijo, E., Crosta, X., De Vernal, A., Dokken, T., ... Turon, J. L. (2009). Constraints on the magnitude and patterns of ocean cooling at the Last Glacial Maximum. *Nature Geoscience*, 2(2), 127–132. <https://doi.org/10.1038/ngeo411>
- Waits, L. P., Luikart, G., & Taberlet, P. (2001). Estimating the probability of identity among genotypes in natural populations: Cautions and guidelines. *Molecular Ecology*, 10(1), 249–256. <https://doi.org/10.1046/j.1365-294X.2001.01185.x>
- Wang, J. (2002). An estimator for pairwise relatedness using molecular markers. *Genetics*, 160(3), 1203–1215.
- Wang, J. (2006). Informativeness of genetic markers for pairwise relationship and relatedness inference. *Theoretical Population Biology*, 70(3), 300–321. <https://doi.org/10.1016/j.tpb.2005.11.003>
- Wang, J. (2014). Estimation of migration rates from marker-based parentage analysis. *Molecular Ecology*, 23(13), 3191–3213. <https://doi.org/10.1111/mec.12806>
- Wang, J. (2017). The computer program STRUCTURE for assigning individuals to populations: easy to use but easier to misuse. *Molecular Ecology Resources*, 17(5), 981–990. <https://doi.org/10.1111/1755-0998.12650>
- Wang, J. (2018). Effects of sampling close relatives on some elementary population genetics analyses. *Molecular Ecology Resources*, 18(1), 41–54. <https://doi.org/10.1111/1755-0998.12708>
- Wang, J., & Whitlock, M. C. (2003). Estimating effective population size and migration rates from genetic samples over space and time. *Genetics*, 163(1), 429–446.
- Wangersky, P. J. (1978). Lotka-Volterra Population Models. *Annual Review of Ecology and Systematics*, 9(1), 189–218. <https://doi.org/10.1146/annurev.es.09.110178.001201>

- Waples, R. S. (1991). Pacific salmon, *Oncorhynchus* spp., and the definition of “species” under the Endangered Species Act.” *Marine Fisheries Review*, 53(3), 11–22.
- Waples, R. S. (1998). Separating the wheat from the chaff: Patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, 89(5), 438–450. <https://doi.org/10.1093/jhered/89.5.438>
- Waples, R. S. (2015). Testing for Hardy – Weinberg Proportions : Have We Lost the Plot ? *Journal of Heredity*, 106(1), 1–19. <https://doi.org/10.1093/jhered/esu062>
- Waples, R. S., & Anderson, E. C. (2017). Purging putative siblings from population genetic data sets: A cautionary view. *Molecular Ecology*, 26(5), 1211–1224. <https://doi.org/10.1111/mec.14022>
- Waples, R. S., & Do, C. (2008). LDNE: A program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Resources*, 8(4), 753–756. <https://doi.org/10.1111/j.1755-0998.2007.02061.x>
- Waples, R. S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, 15(6), 1419–1439. <https://doi.org/10.1111/j.1365-294X.2006.02890.x>
- Ward, J. H. J. (1963). Hierarchical Grouping to Optimize an Objective Function. *Journal of the American Statistical Association*, 58(301), 236–244.
- Ward, R. D., Woodwark, M., & Skibinski, D. O. F. (1994). A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. In *Journal of Fish Biology* (Vol. 44, Issue 2, pp. 213–232). <https://doi.org/10.1111/j.1095-8649.1994.tb01200.x>
- Warton, D. I. (2005). Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. *Environmetrics*, 16(3), 275–289. <https://doi.org/10.1002/env.702>
- Waxman, D. (2012). Population growth enhances the mean fixation time of neutral mutations and the persistence of neutral variation. *Genetics*, 191(2), 561–577. <https://doi.org/10.1534/genetics.112.139220>
- Weir, B. S., & Cockerham, C. C. (1984). Estimating F-Statistics for the Analysis of Population Structure. *Evolution*, 38(6), 1358–1370. <https://doi.org/10.2307/2408641>
- Weir, C. R. (2019). The Cetaceans (Whales and Dolphins) of Angola. In *Biodiversity of Angola* (pp. 445–470). Springer International Publishing. https://doi.org/10.1007/978-3-030-03083-4_16
- Whitlock, M. C., & McCauley, D. E. (1999). Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. *Heredity*, 82, 117–125.
- Whooley, P., Berrow, S., & Barnes, C. (2011). Photo-identification of fin whales (*Balaenoptera physalus* L.) off the south coast of Ireland. *Marine Biodiversity Records*, 4, 1–7. <https://doi.org/10.1017/S1755267210001119>
- Williams, R., Hedley, S. L., & Hammond, P. S. (2006). Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecology and Society*, 11(1), 1.

