Influence of environmental drivers on the movement behaviour of harbour porpoises in the North Sea

Dissertação de Mestrado

Dominique Sabina Stalder

Mestrado em

Estudos Integrados dos Oceanos

SICUT AURORA SCIENTIA LUCET

UNIVERSIDADE DOS AÇORES

Horta
2018

Influence of environmental drivers on the movement behaviour of harbour porpoises in the North Sea

Dissertação de Mestrado

Dominique Sabina Stalder

Orientadores

Dr. Floris M. van Beest

Department of Bioscience – Marine Mammal Section
Aarhus University, Denmark

Prof. Dr. João M. dos Anjos Gonçalves

Departamento de Oceanografia e Pescas
Universidade dos Açores, Portugal

Dissertação de Mestrado submetida como requisito parcial para obtenção do grau de Mestre em Estudos Integrados dos Oceanos

Abstract

The harbour porpoise is a small marine predator with a high conservation status in European waters. In order to protect the species effectively, it is crucial to acquire detailed knowledge on behavioural responses to changing environmental conditions. Here, I investigated the influence of environmental conditions on variation in large-scale movement behaviour of the harbour porpoise population in the North Sea. The movement tracks of 57 satellite-tracked individuals tagged over a total period of 19 years were analysed. For each relocation, the underlying behavioural state (area-restricted or transient state) of the individual was estimated using a state-space modelling (SSM) approach. The behavioural states were then modelled as a function of multiple static and dynamic environmental variables by means of a logistic regression. Harbour porpoises were estimated to spend about 81% of their time in area-restricted state (i.e. movements within feeding areas), while they spent only a small amount of their time (6%) in making fast and long-ranging movements, classified as transient state. These short movement bursts over long distances likely reflected transient movements between foraging grounds. The remaining relocations (13%) could not be assigned unambiguously to either state. Considerable individual differences in the extent of movements were found, with the maximum net displacement from the first location ranging from 24 km to 867 km. Accordingly, the proportion of time spent in transient state (ranging from 0.5% to 20.0%) and resident state (ranging from 50.5% to 99.5%) was highly variable among individuals. The area-restricted state was associated with low levels of salinity, temperature and current velocity; with high levels of chlorophyll a concentrations relative to the seasonal mean; and with intermediate sea bottom slopes. These results indirectly indicate that prey species may aggregate in areas where such environmental conditions are found, therefore serving as feeding grounds to harbour porpoises. Earlier studies on harbour porpoise distribution and abundance support the importance of these environmental drivers. The findings from this study can be used to better inform spatially explicit population models that are currently being developed to study the impact of a changing marine environment with increasing anthropogenic disturbance on harbour porpoise population dynamics.

Resumo

O boto é um pequeno predador marinho com um elevado estatuto de conservação nas águas europeias. Para uma proteção eficaz desta espécie é importante ter conhecimentos detalhados das respostas comportamentais às mudanças das condições ambientais. Neste estudo, investiguei a influência das condições ambientais sobre a variação do comportamento de deslocação de grande escala da população de botos no Mar do Norte. Foram analisados dados de deslocações de 57 indivíduos rastreados por satélite num período de 19 anos. Para cada relocalização, estimou-se o estado comportamental subjacente do indivíduo (residência ou em deslocação) recorrendo a processos de modelação do estado espacial (State-space modelling, SSM). Estes estados comportamentais foram então correlacionados com variáveis ambientais estáticas e dinâmicas através de regressões logísticas. Estimou-se que os botos estão cerca de 81% do seu tempo em áreas circunscritas, passando apenas uma pequena parte do seu tempo (6%) em rápidas deslocações de longa distância, classificadas como estado de deslocação. Esses movimentos de curta duração e longas distâncias refletem provavelmente deslocações entre áreas de procura de alimentação. As restantes relocalizações (13%) não puderam ser atribuídas sem ambiguidade a nenhum destes estados comportamentais. Foram encontradas diferenças individuais consideráveis na extensão destas deslocações, com máximos variáveis entre 24 km e 867 km, relativamente à posição inicial. Consequentemente, a proporção de tempo gasto no estado de deslocação rápida (variando de 0,5% até 20,0%) e no estado residente (variando de 50,5% até 99,5%) foi altamente variável entre indivíduos. O estado residente foi associado com baixos níveis de salinidade, temperatura e velocidade da corrente; com altas concentrações de clorofila-a em relação à média sazonal; e com declives intermédios do fundo. Estes resultados indicam indiretamente que as presas dos botos provavelmente se agregaram em áreas com as condições ambientais referidas, servindo, portanto, como área de alimentação. Estudos anteriores sobre a distribuição e abundância dos botos suportam a importância desses fatores ambientais. Os conhecimentos adquiridos neste estudo podem ser usados para melhorar os modelos populacionais espaciais que estão atualmente a ser desenvolvidos para estudar o impacto do ambiente marinho em mudança, e com as crescentes perturbações antrópicas, que afetam a dinâmica da população de botos.

