

COMMISSIONED REPORT

Commissioned Report No.

The development of a framework to understand dolphin behaviour and from there predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population

For further information on this report please contact:

Ben Leyshon
Scottish Natural Heritage
Fodderty Way
Dingwall Business Park
Dingwall
IV15 9XB
Tel: 01349 865333
E-mail: Ben.Leyshon@snh.gov.uk

This report should be quoted as:

Lusseau, D., New, L., Donovan, C., Cheney, B., Thompson, P.M., Hastie G. and Harwood J. (2011) The development of a framework to understand and predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population. *Scottish Natural Heritage Commissioned Report No.*

The development of a framework to understand and predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population

Commissioned Report No.

Contractor: The University of Aberdeen

Year of publication: 2011

Table of Contents

Contents	Page
EXTENDED EXECUTIVE SUMMARY	6
BACKGROUND.....	6
INTRODUCTION.....	6
MODELLING THE USE OF THE MORAY FIRTH BY VESSELS.....	7
MODELLING THE USE OF THE MORAY FIRTH BY BOTTLENOSE DOLPHINS	8
THE EFFECTS OF BOAT PRESENCE ON BOTTLENOSE DOLPHIN BEHAVIOUR.....	8
THE IMPLICATIONS OF DIFFERENT DEVELOPMENT SCENARIOS FOR BOTTLENOSE DOLPHINS.....	10
MODELLING THE POPULATION CONSEQUENCES OF BOTTLENOSE DOLPHIN BEHAVIOURAL RESPONSES	11
ACKNOWLEDGEMENTS.....	12
THE POPULATION CONSEQUENCES OF DISTURBANCES.....	13
INTRODUCTION.....	13
<i>Predictive v. descriptive scientific advice.....</i>	<i>13</i>
<i>The Moray Firth bottlenose dolphin population</i>	<i>14</i>
AIMS.....	15
OBJECTIVES	16
PART I – A STATE SPACE MODEL STRUCTURE TO LINK BEHAVIOURAL DISTURBANCES IN THE MORAY FIRTH TO POPULATION DYNAMICS OF THE BOTTLENOSE DOLPHIN POPULATION.	17
INTRODUCTION.....	17
<i>Disturbance</i>	<i>18</i>
SIMULATION	19
<i>The Simulation.....</i>	<i>19</i>
<i>Results.....</i>	<i>22</i>
<i>Conclusions.....</i>	<i>24</i>
<i>Dolphin Response to Disturbance.....</i>	<i>24</i>
MODELLING THE DOLPHINS OF MORAY FIRTH	26
PART II – REVIEW OF DATA AVAILABLE TO INFORM THE STATE SPACE MODEL.....	28
DATA TO INFORM MODEL PARAMETER ESTIMATION	28
DATA COLLECTED IN THE MORAY FIRTH.....	29
<i>Autonomous acoustic loggers</i>	<i>29</i>
<i>Photo-identification</i>	<i>30</i>
<i>Photogrammetry.....</i>	<i>30</i>
PART III – AN OBSERVATION MODEL TO INFER DOLPHIN BEHAVIOUR USING DATA FROM AUTOMATED PORPOISE DETECTORS (T-PODS)	32
CONCEPTUAL BACKGROUND.....	32
METHODS	33
<i>Sutors and Aberdeen Harbour: two foraging hotspots.</i>	<i>33</i>
MODELLING APPROACH.....	34
RESULTS.....	35
<i>Consistency across deployments</i>	<i>35</i>
<i>Boat effect.....</i>	<i>40</i>
CONCLUSIONS	42
PART IV – A PREDICTIVE MODEL OF THE WAY BOATS USE THE AREA OF THE MORAY FIRTH	44
OVERVIEW	44
<i>What the model provides</i>	<i>44</i>

DATA AND MODEL DEVELOPMENT	45
<i>Model formulation</i>	45
<i>Basic Distribution models</i>	46
Distribution based on distance from port	47
Transit and stasis times	48
Extending the simple vessel distributions temporally	48
MODEL IMPLEMENTATION	48
<i>R function sets</i>	49
Inputs/outputs	49
Vessel class definitions	49
Port-level	49
Firth-level	50
Individual vessel level	50
<i>Interface options</i>	50
SCENARIOS USING THE MF BOAT MODEL (v0.2)	51
<i>Distribution of the resident recreational vessels</i>	52
SCENARIO 1 – INCREASED TRAFFIC ABOUT NIGG	53
<i>Model inputs for the Nigg scenario</i>	53
<i>Model outputs</i>	54
<i>Summary of scenario 1 Model runs</i>	58
SCENARIO 2 – WHITENESS AS A RENEWABLES FACILITY	59
<i>Model inputs for the Whiteness scenario</i>	59
<i>Model outputs</i>	59
<i>Summary of scenario 2 Model runs</i>	64
SCENARIO 3 – INCREASED CALEDONIAN CANAL VESSELS	64
<i>Model inputs for the increasing caledonian canal traffic</i>	64
<i>Model outputs</i>	65
<i>Summary of scenario 3 Model runs</i>	67
SCENARIO 4 – SINGLE TOUR OPERATOR ADDITION TO INVERNESS	68
<i>Model outputs</i>	69
<i>Summary of scenario outputs</i>	70
ADDITIONAL SCENARIOS	70
DISCUSSION OF THE MFBM	71
<i>Assumptions</i>	71
<i>Data</i>	72
<i>Sensitivities</i>	72
<i>Improvements</i>	73
APPENDICES	74
PART V – A DESCRIPTIVE MODEL OF THE WAY DOLPHINS USE THE MORAY FIRTH	75
CONCEPTUAL BACKGROUND	75
METHODS	75
RESULTS	77
<i>Density estimation</i>	77
<i>Boat exposure scenarios</i>	86
CONCLUSIONS AND OUTLOOK	88
PART VI – SYNTHESIS	90
GENERAL MANAGEMENT GUIDANCE	90
<i>Scenarios</i>	90
OUTLOOK	90
<i>Additional data collection</i>	91
<i>Dolphin ranging models</i>	92
<i>Simulation and parameter fitting</i>	92
<i>Graphical User Interface (GUI)</i>	92
REFERENCES	93

EXTENDED EXECUTIVE SUMMARY

BACKGROUND

Human activities in the marine environment are increasing and diversifying rapidly. We now use coastal waters for recreation, leisure, oil and gas exploitation, renewable energies exploitation, and shipping. This is leading to increased interactions between marine species, such as cetaceans, and these activities. These interactions can lead to behavioural disturbances for these wild populations and therefore we need to manage these activities in order to minimise the biological consequences of these disturbances. However, our current management frameworks are ill-prepared for managing these interactions. Our regulatory frameworks focus on key demographic parameters, such as population growth rate, to assess the significance of the impact of activities. We currently lack the scientific foundations enabling us to predict the population consequences of these disturbances.

Several studies have now shown that behavioural disturbances can affect the condition of the affected populations. In response, a framework was developed in 2005 in the USA to develop the scientific advice needed for managing such impacts. This framework provides mechanistic links, referred to as transfer functions, from behavioural disturbance of individuals to the consequences of those behavioural alterations for vital rates and, ultimately, changes in population structure and population growth.

INTRODUCTION

Two of the main conservation objectives of the Moray Firth Special Area of Conservation (SAC) are to avoid deterioration of the habitats of bottlenose dolphins within the SAC and to prevent significant disturbance to this species. A wide range of coastal and marine developments that could affect these objectives take place or are planned to take place in the inner Moray Firth. In this report we describe a framework that can be used to predict the potential disturbance to bottlenose dolphins that might be associated with the movement of vessels associated with these developments. We then use a preliminary implementation of that framework to investigate the potential impacts of a number of development scenarios. We also describe how the framework can be extended to investigate the consequences of those impacts for the conservation status of the entire dolphin population in the SAC.

In developing this framework we have adopted a standard environmental risk assessment approach. First, we determine the distribution of the potential “hazard” to dolphins (the average length of time that different types of vessel are present in different parts of the Moray Firth), and the distribution of the dolphins themselves within the Moray Firth over the course of a year. We then evaluate how the co-occurrence of vessels and dolphins in the same area may change the feeding behaviour of the dolphins. Finally, we show how the effect of these changes in feeding behaviour on the long-term dynamics of the Moray Firth population can be evaluated and monitored.

MODELLING THE USE OF THE MORAY FIRTH BY VESSELS

This work is described in detail in Part IV of the main report. We divided the waters of the Moray Firth into 6496 1km×1km cells. We then used data from the Moray Firth Vessel database (<http://www.biomitor.org.uk/morayvessels/morayvessels.htm>) provided by Jonathan David & Martin Latimer and collected as part of their contracts with Scottish Natural Heritage and the Whiteness Property Company Ltd, to develop a predictive model (the Moray Firth Boat Model - MFBM) of the way in which vessels in different classes (based on size and type of activity) operating out of 34 ports, harbours, moorings, landings and piers in the Firth use these cells. The model is not intended to accurately predict individual boat trips: no model can do this, except for exceptional cases like regular ferries. Instead, it is intended to provide generalised estimates of average behaviour and uncertainty for each class of vessel.

We assumed that all vessels in the same class operating from a given port or landing used the waters of the Firth in the same way. Data on the movements of commercial vessels within the Inner Moray Firth came from their on-board Automatic Identification Systems (AIS). Data on the movements of smaller, recreational vessels came from Global Positioning Service (GPS) recorders fitted to a sample of boats from selected ports, and from tracking studies by visual observers. Inevitably, given the large number of potential combinations of vessel classes and ports, predictions of the use of space by recreational vessels are based on small samples sizes and must be interpreted with caution. Particularly, further sampling will provide a mean to assess whether our behavioural homogeneity assumption is warranted. This is particularly true for vessels using the Caledonian Canal. However, this situation will improve as more data on the movements of recreational vessels become available, and the MFBM has been designed to accept additional data as they are collected.