<https://doi.org/1>

- Williams, R., Vikingsson, G. A., Gislason, A., Lockyer, C., New, L., Thomas, L., & Hammond, P. S. (2013). Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. *ICES Journal of Marine Science*, 70(6), 1273–1280. <https://doi.org/10.1093/icesjms/fst059>
- Wilson, A. B., & Eigenmann Veraguth, I. (2010). The impact of Pleistocene glaciation across the range of a widespread European coastal species. *Molecular Ecology*, 19(20), 4535–4553. <https://doi.org/10.1111/j.1365-294X.2010.04811.x>
- Wilson, B, Hammond, P. S., & Thompson, P. (1999). Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications*, 9(1), 288–300.
- Wilson, Ben, Reid, R. J., Grellier, K., Thompson, P. M., & Hammond, P. S. (2004). Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Animal Conservation*, 7(4), 331–338. <https://doi.org/10.1017/S1367943004001581>
- Wood, S. N. (2006). Generalized additive models: an introduction with R. In *Chapman & Hall/CRC Press, Boca Raton, FL*. Chapman & Hall.
- Wood, S. N. (2017). Generalized additive models: an introduction with R, 2nd edn. *Chapman and Hall/CRC Press, Boca Raton, FL*.
- Wood, S. N., Pya, N., & Säfken, B. (2016). Smoothing Parameter and Model Selection for General Smooth Models. *Journal of the American Statistical Association*, 111(516), 1548–1563. <https://doi.org/10.1080/01621459.2016.1180986>
- Woodley, T. H., & Gaskin, D. E. (1996). Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. *Canadian Journal of Zoology*, 74(1), 75–84. <https://doi.org/10.1139/z96-010>
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97–159.
- Wright, S. (1943). Isolation by Distance. *Genetics*, 28(2), 114–138.
- Yim, H. S., Cho, Y. S., Guang, X., Kang, S. G., Jeong, J. Y., Cha, S. S., Oh, H. M., Lee, J. H., Yang, E. C., Kwon, K. K., Kim, Y. J., Kim, T. W., Kim, W., Jeon, J. H., Kim, S. J., Choi, D. H., Jho, S., Kim, H. M., Ko, J., ... Lee, J. H. (2014). Minke whale genome and aquatic adaptation in cetaceans. *Nature Genetics*, 46(1), 88–92. <https://doi.org/10.1038/ng.2835>
- Zabel, R. W., Scheuerell, M. D., Clure, M. M. M. C., & Williams, J. G. (2006). The Interplay between Climate Variability and Density. *Conservation Biology*, 20(1), 190–200. <https://doi.org/10.1111/j.1523-1739.2006.00300.x>
- Zanardo, N., Parra, G. J., & Möller, L. M. (2016). Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) in Adelaide's coastal waters, South Australia. *Marine Mammal Science*, 32(4), 1381–1401. <https://doi.org/10.1111/mms.12335>

- Zerbini, A. N., Friday, N. A., Palacios, D. M., Waite, J. M., Ressler, P. H., Rone, B. K., Moore, S. E., & Clapham, P. J. (2016). Baleen whale abundance and distribution in relation to environmental variables and prey density in the Eastern Bering Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 134, 312–330. <https://doi.org/10.1016/j.dsr2.2015.11.002>
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). Mixed Effects Models and Extensions in Ecology with R. *Statistics for Biology and Health*, 579pp.

