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SEI WHALE (*BALAENOPTERA BOREALIS*) ECOLOGY AND MANAGEMENT IN THE NORTH ATLANTIC

by

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ABSTRACT

The current knowledge and data gaps on the biology and ecology of the sei whale (*Balaenoptera borealis*) in the North Atlantic (NA) are reviewed and quantified. Topics where investment is necessary to ensure the proper management of the species are identified and suggestions are made in how to tackle data deficiencies. State of the art ecological research methods are used to characterize the summer habitat of the sei whale off New England and Nova Scotia, the migration and foraging behaviour of the species in the NA, and to investigate the plausibility of existing stock boundaries. It is shown that research on the species has been stagnant for more than two decades. Essential aspects of the sei whale ecology and biology are still mainly derived from whaling records. Movement patterns and winter distribution are not clear and great uncertainty exists about the subdivision of the NA population in further biological units. Abundance estimates in the NA are fragmentary and restricted to a small part of the known part of the species summering habitat. In order to gain insight in the distribution of the sei whale in the north-western Atlantic, a summer habitat suitability model was fit to presence-only data derived from aerial and shipboard sighting surveys, opportunistic sightings and whaling records. The model predicts high habitat suitability for areas of known sei whale aggregation off New England and Nova Scotia but also indicate that other areas, especially along the shelf edge, hold suitable conditions for the occurrence of sei whales in the summer. Further, the model indicates that the sei whale and the right whale (*Eubalaena glacialis*) habitats partially overlap in the studied region, which can translate in possible competition for prey. The migration of the NA sei whales was investigated using satellite telemetry. Results show a migratory corridor between the Azores islands (Portugal) and the Labrador Sea (LS) during the spring. A Bayesian switching state space model was used to investigate the behaviour of sei whales monitored by satellite tags and it is shown that the LS comprises a foraging ground for the species during spring and summer. The most probable origin of those sei whales is the region south or southeast of the Azores, possibly from wintering grounds thought to exist off northwest Africa. The results of the study uncovered unknown patterns about the distribution, movements and habitat use of the sei whale in the North Atlantic, providing new evidence essential to create plausible hypotheses about the stock structure of the species.

SUMÁRIO

O estado actual da investigação e lacunas de conhecimento sobre a biologia e ecologia da baleia sardinheira (*Balaenoptera borealis*) no Atlântico Norte (AN) são revistos e quantificados. As áreas de investimento necessário para suportar a gestão da espécie são identificadas e são feitas sugestões para resolver deficiências de dados. Metodologias modernas de obtenção e tratamento de dados são utilizadas para caracterizar o habitat de verão da baleia sardinheira no Atlântico noroeste, para estudar a migração e comportamento alimentar da espécie no AN e para investigar a plausibilidade das actuais áreas de gestão populacional. Os resultados demonstram que a investigação acerca da baleia sardinheira estagnou há mais de duas décadas. A maior parte do conhecimento sobre aspectos essenciais da espécie baseia-se em dados da baleação. Os padrões de movimentação e a distribuição durante o inverno são virtualmente desconhecidos e subsiste uma grande incerteza quanto à existência e identidade de unidades populacionais no AN. As estimativas de abundância são dispersas e restringem-se a uma pequena parte do habitat de verão da espécie. Para compreender melhor a distribuição da baleia sardinheira no Atlântico noroeste, um modelo foi ajustado a dados de presença obtidos a partir de avistamentos durante campanhas de amostragem navais e aéreas, observações oportunísticas e capturas nas águas da Nova Inglaterra e Nova Escócia. O modelo prevê a existência de habitat favorável em áreas de conhecida agregação da espécie no verão, mas também indica a existência de outras áreas favoráveis, principalmente ao longo do talude continental. Existe alguma sobreposição do habitat da baleia sardinheira com o da baleia franca (*Eubalaena glacialis*), o que pode resultar em competição alimentar. A migração da baleia sardinheira no AN foi investigada utilizando telemetria por satélite. Os resultados demonstram a existência de um corredor migratório entre os Açores e o Mar do Labrador (ML). Um modelo probabilístico Bayesiano de estados num espaço (*state space model*) foi utilizado para investigar o comportamento das baleias, demonstrando que o ML é uma área de alimentação para a espécie. As baleias vistas nos Açores provavelmente passam o inverno em regiões a sul ou sudeste do arquipélago, possivelmente ao largo da costa ocidental africana. O estudo permitiu identificar padrões desconhecidos sobre a distribuição, movimentos e utilização de habitat da baleia sardinheira no AN, provendo informação nova e actualizada, essencial para a criação de cenários plausíveis sobre a estrutura populacional da espécie.