Contents

List of Figures

List of Tables

1. Introduction

1.1 Overview

Marine predators can influence the structure and functioning of marine ecosystems by changing the abundance and behaviour (risk effects) of prey species (Heithaus et al. 2008). Given their position at the top of the food chain, changes in predator abundance can potentially have cascading effects on other trophic levels within ecosystems (Estes et al. 1974, Branch and Williams 2006, Myers et al. 2007). Over the past decades, a decline in the abundance of various marine predator species has been observed as a consequence of targeted fisheries (Pauly et al. 1998, Myers and Worm 2003) and bycatch (Baum et al. 2003). Moreover, marine predator populations are expected to be negatively impacted by several stressors such as pollutants (e.g. Desforges et al. 2018), underwater noise (Madsen et al. 2006) and climate change (Veit et al. 1997). To reduce possible negative human impact and because of their key role in marine ecosystems, great effort is put into the conservation of marine predators, e.g. by establishing marine protected areas (Hooker and Gerber 2004) or measures to mitigate bycatch (Gilman 2011, van Beest et al. 2017). However, in order to implement successful measures for management and conservation of marine predators, detailed knowledge on variation in spatial and temporal movement behaviour and habitat use is critical (Allen and Singh 2016). Recent advances in biotelemetry (Tomkiewicz et al. 2010) and analytical frameworks such as state-space modelling (Morales et al. 2004, Jonsen et al. 2005) offer useful insight into the movement ecology of marine mammals and can thus guide the design of effective conservation measures.

State-space models (SSMs) are time-series models that can be used to infer an individual's behaviour (unobserved state) along its movement track (observed data), thereby offering the possibility to objectively estimate behaviour from satellite tracking data (Jonsen et al. 2013). Based on inherent characteristics of the movement track, the behaviour of the individual is estimated at each relocation. The underlying assumption of this approach is that differences in behaviour are reflected by changes in the animal's movement path (Morales et al. 2004, Jonsen et al. 2005). For example, an animal moving in a relatively fast and directed manner for a period of time is expected to disperse or migrate to another area within its range. In contrast, relatively slow movements with frequent changes in direction could indicate that the animal is searching for prey, i.e. termed area-restricted search behaviour (Turchin 1991). An advantage of SSMs is that error distributions from the observed data (e.g. the satellite locations) can be included, making them suitable for error-prone Argos data (Vincent et al. 2002), which is the technology often used to track movements of marine species (Jonsen et al. 2005, 2013). With this approach, areas that are important for different behavioural types or life stages can be identified and their importance to the species might be assessed (Dulau et al. 2017). Accordingly, SSMs have successfully been used to e.g. identify important breeding grounds of humpback whales (Trudelle et al. 2016, Dulau et al. 2017), describe intermittent foraging of migrating blue and fin whales (Silva et al. 2013) and to identify offshore foraging grounds of killer whales (Reisinger et al. 2015).

The harbour porpoise, *Phocoena phocoena* (Linnaeus, 1758) is a relatively small marine predator occurring throughout the northern hemisphere in both cold temperate and sub-polar waters (Read 1999, Gaskin 1984). The species inhabits mainly shallow, coastal areas (Read 1999), but has recently been documented to use oceanic habitats with waters >2500 m deep in the North Atlantic during winter and spring months (Nielsen et al. 2018). Harbour porpoises are the most abundant cetacean species in the North Sea (Hammond et al. 2002, 2013, 2017). The total number of harbour porpoises in the North Sea was estimated to be about 345 000 individuals and about 42 000 individuals in the adjacent Kattegat and Belt Seas in the Inner Danish Waters during the SCANS III survey in 2016 (Hammond et al. 2017). Despite being abundant in European waters, there are concerns that the species might be negatively affected through high levels of bycatch (Vinther and Larsen 2004) and pollutants (Siebert et al. 1999); as well as by underwater noise from pile-driving during offshore wind-farm construction (Tougaard et al. 2009, Bailey et al. 2010, Dähne et al. 2013), seismic surveys (Pirotta et al. 2014) and shipping (Dyndo et al. 2015, Wisniewska et al. 2018). Accordingly, harbour porpoises are protected in the European Union (EU) through the EU Habitats Directive, where the species is listed in Annex II and IV (EU 1992). This means that the species is strictly protected across its entire range within the EU and deliberate killing, disturbance and habitat deterioration are prohibited (Annex IV). Moreover, special conservation areas have to be established and managed according to the ecological needs of the species (Annex II). In order to implement successful measures for management and conservation of the harbour porpoise populations, detailed knowledge on movement behaviour and habitat use and how these vary over space and time is needed.