Summary

The fields of population ecology, evolutionary biology, and conservation biology are tightly interconnected through their focus on population-level phenomena. This thesis aimed to provide novel insight into the population biology of fin whales (*Balaenoptera physalus*) by employing a range of different approaches from the fields of population and molecular ecology. The focus on fin whales arose from the need for updated assessments of population genetic structuring and demographic trends, with emphasis on North Atlantic and Mediterranean Sea fin whales. A brief introduction on population biology and our current knowledge on fin whales was presented in Chapter 1.

Chapter 2 provided updated estimates of abundance and apparent survival rates of fin whales in the northern Gulf of St. Lawrence. Mark-recapture models were fitted to individual capture histories compiled from a long-term photo-identification data set. I detected a decline in abundance from an estimated 335 (95% confidence interval (CI) 321-348) individuals in 2004-2010 to 291 (95% CI 270-312) individuals in 2010-2016. The decline was corroborated by a concomitant decrease in apparent survival rates from 1990 to 2015. The effects of violating the assumption of equal capture probabilities were assessed in the context of divergent site fidelity patterns among individuals. Large-scale shifts in distribution (causing permanent emigration) and an increase in mortality rates were discussed as potential sources of the observed decline in fin whales in recent years.

Chapter 3 tested the hypothesis that the previously detected decline in fin whale numbers in the northern Gulf of St. Lawrence was the result of changing environmental conditions. Cetacean sighting data from 292 surveys in 2007-2013 were used to fit two distinct generalised additive models in terms of (1) bathymetric and oceanographic variables (the proxy model) and (2) modelled krill biomass (the prey model). Effort was quantified in units of time spent searching for individuals, which required a correction for 'handling time', i.e. the time spent off search effort while collecting auxiliary data. Both models corroborated an annual decline in relative fin whale abundance, but the trend was not correlated to any of the dynamic environmental variables (e.g. sea surface temperature, chlorophyll *a*, modelled krill biomass) included in the models. Failure to identify the underlying cause of the decline was discussed in the context of the small size of the study area, limited availability on fine-scale proxy and prey explanatory variables, and an increase in fin whale mortality rates.

In Chapter 4, a multi-faceted approach employing conventional fixation statistics, kinship- and coalescent-based analyses, was applied to provide detailed insight into the genetic structuring of a 'low divergence' species. The population genetic structure of fin whales in

the North Atlantic and Mediterranean Sea was assessed using multi-locus genotypes and mitochondrial control region DNA sequences from over 1,600 samples. Overall, the population genetic structure was characterised by a stepping stone model, with increased within-area relatedness and likely recurrent gene flow among adjacent areas. Demographic histories inferred from coalescent-based approaches suggested that North Atlantic fin whales underwent a post-glacial population expansion whereas the Mediterranean Sea fin whale population declined during this period. Kinship-based approaches suggested that the range of Mediterranean Sea fin whales includes the Strait of Gibraltar.

Chapter 5 investigated alternative demographic histories to explain the global genomic diversification patterns of fin whales in three ocean basins and two adjacent seas. I hypothesised that Pleistocene glacial-interglacial cycles affected population connectivity and effective population sizes of fin whales. Genome-wide single nucleotide polymorphism data were employed to perform demographic model selection. Population divergence among fin whales from the North Pacific and North Atlantic was best explained by a demographic model with secondary contact, implying a period of gene flow possibly during the last interglacial (~125 thousand years ago). The demographic histories of Northern and Southern Hemisphere fin whales were characterised by a two-epoch model with asymmetric gene flow and changes in effective population sizes. Past demographic histories provided context to contemporary levels of divergence among fin whales from different ocean basins and adjacent seas.