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FIRST CHAPTER

General introduction and dissertation organization

GENERAL INTRODUCTION

Whales and Man throughout history

Cetaceans appear in the fossil record during the Eocene, 52.5 million years ago (Mya), and rapidly radiate to attain the peak in diversity during the middle Miocene (approximately 16 Mya) [1]. After the Miocene, cetacean diversity decreased progressively to the present 90 species (of which one, a river dolphin, is possibly extinct) [2]. The extant cetacean are subdivided in two clades, the Mysticeti (the baleen whales, with 14 species) and the Odontoceti (the toothed whales, with 76 species), all fully aquatic.

Due to the physical characteristics of their environment and macroevolutionary factors most cetaceans became large in comparison to land mammals, with whales attaining the largest sizes in the animal Kingdom [3]. Among many adaptations to the aquatic environment, cetaceans developed a thick sub-dermal adipose layer that would eventually be central in the ecological relation that evolved between those animals and Man.

Their large size means that securing a whale carcass guarantees access to large quantities of meat, fat and raw materials. Thus it is not surprising that Man (*Homo sapiens*) and other hominids started exploiting cetaceans as a resource already in pre-historic times, initially opportunistically as result of strandings [4-7] but soon engaging into active hunting and, in a sense, becoming predators of those animals [8-14]. Due to the sheer size of the animals and the fact that they are strictly aquatic, cetacean hunting is logistically and technically challenging and the activity probably played an important role in technological development and seafaring for some cultures [8,10,13,15]. Nevertheless, some whale species are markedly more difficult to capture than others, due to a combination of anatomy and behaviour, dictating that up to the 1860's only a few species were targeted by most whaling operations. Those were the bowhead whale (*Balaena mysticetus*), the right whales (*Eubalaena glacialis*, *E. australis*, *E. japonica*) the humpback whale (*Megaptera novaeangliae*), the gray whale (*Eschrichtius robustus*), and the sperm whale (*Physeter macrocephalus*) [16,17].

From the 11th Century onwards, starting in Europe, whaling evolved from a subsistence activity to an extractive industry focused mostly on obtaining oil and baleen that were used as raw materials for other industries [16,18]. With industrialization whaling captures became massive, numbering in the tens of thousands, and started impacting the sustainability of the targeted whale populations [19-22]. The mechanization of vessels and technological improvements in catching and processing equipment (introduced in the mid-19th Century) opened the way to the capture of other species that were until then logistically unavailable, giving rise to what is known as "modern whaling" [16,18]. Modern whaling was characterized by a rapid decline in whale populations, with species being depleted successively according to their relative size, from larger to smaller, a reflex of the sole focus of the industry in oil production (larger species yielding more oil per individual) [18].

Due to the important role of whales as marine predators, collapse of whale populations caused by whaling is thought to have affected the functioning of ecosystems across entire ocean basins and along the water column [23-27]. Most (if not all) whale populations that underwent commercial exploitation are believed to still be under recovery but increasing human and environmental pressures threaten that recovery for some species/populations [28-30]. Thus, there is still much uncertainty about how whale populations will behave in the future.

Independently of the direction of population trends, fluctuations in whale abundance are relevant not only at an ecological level, but also under a socio-economic perspective [31]. For example, substantial increases in whale populations will result in sizeable reductions of their prey and may directly or indirectly affect many species currently targeted by fisheries [23,32].

Yet, despite centuries of exploitation, we advanced little in understanding the ecology and ecological role of most whale species. As it will be shown in Chapter Two of this dissertation, some species (of which the sei whale, *Balaenoptera borealis*, is a paradigmatic example) were essentially neglected by modern ecological science. It is thus clear that new approaches to studying whale ecology and to whale management are of paramount importance. Some authors (e.g. [31]) go to the extreme of suggesting that studies on whale ecology might be more useful in whale and ecosystem management than estimation of whale demography. I disagree, and believe that both approaches are complementary and necessary at this stage.