The model assumes that all recreational vessels in a particular size class use the waters around their home port uniformly up to a specified distance for that class, unless there is additional information (for example, from GPS recorders) on their use of space. The model takes account of the complex topography of the Moray Firth and calculates the distance by sea of each 1km×1km cell from a particular port. As a result, the model predicts higher densities of vessels in “bottlenecks”, where there are only a small number of available cells at a given distance from a particular port.

The percentage of recreational vessels from a particular port that are at sea on a particular day is a critical factor in determining the amount of time vessels spend in different parts of the Moray Firth. We assumed this was generally 3%, with a peak of 5% during the months of June, July and August. This is consistent with the estimated deployment rates of 5.4% and 3.3% for Inverness Marina during summer. These assumptions emerged after discussions with interested parties.

In its current form, the MFBM does not distinguish between vessel time spent in transit and time spent stationary, but this distinction can be included in the model as required.

Figure E1 shows the predicted use of the Moray Firth with current levels of vessel traffic.

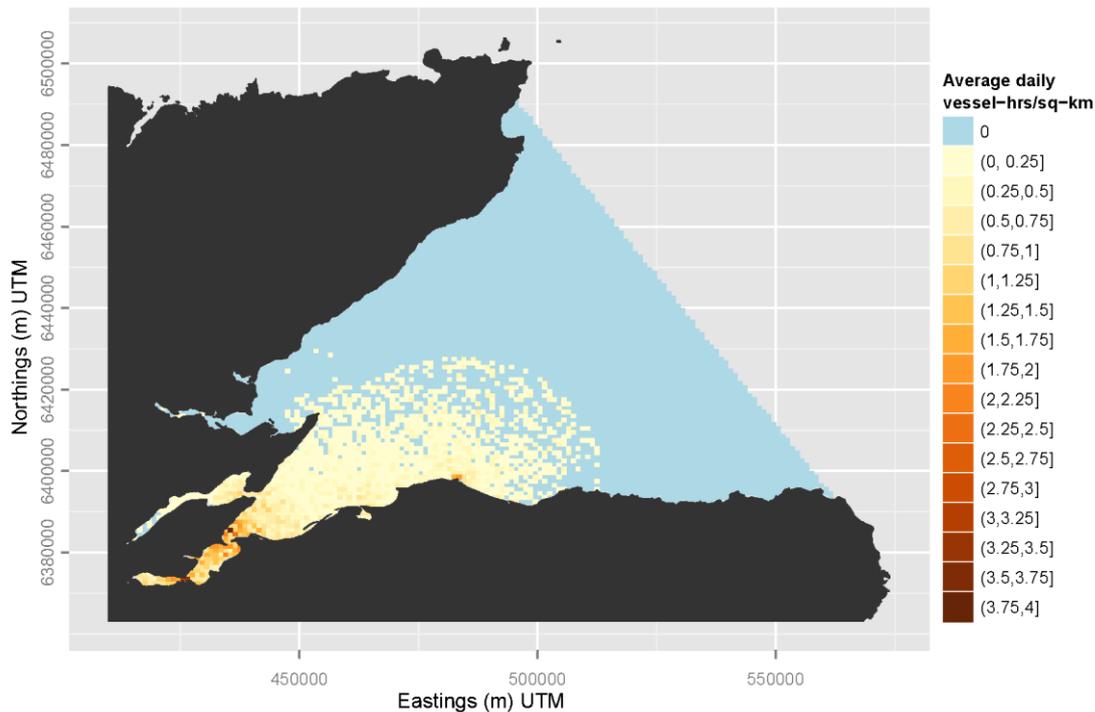


Figure E1. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period including the current pool of recreational vessels and 70 commercial sailings to Nigg.

MODELLING THE USE OF THE MORAY FIRTH BY BOTTLENOSE DOLPHINS

This work is described in detail in Part V of the main report. Although the University of Aberdeen has been studying bottlenose dolphins in the Moray Firth since 1989, the data collection protocols were not designed to provide information on the way in which dolphins use the entire Moray Firth. However, we were able to use new techniques designed for the analysis of the photo-identification data, which has been collected systematically between 2001 (when information on the precise location where each photograph was taken was first recorded) and 2009, to estimate the probability that an individual dolphin will be found in each of the 6496 1km×1km cells used in the analysis of vessel distribution. We found that there were no major differences in the way in which individual dolphins used the Moray Firth within any year. However, there were striking differences between years, with individuals ranging much more widely in some years than others. At present we do not know what environmental factors are responsible for these differences, although they may be linked to the strength of the salmon run. Until we have established this relationship, it is not possible to predict how dolphins will use the waters of the Moray Firth in future years. Nevertheless, we can use the historical data to evaluate the potential impacts of specific proposed developments if they had taken place in years when dolphins were narrowly or widely dispersed.

THE EFFECTS OF BOAT PRESENCE ON BOTTLENOSE DOLPHIN BEHAVIOUR

This work is described in detail in Part III of the main report. Over the past 5 years a number of autonomous acoustic data-loggers, known as T-PODs and C-PODs, have been deployed in the Moray Firth (see Figure E2) and at the entrance of Aberdeen harbour. These devices are

designed to detect the presence of bottlenose dolphins and harbour porpoises by identifying the clicks they use for echo-location. We demonstrate that the interval between these clicks can be used to infer whether or not the dolphins in the vicinity of a T-POD are feeding. Thus, data from T-PODs can be used to determine the behaviour of groups of dolphins in different parts of the Moray Firth at different times of the day and during different periods of the year. In addition, we can compare the acoustic behaviour of dolphins when vessels are present and when they are absent if visual observations have been made at the same location as a T-POD has been deployed. Information of this kind was available from 2005 at the Sutors in the Moray Firth and from 2008 for Aberdeen Harbour. Both sites are known to be foraging hotspots for bottlenose dolphins. We found that dolphins spent 30-40% less time feeding at the Sutors when vessels were present, but no significant effect was detected in at the entrance of Aberdeen harbour. This may be because most of the vessels using the harbour are commercial ones, which have more predictable patterns of movement than the recreational vessels that are normally present around the Sutors. As a result, boat interactions that take place in dolphin foraging hotspots will have a disproportionate effect. Foraging hotspots such as at the Chanonry Narrows, the mouth of the Sutors and the Kessock Channel should therefore be considered sensitive to boat interactions and interactions should be kept at a minimum in these locations. However, this effect is unlikely to be the same throughout the SAC. Feeding disruptions are less likely in locations where most of the boating activity is predictable. That is, locations where boats do not seek interactions with the animals, do not try to approach them, stay on a predictable path, and behave in a predictable way. We therefore cautiously hypothesise that non-touristic commercial activities are less likely to disrupt the feeding behaviour of dolphins than recreational or tourist activity.

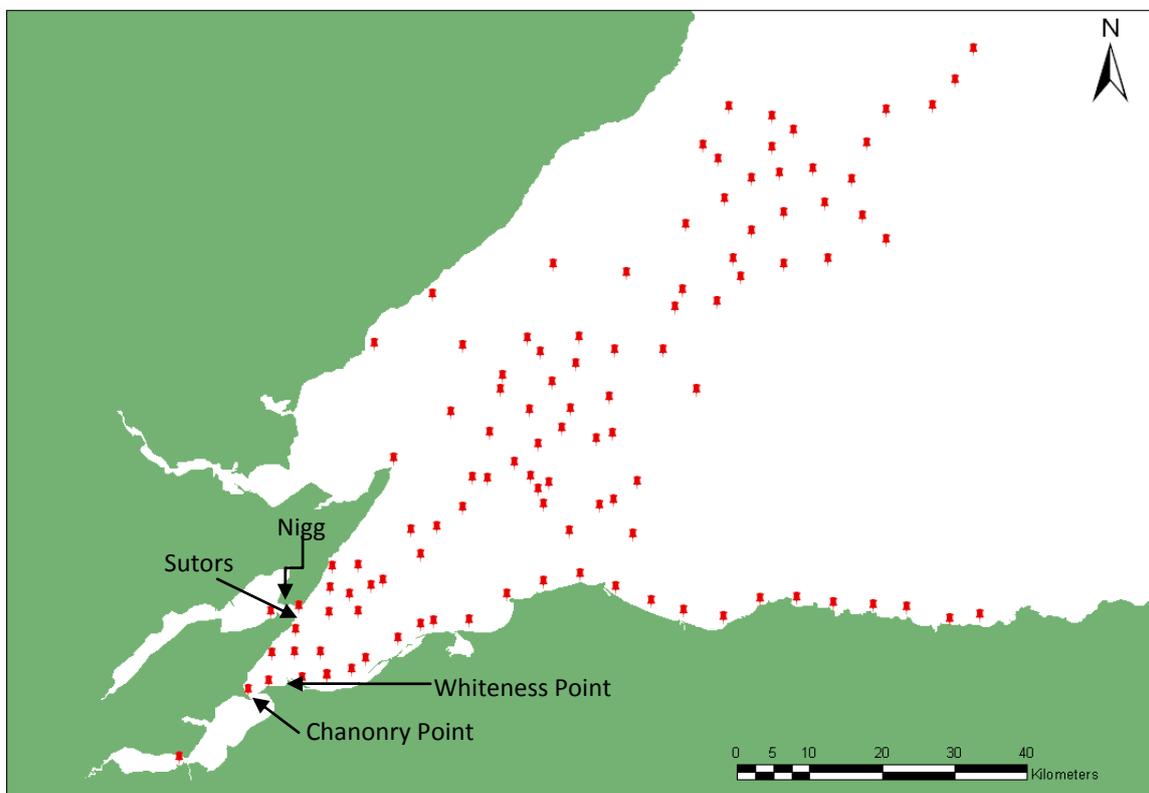


Figure E2. Locations where autonomous acoustic data-loggers (T-PODs and C-PODs) have been deployed since 2005.