Chapter 6 provided a synthesis of the main results presented in this thesis. Demographic effects of changing environmental conditions were highlighted as recurrent theme across all chapters. I provided a discussion on possible implications of my results for population management and future work.

Nederlandse samenvatting

Populatiebiologie van de gewone vinvis: demografische en genetische toepassingen voor het bestuderen van populaties

De onderzoeksvelden populatie-ecologie, evolutionaire ecologie en conservatiebiologie zijn met elkaar verweven door hun focus op fenomenen op het populatieniveau. Dit proefschrift had als doel om nieuwe inzichten te verkrijgen in de populatiebiologie van de gewone vinvis (*Balaenoptera physalus*) door middel van diverse technieken uit de populatie-, en moleculaire ecologie. De focus op gewone vinvissen kwam voort uit de noodzaak voor geüpdatete kennis van hun populatiegenetische structuur en demografische trends, met nadruk op de Noord-Atlantische en Mediterrane gewone vinvis. In Hoofdstuk 1 werd een korte introductie van populatiebiologie en de huidige kennis over de gewone vinvis gepresenteerd.

Hoofdstuk 2 gaf geüpdatete schattingen van populatie-aantallen en overlevingskansen van gewone vinvissen in de noordelijke Golf van St. Laurens. Mark-recapture modellen werden toegepast op individuele vangst-histories gebaseerd op een lange-termijn foto-identificatie-dataset. Ik observeerde een populatie-afname van, naar schatting, 335 (95% betrouwbaarheidsinterval (BI) 321-348) individuen in 2004-2010 tot 291 (95% BI 270-312) individuen in 2010-2016. De afname werd bekrachtigd door een gelijktijdige afname in overlevingskansen tussen 1990 en 2015. De effecten van het niet voldoen aan de aanname van gelijke vangstkansen werden geëvalueerd binnen de context van divergente plaatstrouw onder individuen. Grootschalige verschuivingen in distributie (permanente emigratie veroorzakend) en een toename in sterftcijfer werden bediscussieerd als potentiële oorzaken van de geobserveerde afname in gewone vinvissen in recente jaren.

Hoofdstuk 3 testte de hypothese dat de hiervoor gedetecteerde afname in gewone vinvis-aantallen in de noordelijke Golf van St. Laurens het gevolg was van veranderende omgevingsomstandigheden. Observaties van zeezoogdieren uit 292 surveys in 2007-2013 werden gebruikt om twee verschillende gegeneraliseerde additieve modellen in termen van (1) bathymetrische en oceanografische variables (het proxymodel) en (2) gemodelleerde krillbiomassa (het prooimodel). Inspanning werd gekwantificeerd in eenheden van tijd besteed aan het zoeken van individuen, waarvoor een correctie voor 'handelingstijd', i.e. de tijd niet besteed aan zoeken tijdens het verzamelen van auxiliaire data. Beide modellen ondersteunden een jaarlijkse afname in het relatieve aantal gewone vinvissen, maar de trend correleerde met geen enkele dynamische omgevingsvariabele (zoals temperatuur van het zeewateroppervlak, chlorofyl a of gemodelleerde krillbiomassa) in de modellen. De mislukte

identificatie van de onderliggende oorzaken van de afname werden bediscussieerd in de context van het kleine formaat van het studiegebied, beperkte beschikbaarheid van nauwkeurige onafhankelijke proxy-, en prooivariabelen, en een toename in het sterftecijfer van de gewone vinvis.