The sei whale

The sei whale is one of the eight species in the Family *Balaenopteridae*, the rorqual whales [2]. The taxonomy of the sei whale was a complex affair from the very beginning. On February 21, 1819 a whale stranded in the shore of Holstein, Germany, and was transported to Hamburg where it was on paid display during two months, until the stench drove away even the bravest visitors and put an end to the profitable business. It was only then that the eminent scholar from the University of Berlin Karl Asmund Rudolphi acquired the decayed carcass and took it back with him to Berlin to be studied. Rudolphi published his anatomical notes on this specimen in 1822 [33], but erroneously described it as *Balaena rostrata* Fabricius, 1780 – an early synonymous of the common minke whale *Balaenoptera acutorostrata*.

In 1823 Georges Cuvier referred to Rudolphi's specimen as "Rorqual du Nord" but did not use a binomial Latin name, and despite noting several anatomical differences it is unclear if he suspected that it should belong to a different species [34]. It was not until 1828 that Réne Primevère Lesson converted the Cuvier's vernacular designation of "Rorqual du Nord" into Latin as *Balaenoptera borealis*, finally coining the formal binomial designation [35].

Regardless of his mistake, for a long time the English vernacular designation of the species was "Rudolphi's rorqual", honouring the original describer of the holotype. However, the vernacular name most widely used to designate the species is the Norwegian derived "sei whale" (*Sejhval*), in a reference to the arrival of these whales upon the coasts of northern Norway at the same time as the *"seje"* or pollock (*Pollachius virens*).

In the following decades after the description of the species, at least a dozen new similar species and subspecies were described, but eventually all were identified as synonyms to the sei whale. Currently there are two subspecies recognized, although morphological and genetic support for the southern-hemisphere subspecies is weak. The two subspecies are:

- *Balaenoptera borealis borealis* Lesson, 1828 referring to the Northern hemisphere sei whale. The holotype, the specimen collected by Rudolphi, was stored in the Berlin Museum of Natural History but is presumed destroyed as a consequence of bombings during WWII.
- *Balaenoptera borealis schlegellii* Flower, 1865 that refers to all sei whales from the southern hemisphere. The holotype of this subspecies is in the Leiden Museum of Natural History.

Sei whales are around 4.5 m when they are born. As with other baleen whales, adult females grow slightly larger than males with sizes ranging from 13.4 to 19.5 m. Males range between 12.8 to 18.6 m. The larger sizes are attained by the Southern Hemisphere individuals. Adult weights range between 20 to 30 metric tons [36]. They have a slender body and lack complex pigmentation patterns. They are dark grey over most of the body and white on the underside. The body is often covered with round scars presumably from cookie-cutter sharks (*Isistius brasiliensis*).

The dorsal fin is tall and falcate, normally making an angle with the back in excess of 45º. In some individuals the dorsal fin has one or more circular holes near the trailing edge, possibly caused by burying parasites [37]. The rostrum is somewhat pointed and is slightly pitched, having a single ridge in the middle that runs from the splash guard of the blowholes to the tip of the mouth. In the field and at close range, the single ridge on the head is the most reliable feature in distinguishing the sei whale from the very similar Bryde's whale, which has three ridges [38].

Sei whales have 340 to 350 plates of dark grey baleen with light bristles, measuring between 75 and 80 cm in length. Some individuals can have some white plates near the tip of the rostrum [38]. The ventral grooves (or pleats) that allow the mouth to expand during feeding, end well before the navel, unlike what happens in most other Balaenopteriid whales (except for the minke whale) [36].

Despite their cosmopolitan distribution and having been heavily exploited throughout the world by whaling operations, we are still ignorant of many aspects of the lives of sei whales. Some whale species came under the focus of intense research over the last decades for diverse reasons: for being highly endangered; for having coastal habits which increases study opportunities; for being iconic; for being commercially exploited; or for a combination of those. The sei whale does not fall into any of those categories. Research on the sei whale in the past was mostly fuelled by whaling. When whaling came under intense public scrutiny, the sei whale came out of the research spot-lights as a result of the moratorium on all commercial whaling activity declared by the International Whaling Commission from the 1985–86 pelagic and 1986 coastal seasons [39]. In the last decades, in the North Atlantic (NA), only few localized and short-termed studies exist that focused or included this species (some examples are presented in the Second Chapter).

Currently any attempt for science driven management of the species at the scale of the North Atlantic is bound to be unsuccessful due to the limited and obsolete nature of the data.