Seasonal shifts in harbour porpoise density have been observed in various populations across the range of the species, e.g. in the North Sea (Sveegaard et al. 2011, Gilles et al. 2016), the adjacent Belt Sea and Baltic Sea (Sveegaard et al. 2011), as well as in the Bay of Fundy and Gulf of Maine, Canada (Read and Westgate 1997). The reasons for these variations are not well understood but are likely linked to changes in prey distribution (Gilles et al. 2016). Considerable individual differences in the extent of movements have been observed (Read and Westgate 1997) and seasonal displacements seem to be gradual and individual-specific rather than coordinated mass migrations (Read and Westgate 1997, Sveegaard et al. 2011). Indeed, Sveegaard et al. (2011) found that tagged harbour porpoises occupied mainly areas close to the tagging sites in Kattegat and Skagen (i.e. high site fidelity) though some individuals left the area and traversed large distances across the North Sea. To date, it is unknown what triggers such long-range movements. Despite the ability of harbour porpoises to move over extended distances in a short period, their focal areas have been found to be relatively small (Johnston et al. 2005) and strongly associated with areas where prey species presumably aggregate. Such areas include for example islands and headland wakes, where primary production is high due to enhanced vorticity during flood tides (Johnston et al. 2005). Several other studies found high densities of harbour porpoises in sites with high tidal currents, e.g. in tidal estuaries used by prey species to exploit increased food availability (IJsseldijk et al. 2015) or next to trenches in the seabed where prey species are funnelled and transported towards the waiting harbour porpoises by the tidal current (Pierpoint 2008).

Furthermore, harbour porpoise abundance has also been explained by various environmental conditions, including water depth (Marubini et al. 2009, Isojunno et al. 2012, Booth et al. 2013, Gilles et al. 2016, Díaz López and Methion 2018), sea bottom slope (Isojunno et al. 2012, Booth et al. 2013), distance to coast (Marubini et al. 2009, Edrén et al. 2010, Booth et al. 2013, Gilles et al. 2016), tidal cycle and current velocity (Marubini et al. 2009, Embling et al. 2010, IJsseldijk et al. 2015), temperature (Gilles et al. 2016, Wingfield et al. 2017, Díaz López and Methion 2018), sea surface chlorophyll a concentration or primary production (Gilles et al. 2011, Wingfield et al. 2017), time of day (IJsseldijk et al. 2015, Wingfield et al. 2017) and seasonality (Haelters et al. 2011, Peschko et al. 2016, Gilles et al. 2016, Wingfield et al. 2017). However, the above findings are largely based on aerial surveys and opportunistic observations. Much less effort has been done on studying variation in movements patterns of individual porpoises and the relation to environmental conditions (but see van Beest et al. 2018 on fine-scale movement behaviour of harbour porpoises).

1.2 Aims and hypotheses

The aims of this study were to quantify variation in the movement behaviour of harbour porpoises in the North Sea and to identify environmental features that influence the behavioural state of tagged individuals. To do so, I capitalized on an on-going long-term Argos satellite tracking dataset (starting in 1997) including movement tracks of 57 harbour porpoise individuals tagged along the Danish coastline. I first applied a SSM to the movement data to detect one of two behavioural states, namely restricted search behaviour or transient behaviour, for each relocation. A logistic regression was then used to assess how environmental variables influence the probability of being in one of these behavioural states. Doing so will provide a better understanding about the influence of environmental conditions on harbour porpoise movement and behaviour and how they change over time.

The following hypotheses were tested:

1) Harbour porpoises have a high energy demand due to their distribution in cold and temperate waters and small body size leading to high metabolic rates (Kastelein et al. 1997, Lockyer and Kinze 2003). I therefore expect that the tagged individuals use area-restricted behaviour (likely to be feeding) most of the time interrupted only by short transient movements (movements between feeding areas and unlikely to be feeding).

2) Although little data exists on which environmental conditions harbour porpoises prefer or follow while in transient behaviour, travelling behaviour has previously been found to occur along isobaths in the Bay of Fundy (Read and Westgate 1997) and I expect to find similar patterns in areas of the North Sea with a steep bathymetry gradient e.g. along the Norwegian Trench.

3) Harbour porpoises are assumed to closely follow the distribution of their prey and exploit oceanographic features where prey species aggregate (Johnston et al. 2005). I, therefore, expect an increasing likelihood of observing relocations in the area-restricted search state in areas with high primary productivity, e.g. coastal areas or the Doggerbank (Brockmann et al. 1990, Gilles et al. 2016). In addition, van Beest et al. (2018) found that harbour porpoises in the North Sea used fine-scale movements indicative of foraging behaviour in shallow and saline waters, so I expect relocation in the area-restricted search state to follow the same pattern.