THE IMPLICATIONS OF DIFFERENT DEVELOPMENT SCENARIOS FOR BOTTLENOSE DOLPHINS

This work is described in detail in Parts IV and V of the main report. We considered the potential implications of four development scenarios for bottlenose dolphins in the Moray Firth:

1. A new offshore renewables fabrication facility at Nigg in the Cromarty Firth that would result in an additional 100, 200 or 400 extra vessel movements in the Firth each year. The vessels would comprise barges and other large commercial vessels. These vessels movements could either occur at roughly even rate throughout the year or predominantly during the summer months.
2. A new renewable fabrication facility at Whiteness Point, Ardersier that would result in an additional 100, 200 or 400 commercial vessel movements in the Firth each year. These vessels movements could either occur at roughly even rate throughout the year or predominantly during the summer months.
3. A 5%, 10% and 20% increase in the number of leisure craft less than 10m using the Caledonian Canal and entering the Moray Firth.
4. A tour boat operator based at Inverness operating a 10m Rigid-Inflatable Boat (RIB). The vessel would make an average of 3 journeys per day and not travel more than 30km from its home port.

We were also asked to consider a scenario in which two new commercial dolphin watching operators want to start business based at the new marina in Inverness. In order to implement this scenario we required specific information on the projected activities of these vessels. However, the operators did not respond to repeated requests from SNH for this information, and we were unable to consider this scenario.

None of the variants of scenario 1 resulted in an appreciable change in vessel distribution within the Moray Firth, although the average amount of time spent by vessels in the most heavily used cells each day was likely to increase by up to 20 minutes during the summer months. This is relatively small compared to the use of these cells by recreational boats. We combined this information with the data on the estimated probability of the presence of dolphins in each cell in 2004 (when dolphins were widely dispersed) and 2003 (when their distribution was more restricted). None of the scenarios resulted in an increase in the amount of time vessels were in the vicinity of dolphins of more than 1 hour per year.

All of the variants of scenario 2 resulted in an appreciable change in vessel distribution over the entire Moray Firth, because sailings from Whiteness Point are likely to traverse areas of the Moray Firth that currently experience relatively low levels of vessel activity. However, the average daily increase in vessel usage of the most heavily utilised cells within the commercial traffic route under the scenario with the greatest increase in traffic in summer was only 28 minutes. Most of the variants of this scenario resulted in an increase in the amount of time vessels were in the vicinity of dolphins that was less than 1 hour per year

per dolphin. However, if the number of vessels using Whiteness Point was increased to 400 and most of this traffic was in the summer, the increase was up to 2 hours per year. The difference in predicted increase in exposure between the two sites is trivial at lower level of simulated shipping activity. However, when the increase in activities reaches the upper simulated levels, we see that the difference between the two sites diverges and becomes more substantial (2h v 1h). If such levels of activity were envisaged at Whiteness, then we currently have little confidence to draw conclusions about their potential population-level consequences.

If both the Nigg and Whiteness Point developments take place, and both result in an extra 400 vessel movements that mostly occur in summer, then the amount of time dolphins spend in the vicinity of vessels will increase by around 2.5 hours per year. We cannot reach any conclusions at this stage about the likely consequences of such an increase in activity. Therefore, if such a development was to take place, further investigations would be required to ascertain the likely effect of 2.5h increase in exposure for the vital rates of dolphins.

Predictions of the effects of scenario 3 are more difficult because we have only limited data on the behaviour of recreational vessels that have passed through the Caledonian Canal. We assumed that these vessels distributed themselves across all of the ports in the Moray Firth where there are recreational vessels that they were substantially more active than resident vessels, and that most of them arrived in the Moray Firth between May and September. Even the most extreme scenario only resulted in an increase in usage of approximately 1 minute per day across all the cells utilised by these vessels. Nevertheless, the greatest increase in traffic resulted in an increase in the amount of time that dolphins were likely to spend in the vicinity of vessels of up 9 hours per year, if the distribution of dolphins was similar to that observed in 2003. This was because the areas around the ports likely to be used by these additional vessels are heavily used by dolphins.

Scenario 4 resulted in an average increase of approximately 1 vessel-minute within the area of operations of the tour vessel. However, increases in the average usage for specific cells in this area could be as high as 7 vessel-minutes per day. This additional use is predicted to result in an increase of 1-2 hours in the amount of time dolphins spent in the vicinity of vessels. As with scenario 3, this was because the area likely to be used by the tour vessel is also heavily used by dolphins.

MODELLING THE POPULATION CONSEQUENCES OF BOTTLENOSE DOLPHIN BEHAVIOURAL RESPONSES

Studies of other coastal populations of bottlenose dolphins in Australia and New Zealand have revealed that frequent encounters with tourist boats can result in a decrease in the amount of time that dolphins spend resting. If continued, this disturbance can lead to a decline in the survival of dolphin calves and an increase in the interval between successive pregnancies, resulting in a decline in population size.

It seems unlikely that the predicted increase in the amount of time that dolphins in the Moray Firth are likely to spend in the vicinity of vessels as a result of the renewable development scenarios investigated in this report is likely to result in population effects of

this kind. The proposed developments at Nigg and Whiteness Point (Figure E2) involve an increase in commercial vessel traffic leading to a few minutes of added exposure for the dolphins. In addition, predictable commercial traffic is likely to have less effect on dolphin behaviour than the less predictable movements of recreational and tour operating vessels. The predicted increase in time spent in the vicinity of vessels associated with the largest increase in traffic through the Caledonian Canal could conceivably have a greater effect. However, these predictions rely on a large number of assumptions that do not have a strong factual basis. Much more research on the behaviour of vessels emerging from the Canal is required before these predictions could be used as the basis for planning decisions. Nevertheless, it is important to establish a framework that can be used to evaluate the population-level consequences of increases in the time dolphins spend in the vicinity of vessels of this, and potentially greater, magnitude.

In Part I we describe how such a framework can be developed. The key requirements of this framework are information on the behaviour of dolphins in different parts of the Moray Firth, information on the effect of the presence of vessels on this behaviour in order to construct a “dose-response relationship”, and information on changes in the body condition of individual dolphins (particularly mature females) over time. In Part II we describe how all of this information can be collected using monitoring techniques that are already in use within the Moray Firth SAC.

ACKNOWLEDGEMENTS

We would like to thank the many colleagues that have contributed to the data collection at the University of Aberdeen Lighthouse Field Station over the past 22 years. We would like to particularly thank Tim Barton for his instrumental help in designing and carrying out acoustic and photo-identification sampling. Thanks also to Elizabeth Coates and Andrea Powell who collected visual observations in conjunction with TPOD deployments for their MSc theses.

The population consequences of disturbances

INTRODUCTION

The way in which we use the marine environment is diversifying rapidly. One consequence of this is the ensonification of the oceans, which is likely to affect cetaceans, directly and indirectly, by disturbing their behaviour. However, we currently lack the scientific foundations to predict how this anthropogenic disturbance will influence the dynamics of cetacean populations. Several studies have now shown that such disturbance can indeed affect the condition of populations which led the International Whaling Commission to state: “The fitness of individual odontocetes repeatedly exposed to tour vessel traffic can be compromised and this can lead to population level effects. In the absence of data, it should be assumed that such effects are possible until indicated otherwise – particularly for small, isolated and resident populations.” (IWC 2006). In 2005, the US National Research Council developed a conceptual framework that could be used to help establish this foundation, which they called the Population Consequences of Acoustic Disturbances framework (PCAD, Figure 1) (National Research Council 2005). This framework provides mechanistic links, referred to as transfer functions, from behavioural disturbance of individuals to the consequences of those behavioural alterations for vital rates and, ultimately, changes in population structure and population growth.

Here, we focus on linking behavioural changes to their biological costs. To do so, we develop a general statistical modelling framework in which we can use observed behaviour to infer the hidden motivation systems that underlie the behavioural ecology of cetaceans (McFarland & Sibly 1975). This model can be later on used to infer the physiological costs of anthropogenic disturbance and inform the mechanistic links between behavioural changes and vital rates.

This project aimed to progress the development of a management tool that can be used to make robust decisions about the expected effects of new developments in an area occupied by cetacean populations that have been the focus of behavioural studies. This approach is attractive for two reasons. First, it provides a measure of the likely effects of development on biological signals that are relevant to regulatory frameworks such as the Habitat Directive. Second, it provides means to infer the uncertainty surrounding these decisions, given the information available to make them, and the relative contribution of different processes to this uncertainty; providing means to focus research effort efficiently (Harwood & Stokes 2003).

Here, we apply these conceptual and analytical developments to the special case of the bottlenose dolphin population in the Moray Firth.

Predictive v. descriptive scientific advice

Non-lethal interactions between human activities and wildlife populations are currently governed using a descriptive approach. That is, the impact an activity can have is assessed, the consequences of those impacts is inferred, and decisions are reached on the levels of activity that can be deemed safe (Higham et al. 2009). However, this approach has serious shortcomings. Firstly, legal frameworks in place to manage wildlife populations set population trajectory targets such as population growth rate. Therefore the most crucial element of the decision-making process, the biological relevance of the observed impact, is often the least informed using a traditional approach. This leaves situations open to interpretations and challenges, wasting time and resources for all parties involved. Secondly, this reactive approach minimises our ability to extrapolate from one assessment to the next. We are therefore often left with piecemeal case studies that are difficult to meta-analyse to draw general conclusions that are necessary to provide sound scientific foundations to management decisions.