This dissertation examines some aspects of the sei whale ecology in the NA using state of the art data collection and analytical techniques. The motivation of the dissertation is not only to contribute for a better understanding of the ecology of the species in the NA but also to demonstrate that with modern research techniques it is possible to properly inform management decisions, even for intractable species such as whales. By careful use of state of the art techniques I show how it is possible to obtain *much out of little*, in order to improve our understating about the ecology and ecological roles of whales and to aid in the management of these animals and their ecosystems in a cost-effective manner. The results provide much needed information about the ecology of the sei whale in the North Atlantic and show that similar techniques can be invaluable to the study and management of other taxa facing the same problems of data scarcity.

DISSERTATION STRUCTURE

This dissertation is composed by four research chapters, plus the General Introduction and Discussion chapters. The research chapters are intended to stand alone as publishable units and as a result some redundancy in the introduction and methods sections can be found. For the same reason, no cross-references are made between research chapters, but references to published and "In Press" chapters may be found in the text.

By their nature, some chapters made heavy use of references. For the sake of readability references are presented as numbered endnotes to each chapter using the PLoS style.

The Second Chapter, "*The forgotten whale: a bibliometric analysis and literature review of the North Atlantic sei whale (*Balaenoptera borealis*)*" was published in

Mammal Review (DOI: 10.1111/j.1365-2907.2011.00195.x) and is presented as part of this dissertation with acknowledgement to the co-authors, David Janiger, Mónica A. Silva, Gordon T. Waring and João M. A. Gonçalves.

The Fourth Chapter, "*Assessing performance of Bayesian state-space models fit to Argos satellite telemetry locations processed with Kalman filtering*" has been accepted for publication in PLoS ONE (DOI: 10.1371/journal.pone.0092277) and is presented as part of this dissertation with acknowledgement to the co-authors, Mónica A. Silva, Ian D. Jonsen, Deborah J. F. Russell, Dave Thompson and Mark F. Baumgartner.

The Fifth Chapter, "*Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry*", has been accepted for publication in Endangered Species Research (DOI:10.3354/esr00630) and is presented as part of this dissertation with acknowledgement to the co-authors, Mónica A. Silva, Gordon T. Waring and João M. A. Gonçalves. Results of this chapter were also included in a working paper presented to the 64th meeting of the International Whaling Commission Scientific Committee (working paper SC/64/RMP6, available from http://iwc.int/iwc64docs), in the scope of the discussion over a proposal by Iceland for the pre-implementation of a management procedure for the eventual resumption of sei whaling by that country.

DISSERTATION OUTLINE

First Chapter: General introduction and dissertation structure

The First Chapter lays down the motivation of the thesis, describes the form of the dissertation and briefly introduces the aims and hypotheses of each of the research chapters.

Second Chapter: The forgotten whale: a bibliometric analysis and literature review of the North Atlantic sei whale (*Balaenoptera borealis*)

In the Second Chapter, I assess the state of the art in North Atlantic sei whale research. This chapter is more than a mere review of published and unpublished information. By using bibliometric techniques I show that research on the sei whale is stagnant in comparison to other similar species. I also clearly quantify the scientific production by subjects and regions of the World, showing where are the greatest deficiencies in knowledge and which are the more relevant issues to resolve for the proper management of the species and the ecosystems it integrates. Research and management funding is limited and understandably funding agencies want to maximize the outcome of their investment and restrict spending to solving essential problems. The approach taken in the Second Chapter is the first step in tackling the data deficiency problem posed by the sei whale. By clearly showing that existing data on sei whale is insufficient for its management and laying down the most appropriate lines of research that should be followed to obtain that data, the Second Chapter makes a better case in defending investment on this species.

Objectives

2.1 To give an in-depth review on the state of the art on the North Atlantic sei whale.

2.2 Provide a clear quantification of the knowledge on the sei whale biology and ecology and research needs to inform management decisions.

2.3 Identify lines of research necessary to resolve the data deficiency.

Hypotheses

2.1 Existing data on the North Atlantic sei whale is insufficient and inappropriate for its proper management.

2.2 Existing level of research on the North Atlantic sei whale is insufficient to solve data deficiencies.

Third Chapter: Habitat suitability of the sei whale (*Balaenoptera borealis*) in New England and Nova Scotia using presence-only modelling

In the Third Chapter, sighting and whaling data are combined to create a model of summer habitat suitability for the sei whale off New England and Nova Scotia. To achieve that goal a Maximum Entropy algorithm was employed to enable the use of presence-only data. Pooling the data from several sources and using low-cost opportunistic data enabled the creation of cost-efficient and credible habitat suitability maps. The study also unveiled overlap of feeding habitats in the study region and potential competition between the sei whale and the endangered North Atlantic right whale (*Eubalaena glacialis*). Finally, the model limitations are discussed and improvements suggested so that it can be properly used when informing management decisions.