In Hoofdstuk 4 werd een veelzijdige aanpak gebruikt waarbij conventionele fixatiestatistieken, verwantschap en coalescentie-gebaseerde analyses werden toegepast om een gedetailleerde inzage in de genetische structuur van een 'laag-divergente' soort. De populatiegenetische structuur van Noord-Atlantische en Mediterrane gewone vinvissen werd uitgezocht met behulp van multi-locus genotypering en mitochondriaal DNA uit ruim 1,600 monsters. De populatiegenetische structuur werd over het algemeen gekenmerkt door een stepping stone model, met verhoogde verwantschap binnen gebieden en recurrente genoverdracht tussen gebieden. Demografische histories afgeleid uit coalescentie-gebaseerde analyses suggereerden dat Noord-Atlantische gewone vinvissen in aantal toenamen na de vorige ijstijd, terwijl Midderraanse gewone vinvissen afnamen in deze periode. De verwantschapsanalyse suggereerde dat de Straat van Gibraltar binnen het bereik van Mediterrane gewone vinvissen ligt.

Hoofdstuk 5 onderzocht alternatieve demografische histories om de wereldwijde genomische diversificatie van gewone vinvissen in drie oceanen en twee aangrenzende zeeën te verklaren. Ik hypothesizeerde dat de cycli van de ijstijden tijdens het Pleistoceen van invloed waren op de populatieconnectiviteit en effectieve populatiegrootte van gewone vinvissen. Genoomwijde enkel-nucleotide polymorfismen werden gebruikt om demografische modelselectie uit te voeren. Populatie-divergentie tussen Noord-Pacifische en Noord-Atlantische gewone vinvissen was het best te verklaren volgens een demografisch model met secundair contact, wat een mogelijke periode van genoverdracht tijdens het vorige interglaciaal (~125 duizend jaar geleden) impliceert. De demografische histories van gewone vinvissen in het noordelijk-, en zuidelijk halfrond werd gekenmerkt door een two-epoch model met asymmetrische genoverdracht en veranderingen in effectieve populatiegrootte. De demografische histories geven context aan hedendaagse niveaus van divergentie tussen gewone vinvissen in verschillende oceanen en aangrenzende zeeën.

Hoofdstuk 6 geeft een synthese van de hoofddresultaten gepresenteerd in dit proefschrift. De demografische effecten van veranderende omgevingsomstandigheden werden benadrukt als terugkerend thema in alle hoofdstukken. Ik bediscussieer de mogelijke implicaties van mijn resultaten voor populatiemanagement en toekomstige studies.

(translated by Dr Jurjan van der Zee)

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About the author

Anna Schleimer is a Luxembourgish marine biologist specialised in baleen whale population biology. She received a Bachelor of Science in Marine Biology from the University of Plymouth in 2013. She conducted her undergraduate thesis under the supervision of Dr Simon Ingram (University of Plymouth) and Dr Dave Duffus (University of Victoria) on maternally directed feeding site fidelity in gray whales. She continued her studies at the University of St Andrews with a Master of Research degree in Marine Mammal Science. Under the supervision of Prof. Philip S. Hammond, she wrote a dissertation entitled 'The effect of changing environmental conditions on the distribution of fin whales in the northeast Atlantic'.

Anna's research experience is not limited to cetaceans. In 2015, she spent six months studying the effects of provisioning on the behaviour of whale sharks with the Large Marine Vertebrates Research Institute in the Philippines. Before the start of her PhD, she worked in the molecular laboratory of the National Museum of Natural History in Luxembourg, where she was involved in projects led by zoology curator Dr Alain Frantz on population connectivity in raccoons, bats, and foxes. She takes pride in having helped to uncover the murder of a hunting dog using genetic barcoding.

In 2015, she joined the team of the Mingan Island Cetacean Study on the North Shore in Québec, where she developed initial ideas for a PhD project with the research coordinator Dr Christian Ramp. Over the course of her PhD, Anna returned to the research station four times for field work. In 2016, Anna was awarded funding for her PhD project on the population biology of fin whales by the Luxembourg National Research Fund. The co-tutelle project was supervised by Prof. Philip S. Hammond at the University of St Andrews, Prof. Per J. Palsbøll and Dr Martine Bérubé at the University of Groningen, and Dr Christian Ramp from the Mingan Island Cetacean Study.