The impact of traditional activities exploiting wildlife populations, such as hunts or unintentional kills, is straightforward to interpret in terms of population dynamics and therefore this descriptive approach has been sufficient to manage these activities (Punt & Donovan 2007). But a paradigm

shift is now crucial to manage adequately non-lethal interactions between wildlife and human activities. To achieve this, we need to invest in a new approach to scientific advice: focusing on developing predictive power in our management of natural resources. Such a change is needed because non-lethal interaction is quickly overtaking traditional exploitation in the animal's landscape (Lusseau et al in revision). This is particularly crucial for the management of cetacean populations which are increasingly exposed to a wide variety of industries that can affect their behaviour, with potential population-level consequences. The approach we advocate here provide a mean to directly estimate the effects of non-lethal impacts on an unbiased metric, population growth rate, and therefore reduces the problem to traditional management of wildlife population exploitation (lethal takes).

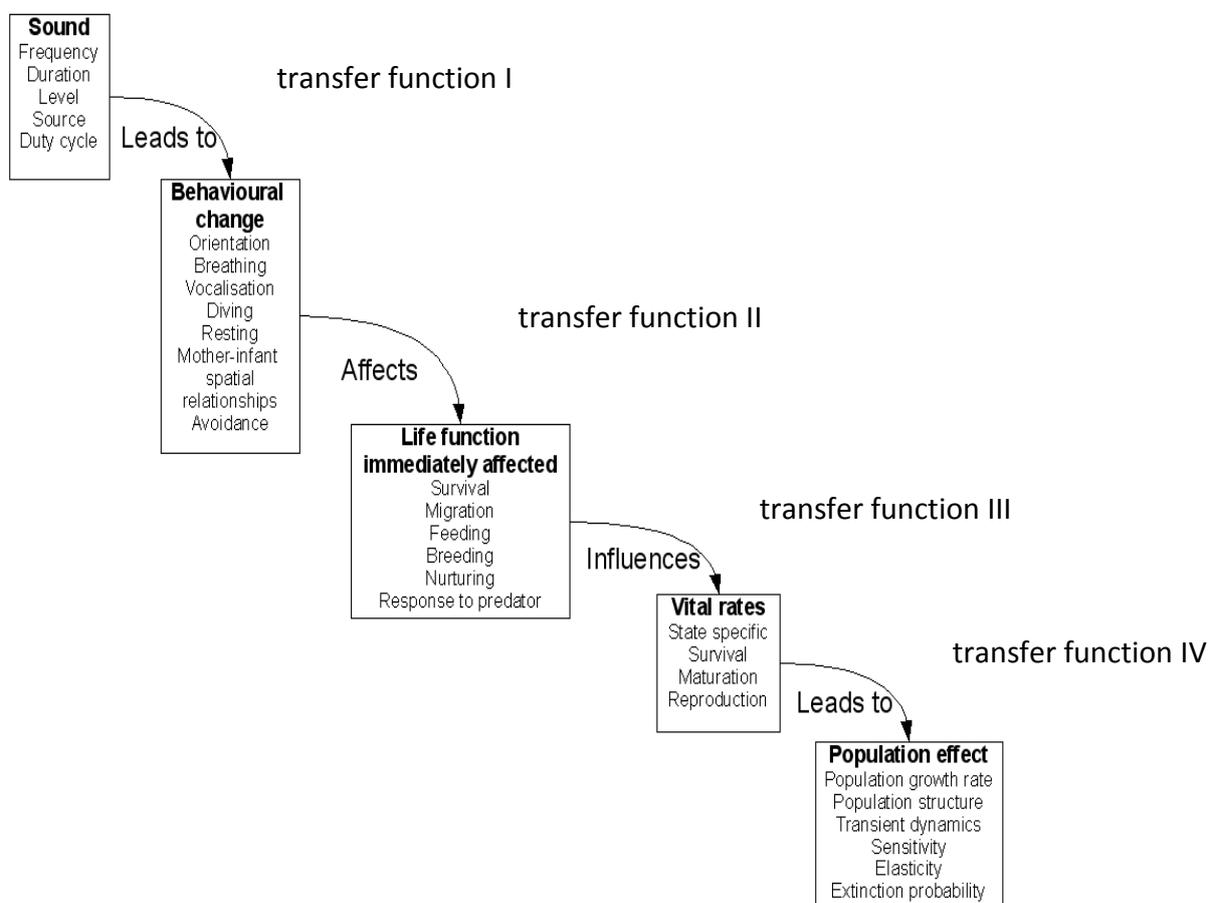


Figure 1. The Population Consequences of Acoustic Disturbance framework developed by the US National Research Council, adapted from NRC (2005).

The Moray Firth bottlenose dolphin population

Bottlenose dolphins (*Tursiops truncatus*) are a globally distributed species found across a wide range of countries and temperatures from the Moray Firth, Scotland in the north to Fiordland, New Zealand in the south. All of the populations studied have shown a pattern of relationships described as fission-fusion (Connor, et al. 2000), in which an individual's membership in a social

group is fluid and the group composition can change several times per day. The pattern of the associations changes across the different populations, mostly among the females, and seems to have some dependence on environmental resources (Lusseau, et al. 2003). School size in bottlenose dolphins is typically between 2-15 individuals, although larger groups are often observed and in-shore populations tend to form smaller groups than those found off-shore (Connor et al. 2000). Additionally, while school formation is dependent, in part, on chance, its size is affected by prey availability (Lusseau et al. 2004). Schools are active during both the day and night, changing behaviours according to various factors, such as tide, season, and physiological state (Perrin, Würsig and Thewissen 2009). The general class of behaviours in which dolphins engage are: diving (feeding), travelling, resting, milling and socialising (Lusseau 2006b). Physically, bottlenose dolphins range in size from 2.5-4.5 m, with much of the variation being due to geographic region. They are a long-lived species that reproduces slowly, with females being known to live more than 57 years, and the males up to 48 years (Perrin, Würsig and Thewissen 2009). In general, changes in the homeostasis of cetaceans can be indicated by changes in an individual's surfacing and movement behaviour. Most of a dolphin's physical growth occurs during the first two years of life, when the calves are still being suckled by their mothers. This observed extra energy demand may result in some differences in behaviour between male and female dolphins, especially since the calf's dependence on its mother may last for up to six years. Age at sexual maturity also varies between the sexes, with females becoming sexually mature at a younger age. The breeding season can be year-round, although there tend to be peaks in the spring and summer months. Gestation is close to a year and therefore the calving season overlaps with breeding. The dolphins' reproductive life-span is long, with males and females over 40 years of age having been known to successfully produce calves (Perrin, Würsig and Thewissen 2009).

The Inner Moray Firth, Scotland is a Special Area of Conservation (SAC) designated, in part, to protect the population of bottlenose dolphins found in the area through the EU Habitats Directive (Bailey et al. 2010b, Thompson et al. 2000). This protection is not geographically limited and follows this dolphin population wherever they go. Bottlenose dolphins can be found in the Moray Firth year-round, and this is the only known resident population in the North Sea. However, resident, individually-identified dolphins have been found as far south as the Firth of Forth and even Newcastle (Wilson et al. 1997; pers. obs.). The population size is currently estimated to be 195 dolphins (Thompson et al. 2011). The combination of a relatively small population and its isolation, may make the dolphins more susceptible to disturbance (Thompson et al. 2000). Under the Habitats Directive any new activities taking place in the range of this population should not affect the integrity of the SAC. This means in particular that the population growth rate should not be affected so as to threaten population viability.

AIMS

We propose to use a two-pronged approach to develop scientific advice for managing human activities that could affect the condition of the Moray Firth bottlenose dolphin Special Area of Conservation.

First, we propose to develop methods to assess the population consequences of disturbances using a spatially explicit approach (Figure 2). This approach will increase the flexibility of scenario development. Second, we propose to develop a simulation platform on which scenarios can be run to assess the potential impact of future developments. The goal of this study is to instigate this process by defining methods and providing preliminary estimation of the mechanisms that could

lead to population-level consequences. We are also developing baseline management advice that can be adapted as this simulation platform is developed.