Objectives

3.1 To assess the feasibility of using presence-only data derived from distinct sources to develop a habitat suitability model for the sei whale.

3.2 To provide habitat suitability maps of the sei whale to advance scientific knowledge on the species and to inform management decisions.

Hypotheses

3.1 Presence-only data of sei whales is sufficient to produce a habitat suitability model that performs better than random.

3.2 Summer habitat suitability for the sei whale is not homogeneous within the study region.

Fourth Chapter: Assessing performance of Bayesian state-space models fit to Argos satellite telemetry locations processed with Kalman filtering

The Fourth Chapter is a more technical chapter, but essential to back the analysis made in the Fifth Chapter. In the Fourth Chapter the reliability of fitting Bayesian state-space models (SSMs) and switching state-space models (SSSMs) to marine mammal satellite tracking data processed with a recently released location algorithm (Kalman Filter; KF) is investigated. This study is relevant since although SSMs and SSSMs have been used to model animal movement and behaviour using an older location algorithm (Least Square; LSq), the implications of using these models with the new algorithm were not known and could lead to biased estimates of movement parameters and behavioural states. The results presented in that chapter show that fitting SSMs and SSSMs to KF derived data offer clear advantages over LSq derived data. Since the KF algorithm can considerably increase the number of received positions and prolong the tracking periods, the results presented in the Fourth Chapter are of the upmost relevance to studies where few messages are received, which applies to many marine and dense forest species.

Objectives

4.1 To assess the spatial accuracy of locations from models fit to data derived from LSq and KF processing algorithms.

4.2 To determine how spatial accuracy varies with observation frequency, temporal resolution and reported precision of Argos locations.

4.3 To investigate how the quality of tracking data affected the similarity of the output from SSSMs fit to LS and KF data.

Hypotheses

4.1 Spatial accuracy of locations from SSM models fit to KF processing algorithm derived data is similar or better than from LSq derived data.

4.2 Data quality has the same effect in the accuracy of the results from SSM models fit to LSq and KF data.

4.3 Parameters of SSSM models fit to LSq and KF data are similar both for location and behavioural estimation.

4.4 Fitting SSM models to KF derived data brings advantages over LSq derived data.

Fifth Chapter: Of rooks, bishops and queens. Sei whale movements in the North Atlantic chessboard

In the Fifth Chapter satellite telemetry technology is used to gain insight in the migratory and foraging behaviours of the sei whale in the North Atlantic (NA) and to address a management problem regarding the stock composition of the population. Using a Bayesian switching state-space model (SSSM) whale tracks were reconstructed and movement parameters were investigated to infer behaviour. The method enabled the distinction of two discrete movement phases, corresponding to migratory and foraging behaviours. The study demonstrates that the Labrador Sea is an important feeding ground for the sei whale and also resolved the origin of sei whales seen in that region. More importantly, the results presented in the Fifth Chapter offers un unprecedented view about the large scale movements of the sei whale in the North Atlantic, challenging some pre-conceived notions and offering much needed information for the proper management of the species. The Fifth Chapter is also an example of the power of state of the art techniques in obtaining cost-effective, meaningful data that is useful both to gain insight into the ecology of challenging species and to inform management decisions.

Objectives

5.1 To investigate the migratory destinations and behaviour of sei whales seen off the Azores.

5.2 To identify foraging areas for this species.

5.3 To identify wintering areas for this species.

5.4 To assess the pertinence of existing theories on population structure for the species in the North Atlantic.

Hypotheses

5.1 Whales seen in the Azores during the spring are *en-route* to foraging grounds.

5.2 Known feeding grounds of the sei whale in the North Atlantic are discrete.

5.3 Migration of sei whales in the North Atlantic is restricted to movements along a north-south axis, supporting a latitudinal structuring of the population.

5.3 Satellite telemetry can be used to identify plausible hypotheses about movements and stock structure of whales to inform management decisions.

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