In Luxembourg, she is the co-founder and vice-president of ODYSSEA, a non-governmental organisation committed to marine conservation, research and awareness. She has participated with ODYSSEA in national science outreach events and has represented Luxembourg at international conventions.

Publication list

- Kimmig, S. E., Beninde, J., Brandt, M., Schleimer, A., Kramer-Schadt, S., Hofer, H., Börner, K., Schulze, C., Wittstatt, U., Heddergott, M., Halczok, T., Staubach, C., & Frantz, A. C. (2020). Beyond the landscape: resistance modelling infers physical and behavioural gene flow barriers to a mobile carnivore across a metropolitan area. *Molecular Ecology*, 00, 1–19. <https://doi.org/10.1111/mec.15345>
- Osten-Sacken, N., Heddergott, M., Schleimer, A., Anheyer-Behmenburg, H. E., Runge, M., Horsburgh, G. J., Camp, L., Nadler, S. A., & Frantz, A. C. (2018). Similar yet different: Co-analysis of the genetic diversity and structure of an invasive nematode parasite and its invasive mammalian host. *International Journal for Parasitology*, 48, 233–243. <https://doi.org/10.1016/j.ijpara.2017.08.013>
- Penketh, L., Schleimer, A., Labaja, J., Ponzo, A., Araujo, G., & Snow, S. (2020). Scarring patterns of whale sharks, *Rhincodon typus*, at a provisioning site in the Philippines. *Aquatic Conservation: Marine and Freshwater Ecosystems*. <https://doi.org/10.1002/aqc.3437>
- Ramp, C., Gaspard, D., Gavrilchuk, K., Unger, M., Schleimer, A., Delarue, J., Landry, S., & Sears, R. (2021). Up in the air: drone images reveal underestimation of entanglement rates in large rorqual whales. *Endangered Species Research*, 44, 33–44. <https://doi.org/https://doi.org/10.3354/esr01084>
- Schleimer, A., Araujo, G., Penketh, L., Heath, A., McCoy, E., Labaja, J., Lucey, A., & Ponzo, A. (2015). Learning from a provisioning site: code of conduct compliance and behaviour of whale sharks in Oslob, Cebu, Philippines. *PeerJ*, 3, e1452. <https://doi.org/10.7717/peerj.1452>
- Schleimer, A., Frantz, A. C., Lang, J., Reinert, P., & Heddergott, M. (2016). Identifying a hunter responsible for killing a hunting dog by individual-specific genetic profiling of wild boar DNA transferred to the canine during the accidental shooting. *Forensic Science, Medicine, and Pathology*, 9–14. <https://doi.org/10.1007/s12024-016-9806-9>
- Schleimer, A., Ramp, C., Delarue, J., Carpentier, A., Bérubé, M., Palsbøll, P. J., Sears, R., & Hammond, P. S. (2019). Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence. *Ecology and Evolution*, 9(7), 4231–4244. <https://doi.org/10.1002/ece3.5055>
- Schleimer, A., Ramp, C., Plourde, S., Lehoux, C., Sears, R., & Hammond, P. (2019). Spatio-temporal patterns in fin whale *Balaenoptera physalus* habitat use in the northern Gulf of St. Lawrence. *Marine Ecology Progress Series*, 623, 221–234. <https://doi.org/10.3354/meps13020>

Víkingsson, G. A., Pike, D. G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B. Á., Mikkelsen, B., Øien, N., Desportes, G., Bogason, V., & Hammond, P. S. (2015). Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? *Frontiers in Ecology and Evolution*, 3, 1–18. <https://doi.org/10.3389/fevo.2015.00006>

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Douglas Adams, *The Long Dark Tea-Time of the Soul*

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