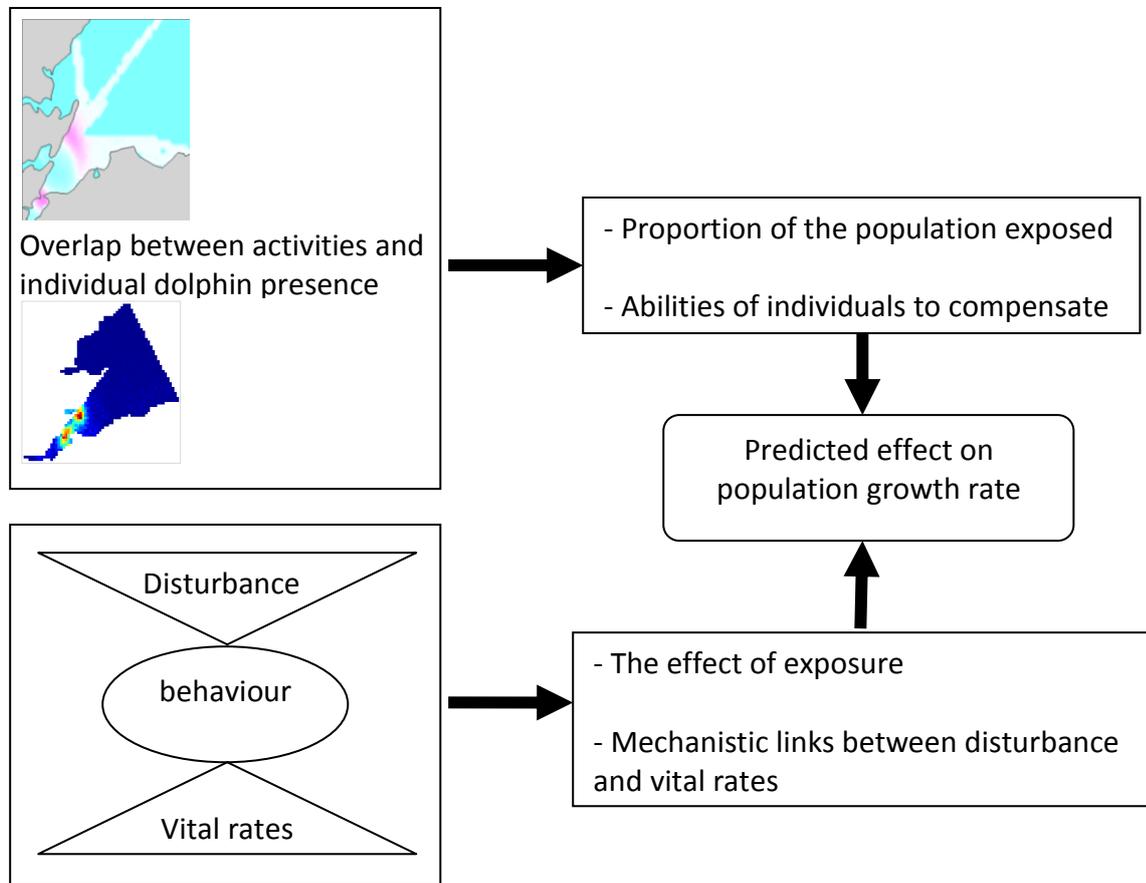


Figure 2. The components needed to advise on the population consequences of disturbances (arrows represent influences): (i) the overlap (in space and/or time) of the disturbing activities and all individual dolphins and (ii) a model to mechanistically link behavioural disturbances to potential alteration in individual vital rates. Once this framework is informed with data, it can be used to predict the likely population-level consequences of disturbances, and the uncertainty surrounding this advice, of any scenario using simulations.

OBJECTIVES

Following our aim, we develop five objectives to achieve it.

1. Develop a state space model structure, based on existing generic models, to link behavioural disturbance in the inner Moray Firth to population dynamics of the NE Scotland bottlenose dolphin population.
This model structure will help to understand data needs and requirements to achieve our aim. Once data will be collected, we can then fit the model in order to estimate its coefficients and therefore the overall effects of human activities.

With this model structure in mind we could then assess data availability and develop statistical models to use this data to inform the model functions as well as simulations based on this model to inform the variability with which individuals are exposed:

2. Review data available to inform this model and assess how well existing data inform the different model functions.
3. Develop an observation model to infer dolphin behaviour using data from Automated Echolocation Detectors (T-PODs) to inform the model in objective 1.
4. Develop a predictive model of the way boats use the area of the Moray Firth.
5. Develop a descriptive model of the way individual dolphins use the Moray Firth and use it to make preliminary estimation of dolphin exposure to boat traffic.

PART I – A state space model structure to link behavioural disturbances in the Moray Firth to population dynamics of the bottlenose dolphin population.

INTRODUCTION

A number of mechanisms have been identified as possible pathways for disturbance to influence the vital rate of individuals, and therefore ultimately the growth rate of their population (Lusseau & Bejder 2007). The research team held a workshop in December 2010 to identify plausible mechanisms for the Moray Firth situation that could be informed using existing data from the Moray Firth or data that could realistically be obtained from this population. This does not mean that other mechanisms (eg. immune-competence challenges caused by chronically elevated stress hormones) were deemed unimportant. However, sampling techniques to inform these other mechanisms are in their infancy, and it would therefore be challenging at present to include them in any meaningful way in parameter estimation.

The only documented effect of disturbance and environmental perturbation on vital rates of bottlenose dolphins is a reduction in the survival and condition of calves (Lusseau et al. 2006; Bejder 2005). Importantly, those effects can influence population growth rate (Currey et al 2008). This change appears to be caused by reduced availability of energy to adult females in response to behavioural changes associated with disturbance or altered prey availability. Bottlenose dolphins are income breeders and therefore rely on continuous energy acquisition during the calf-rearing period to maintain their investment in their offspring. We therefore agreed to focus on a model of the effect of behavioural changes on individual energy budgets and the potential effect of changes in energy budgets on calf condition and survival (Figure 1.1). We agreed to develop models of an individual's energy gain and expenditure using a state-space modelling framework in which the activity state of an animal is interpreted as an observation of its underlying motivational state (McFarland and Sibly 1975). These motivational states can be considered as equivalent to the "life functions" in the NRC PCAD model (Figure 1). An underlying process model is then used to describe the transition from one motivational state to another. This transition is likely to be affected by the individual's physiology, the motivational state of other dolphins in its social group, and its environment (which includes disturbance). The parameters of the underlying process model can then be estimated from a time series of observations of an individual's activity state and a matching set of covariate data. To complement this individual-based behaviour-physiology model (BehPhys)

we also agreed to develop a model of the link between energy gain and demography using an integrated statistical model that can be used to investigate the effects of changes in condition on the investment that mothers make in calves (PhysDem model). The model can look at the effects of changes in survival and calving success on the population's demography, taking account of the effects of environmental conditions (Figure 1.1).

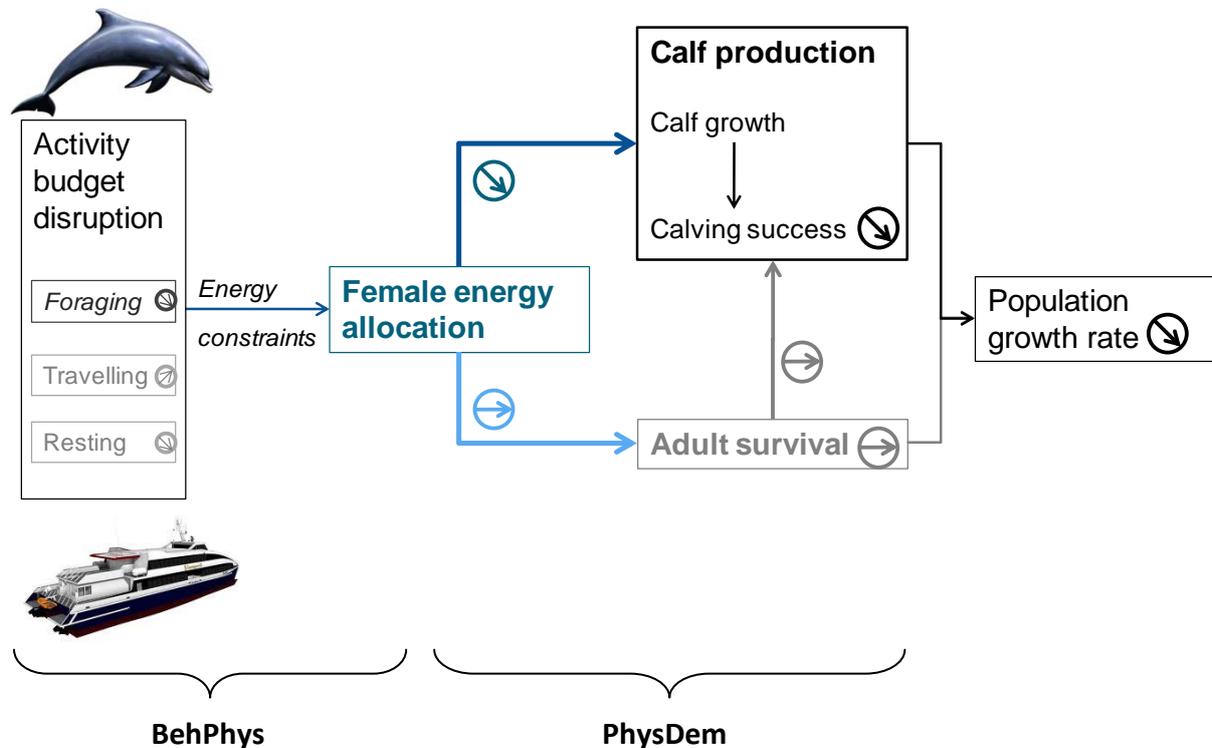


Figure 1.1. Mechanisms through which behavioural disturbances can lead to site condition deterioration. This represents the assumed mechanisms for this model. The arrows represent the likely mechanistic linkages leading disturbances to affect population growth rate. Arrow symbols (arrows in circles) represent the likely effect: decreasing, increasing, or no effect (constant). The section of the conceptual model in blue is a hidden process that can only be inferred.

Disturbance

The dolphins in the Moray Firth are potentially affected by a number of anthropogenic disturbances. Of recent concern is the construction and operation of wind-turbines for renewable energy (e.g., Bailey et al. 2010b), but more traditional sources of disturbance are due to boat traffic. In general, bottlenose dolphins, like other cetaceans, change their activities to avoid boats by engaging in avoidance tactics (Lusseau 2003a, Lusseau 2004). This disruption of their normal activity affects the amount of time that individuals spend engaged in different activities and therefore can jeopardise their life functions. Activities, and their disruptions, can be observed and measured in a wide number of ways.

Traditionally, observers follow focal schools of dolphins visually and record changes in activity states observed. However, we can also infer broad categories of dolphin activities, which are relevant to their life functions, using acoustic methods because they rely on echolocation to sense their environment (Au 1993). This simulation is developed under the premise (see part II) that the behaviour of the Moray Firth bottlenose dolphins can be inferred using spatially-fixed loggers of echolocation clicks (T-PODS). These are stationary devices placed within the Firth that can record the echolocation clicks made by cetaceans in the area (Bailey et al. 2010a). As well as providing a

measure of the presence/absence of dolphins within a given area, the clicks recorded on T-PODs can be used to identify feeding events (e.g. Hastie et al. 2006). Activity states are defined as 'mutually exclusive and cumulatively inclusive,' (Lusseau 2003), so dolphins could only take part in one behaviour, making it easier to define feeding events and a behavioural budget of dolphins.

SIMULATION

This simulation is based on parameters taken from the literature. It has not been fitted to data to provide precise parameters for all the mechanistic processes described below. However, this fitting process will be possible once all the other components of this framework have been completed (Figure 6.1).

The Simulation

The purpose of the simulation was to use mathematical formulations to reconstruct the behaviour of bottlenose dolphins in the Moray Firth, Scotland to support future work that will fit models of dolphin behaviour to locally collected data. Therefore, the simulation was built with a specific population in mind, although many of the assumptions could be relaxed for other dolphin populations, as necessary.

Lusseau (2006b) defines five activity states (diving, travelling, socialising, resting and milling) but we reduced this to four states in our simulation by combining milling and travelling into one state of travelling. We also re-labelled diving as 'feeding.' Each individual also has underlying motivational states comprised of their energy level, fear, social desire and condition (McFarland & Sibly 1975). These motivational states change according to the activity state of the school (Figure 1.2). Therefore, individual dolphins will need to balance their personal desire to partake in a particular behaviour (e.g. desire to rest) against the safety of being in a school whose collective behaviour (e.g. feeding) does not reflect their personal desire (Sueur et al 2011). Should individuals decide to leave the school, they would need to join another group, or form a new group, depending on the level of association they have with other schools.

The simulation begins by randomly choosing the number of groups into which the population is divided, with the maximum number of groups equal to one-half of the population size. *This is based on the assumption that the minimum school size is two individuals, since being alone confers no advantages to the individual dolphin.* Once the number of starting groups is known, individual dolphins are randomly placed into each group, and each school is assigned one of the four possible activity states at random. Although frequency distributions are available for group size (Lusseau et al. 2004), these were not accounted for in the simulation. This choice was made deliberately to see if the simulation could mimic the observed dolphin social behaviour. In addition, each school is assigned a random starting location within the most heavily utilised portions of the Firth. As well as being assigned to a school, each dolphin is assigned random starting values for their motivational states. Since the population is not homogenous, we define three 'types' of dolphins: mothers with calves, adult males and adult but non-breeding females, and juveniles. *The highest associations are assumed to occur within a group, while neutral association is assumed between adults and non-breeding females and the other two groups. Juveniles and mothers with calves are assumed to be negatively associated. Within these constraints, each individual is assigned a random association value (between -1 and 1) with every other individual in the population.*

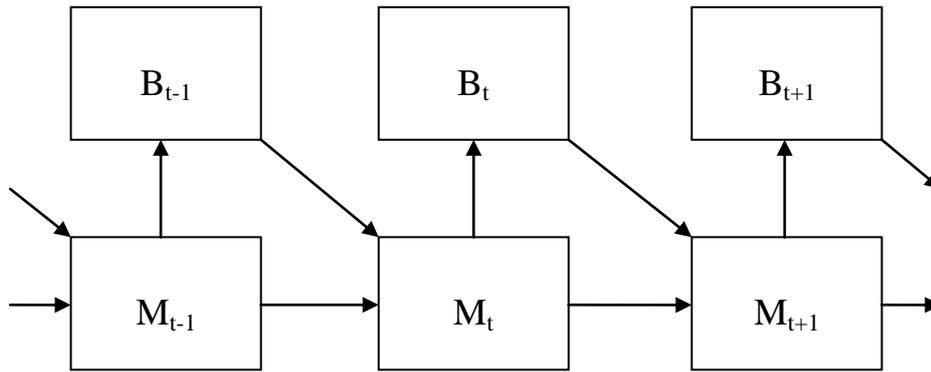


Figure 1.2. The relationship between motivational state (M) and behaviour (B), as they change through time (t).

An individual's motivational state is a unit-less measurement centred around zero. Negative values indicate that an individual is not strongly motivated by that particular state, that they are 'satisfied,' i.e., an animal is satiated, in peak condition, completely rested, or experiencing no fear. A positive value would indicate that an individual is highly motivated to perform the behaviour associated with a given state, that they are 'discontented,' i.e., the individual is hungry, in poor condition, exhausted, or terrified. At the start of a time step, all individuals experience the cost and benefits of taking part in the school's current behaviour, plus some random variation due to the individual. *Feeding is assumed to decrease the motivation to feed, while increasing fear. Travelling is assumed to decrease fear, but increase hunger. Resting increases hunger, but decreases fear. Finally, socialising increases fear and hunger, but decreases social needs.* The motivation to feed is also affected by the season. *We assume that individuals will feel less need to feed in warmer weather because food will be more readily available, of higher quality and the energetic costs of maintaining body temperature will be lower.* Thermoregulation is a major energetic cost in cetacean energy budgets (Lockyer 2007, Brodie 1975). The magnitude of the cost/benefit to each state can vary according to the behaviour. For example, being social increases the motivation to feed more rapidly than travelling because social behaviours, such as sexual displays, require more energy than swimming at a steady pace (Yazdi, et al. 1999). An individual's condition is not affected directly by its behaviour, but indirectly by its motivation to feed. When an individual is not being driven by hunger, this implies it is satiated and therefore able to maintain good condition. This also allows condition to change at a slower rate than hunger, as we would expect to see in nature (Figure 1.2).

Table 1.1. A matrix indicating how each behaviour may increase (+), decrease (-) or fail to affect (0) an individual's motivation.

	Hunger	Fear	Condition	Social Needs
Travelling	+	-	0	0
Feeding	-	+	+	0
Resting	0	+	0	+
Socialising	+	+	0	-

An individual will want to change behaviours if any of its motivational states cross a set threshold. However, the school will only change behaviour if at least half of its members desire such a

change (Sueur et al. 2011). Dolphins that have more than one motivational state above this threshold are given extra weight, since these individuals could conceivably be more forceful in imposing their needs onto those of the group. Should the school decide to change behaviours, they may also need to change location. Therefore, although the school may wish to feed, its actual behaviour will be travelling until it reaches an appropriate location. Therefore, the desired behaviour may not match the observed behaviour (Figure 1.3).

Dolphins in the Moray Firth do not show spatially explicit behaviours, so different locations can have multiple uses, although not all locations are suitable for all behaviours. It is therefore necessary to explicitly model the location and movement of each group. Each group moves according to a directed random walk, choosing a new location at each time step according to a probability based on the suitability of neighbouring locations for the group's desired behaviour (e.g., feeding), as well as their proximity. Smaller distances are travelled when the group is feeding, resting or socialising.

After the school's behaviour for a particular time step has been defined, the individuals forming the school must decide if they wish to remain with the school. A dolphin's decision to consider changing schools is based upon its motivational states over time t and $t-1$. If, over these time steps, half or more of the motivational states show that an individual has been fully satisfied with its energy level, fear and social needs, or completely dissatisfied with any of the four states, then the individual may wish to change school. Satisfaction with condition does not play a role in the decision to change schools, since an individual would not normally leave a group that was helping it to maintain excellent condition. Another factor the individual will consider is the current size of its school. Up to a certain threshold, larger schools provide more protection from predation risk (Acevedo-Gutiérrez 2002), so a dolphin will be more likely to leave a small or extremely large school, compared to one closer to the size of the threshold. Furthermore, since dolphins tend to form associations with particular individuals, should one dolphin choose to leave a school, the dolphin with which it is the most closely associated will leave the school with it. Finally, if an individual's school has just changed behaviour, it will not seek to change school, since it has yet to experience any of the possible benefits of the behaviour change.

The reasoning behind the mechanism for the decision to consider leaving a group is based on the concept that individuals need to balance their different motivational states. For example, if an individual is satiated, it will no longer need to build energy levels – instead it might seek to 'spend' some of the energy it has acquired in socialising. On the flip side, if an individual's need to rest is not being met because the group is travelling, the individual will want to change behaviours. Should the school change behaviours, the individual will then feel content, for at least one time step, that those needs were acknowledged, even if the shift in behaviour does not meet all of its needs.

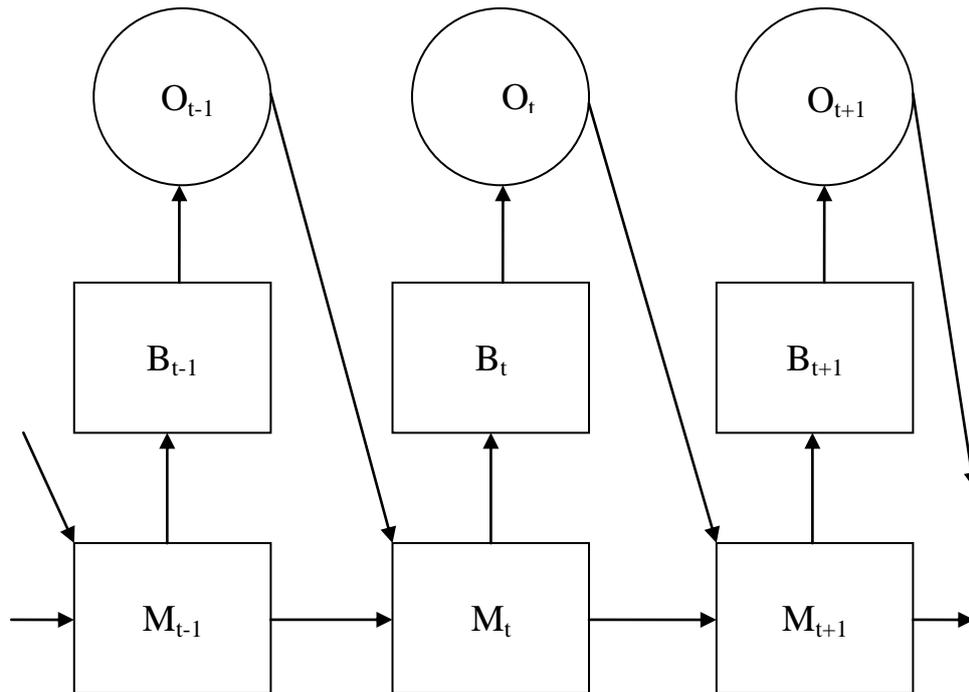


Figure 1.3. The relationship between motivational state (M), desired behaviour (B), and observed behaviour (O) as they change through time (t). It is possible for the observed behaviour and desired behaviour to be equal.

If a dolphin meets the criteria at which it may change schools, it will do so with a probability based on its current school size, which plateaus for schools larger than 20 dolphins. Should the decision to leave the school be made, the individual will join a new school based on the proximity to existing schools, its desired behaviour and the average association with the members of these schools.

A new school will form if the average association between those individuals wishing to leave an existing school is higher than their association with any existing school, or if no existing school is within a biologically plausible distance of travel. If, by chance, an individual is left without a school at the end of the time step, it will join the closest existing school, no matter how far away it may be. *The assumption, again, is that the benefits of being in a group outweigh being alone.* Lone dolphins are exceptionally rare in the Moray Firth, and group-living benefits in these species have been demonstrated many times (Lusseau et al. 2004).

This fission-fusion behaviour occurs at the end of the time step, after which the process begins again for however many time steps are deemed appropriate.

Results

The simulation was run for 360 time steps, which is one year if the time steps are taken to be one day. We found that the simulation generated a distribution school sizes similar to that expected in nature (Figure 1.4) even though the simulation used crude parameters (Lusseau et al. 2004).

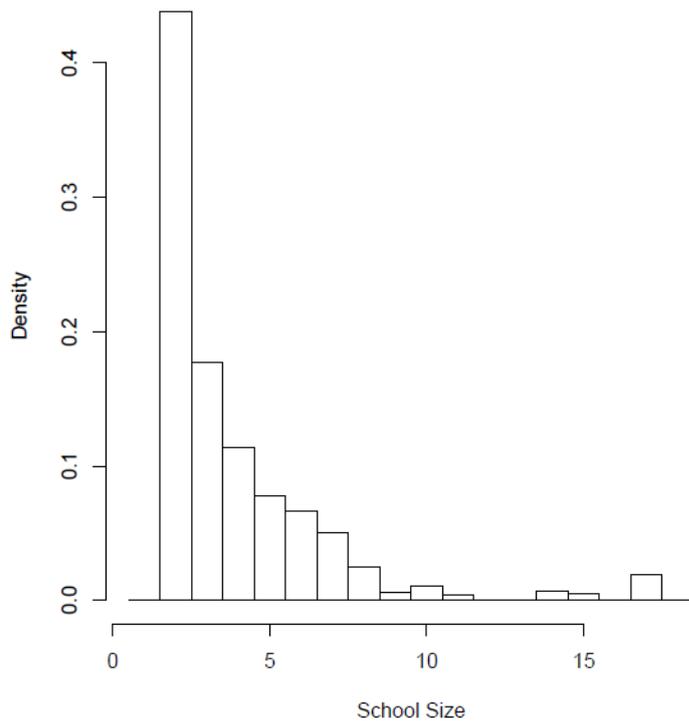


Figure 1.4. The distribution of school sizes as predicted by the simulation.

The simulated distribution of dolphins appears to match observed data (Figure 1.5, Figure 5.1), with the highest concentrations being in the area of the Moray Firth known as Inverness Firth and at the mouth of Cromarty Firth. This is a function of the underlying vague prey distribution provided to the simulation estimated from the literature and incorporated at this stage as a simple regional binary information (foraging hotspot or not) (Hastie et al. 2004, Bailey and Thompson 2010). Should shifts in prey availability occur, these factors can be taken into account. Once the model is fitted to observed dolphin movement, it may not be necessary to invoke this covariate in the model specification.

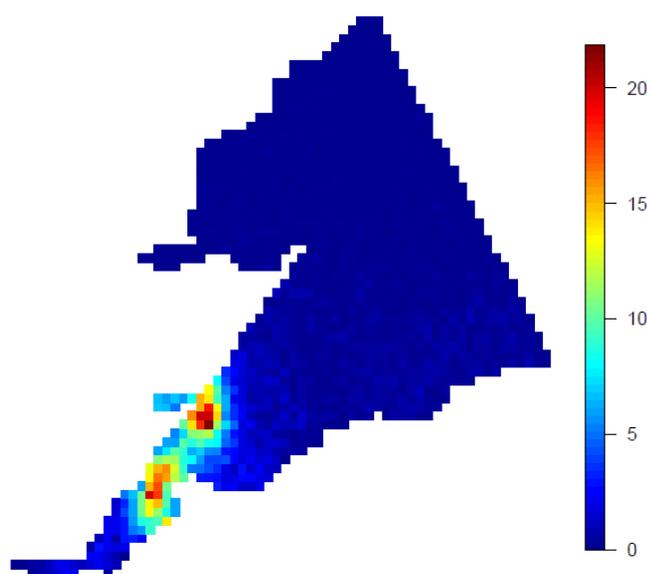


Figure 1.5. The density of dolphins schools in the Moray Firth as predicted by the simulation is similar to the observed distribution of individuals in most years (see Figure 5.1).

Finally, the time budget of the dolphins is biologically realistic, showing similar patterns to those observed in other bottlenose dolphin populations (Lusseau 2003c, Figure 1.6).

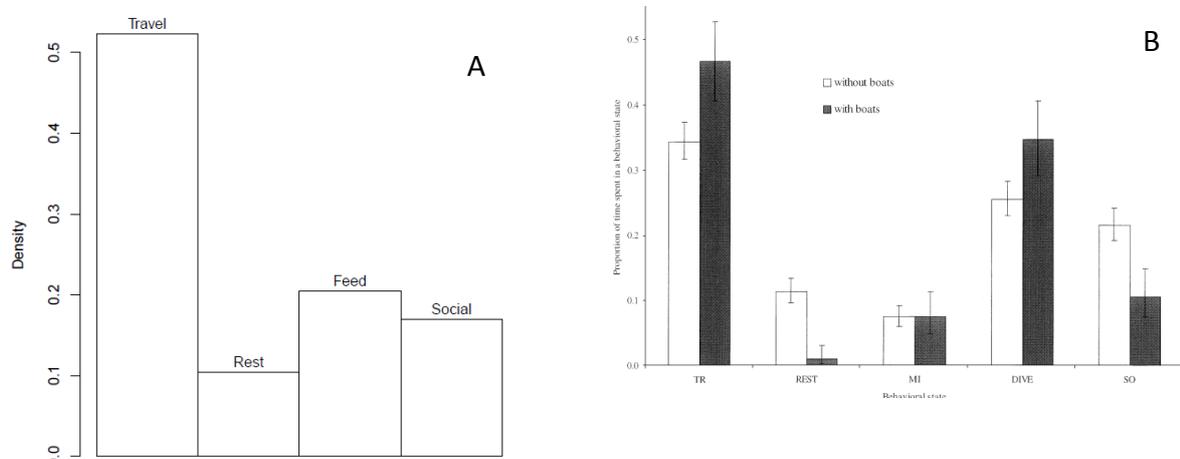


Figure 1.6. The behavioural time budget of bottlenose dolphins predicted from the simulation (A) and observed in Doubtful Sound, NZ (Lusseau 2003) (B) (TR = travelling, REST = resting, MI= milling, DIVE = feeding, SO = socialising).

Conclusions

These simulations are currently not informed by data collected in the Moray Firth, yet we are able to predict behavioural budgets and school-size frequency distribution that are biologically reasonable. This shows that the mechanistic processes on which the simulations rely (the relationships between motivations and observed behaviour) are reasonable. We therefore have here the skeleton of the simulation platform whose parameters will now need to be informed by fitting the mechanistic models to actual data such as habitat use and POD time series (see next sections).

Dolphin Response to Disturbance

The initial simulations focussed on investigating whether the conceptual framework for dolphin behaviour was capable of recreating the observed dolphin behaviour, group size distribution and spatial distribution. Having simulated biologically realistic dolphin behaviour, we are next interested in simulating the dolphins' response to disturbance. In this case, disturbance takes the form of boat traffic moving through the Moray Firth to and from the various ports in the area (Figure 1.7). Spatial models developed in part IV and V form the basis of the information for this section of the model.

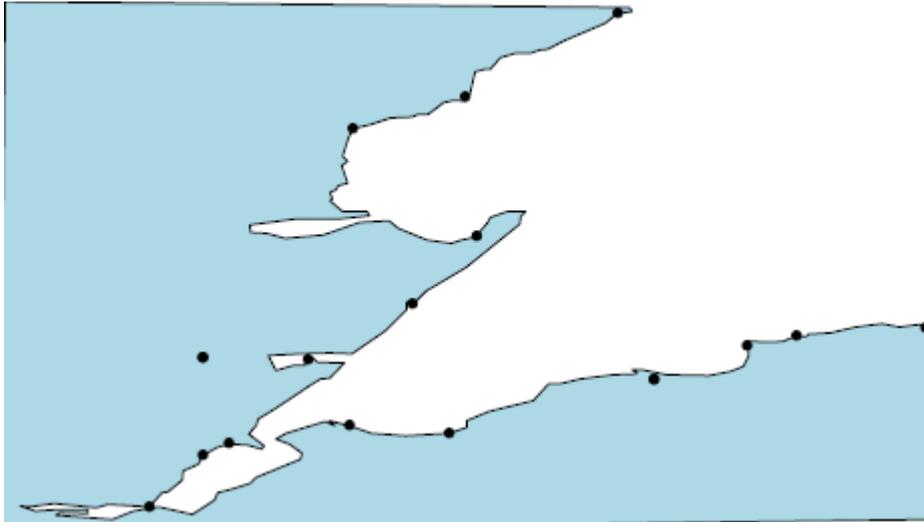


Figure 1.7. A map of the Moray Firth area with the ports marked as black circles. Blue indicates land. The one port that appears to be located inland is on an estuary not considered in our simulations.

Bottlenose dolphins can detect anthropogenic sounds over a range of up to several km. However, they do not immediately react to the disturbance in a visible way. Instead, as the source of this sound gets closer to the dolphins, their level of ‘fear’ motivational category in the simulation increases. Eventually, the dolphins’ fear outweighs their other motivations and the group will move away from the disturbance. Alternatively we can also make the assumption that if the boat comes within a set distance of the dolphins, the disturbance is considered more immediate, and the dolphins are more likely to move away from the boat no matter what their level of fear is. If the group is feeding when disturbed, the probability that they will move away from the area is also dependent on their motivation to feed and their condition. Groups more highly motivated to feed or in poor condition are less likely to stop feeding, since their need to increase their condition will outweigh their fear. We can therefore incorporate the effect of boat disturbances as a covariate in the simulation model influencing the motivational state of individuals, and therefore ultimately with the possibility to influence their activities. The advantage of this mechanistic approach to accounting for disturbances is that we can model shifts in activities as well as no observable response to boat interactions, depending on the motivational state trade-offs. Therefore we can reproduce all possibly observed outcomes to a boat interaction. As in the previous section, it is now necessary to estimate the parameters of the relationship between this disturbance covariate and motivations. We can achieve this using a state space modelling approach (see PART III) in which motivational states are hidden processes linked to observable behaviour under different disturbance conditions. Using these structural relationships we can estimate the parameters and consequently use those estimates in this simulation.

The dolphins’ reproductive rate is the vital rate most likely to be impacted by disturbance, either through increased inter-calf interval or decreased calf survival. Changes in the animals’ energy intake or expenditure will affect their condition, reducing the resources available to females to either produce or maintain calves (Figure 1.8). While any disturbance will result in increased energy expenditure through increased movement, disturbances during feeding events will also decrease energy intake, compounding the effect of the disturbance.

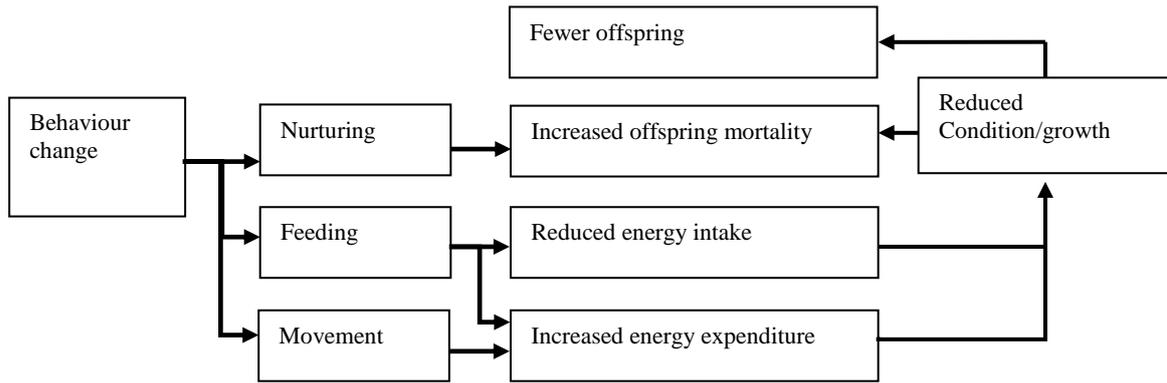


Figure 1.8. A flowchart illustrating how disturbances resulting in behaviour change could affect bottlenose dolphin populations through reduced reproduction.

MODELLING THE DOLPHINS OF MORAY FIRTH

The simulations described in part V of this report can be used to simulate the type of data observed from the Moray Firth, as well as the possible effects of boat traffic on dolphin behaviour and distribution. We can estimate when dolphins are feeding and when they are taking part in other behaviours using remote acoustic logger data time series (such as T-PODs). There are a set number of activity states (N) that can occur within a day. The number of times dolphins are recorded feeding in one location, within a day ($B_{f,t}$), is dependent on covariates such as water depth (W), gradient (G) and time (T) (Hastie et al. 2004), as well as the number of feeding events that have already occurred in that location. This accounts for prey depletion and/or satiation of a dolphin school. Mathematically, this can be written as,

$$B_{f,t} = \alpha_0 W + \alpha_1 G + \alpha_2 T - \alpha_4 B_{f,t-1},$$

The water depth and gradient do not vary with time, since they are permanent features of the landscape reflecting prey availability and location.

All other dolphin behaviours, travelling, resting and socialising, cannot be distinguished in the clicks recorded by the T-PODS. Therefore, the number of times a dolphin will take part in any other behaviour ($B_{o,t}$) in a set area is dependent on the suitability of that habitat for dolphins. For example, areas farther from the mouth of an estuary (D) may be less likely to hold dolphins. Season (S), which can be modelled as a one for the warm season and a zero for the cold season, will increase the amount of time dolphins spend in other behaviours, since food will be more available and better quality when the animals do spend time feeding. Finally, there are other relevant environmental covariates (E) that could be considered, such as tidal fronts (e.g. Bailey & Thompson 2010), that may make the habitat more suitable for bottlenose dolphins. D , S and E can be informed using dolphin ranging predictive models fitted to data using a spatially explicit mark recapture density estimation approach (see PART V).

$$B_{o,t} = \alpha_5 E - \alpha_6 D + \alpha_7 S.$$

The amount of time a location is empty ($B_{e,t}$), is therefore,

$$B_{e,t} = N - B_{f,t} - B_{o,t}.$$

TPODs record the clicks of individual dolphins. However, it is not possible to identify individuals from their clicks. Therefore, we cannot estimate individual condition and must instead consider condition at the population level. In addition, since we do not have direct measures of condition, such as blubber layer, we must instead estimate an index of condition. We have identified that we should in future be able use photogrammetry to estimate these variables (see PART II). As a result, condition is modelled as the ratio of the number of feeding events to none feeding events, with some effect of season. Season is incorporated in the condition equation, since we assume that the dolphins will need to feed less in the summer months when food is more available and higher quality. Mathematically, the index of condition can be written as,

$$C_t = \frac{B_{f,t}}{B_{o,t}} + \beta S,$$

where condition will be increased in the warm season.

The observations of dolphin behaviour (O_t) are recorded with error. In particular, it is possible that we failed to detect the dolphins on the TPOD, even though the animals were present. Therefore, the observed values of number of times a location is empty is inflated compared to the true $B_{e,t}$. This results in four possibilities for each observation within a time-step: the animal is feeding, the animal is in any activity state other than feeding, and the animal was present, but undetected by the TPOD, and the animal is truly absent. This gives a multinomial distribution on the observations where,

$$O_t \sim \text{multinom}(N, \mathbf{p}_t),$$

and \mathbf{p}_t is a vector of probabilities for each possible type of observation, based on the values of B_t . $B_{e,t}$ can give an estimate of the proportion of time the location is empty, while $B_{f,t}$ and $B_{o,t}$ would provide an estimate for how often the location is occupied. However, some of these periods of occupation will be missed. *If we assume that we are equally as likely to fail to record clicks during $B_{f,t}$ as $B_{o,t}$, then we can model this as,*

$$\begin{aligned} p_{e,t} &= \frac{B_{e,t}}{N} \\ p_{m,t} &= (1 - p_{e,t})p_c \\ p_{f,t} &= \frac{B_{f,t}}{N} - 0.5p_{m,t}, \\ p_{o,t} &= \frac{B_{o,t}}{N} - 0.5p_{m,t} \end{aligned}$$

where p_c assumes that a constant proportion of the clicks will be missed.

PART II – Review of data available to inform the state space model

DATA TO INFORM MODEL PARAMETER ESTIMATION

Activity state from acoustics

Field sampling of the Moray Firth bottlenose dolphin population has traditionally focused on collecting data to understand their population biology. There is therefore no behavioural information that has been collected systematically over prolonged periods, using focal follow of dolphin schools. However, behaviour can be inferred from time series of dolphin echolocation click detection on autonomous acoustic loggers (T-PODs). This spatially-fixed information can be used to inform the dynamics of activity states in the home range of the population and, in conjunction with either visual observation or additional acoustic loggers, estimate the effect of anthropogenic activities on behaviour (Figure 2.1). There are three main drawbacks with regards to using data from T-PODs. First, the area in which dolphins can be detected is limited, we do not know what is occurring in those areas not covered by the recorders. However, non-sampled locations can be thought of as the hidden component of the home range use which we can try to infer. Second, the absence of a click may be due to the true absence of a dolphin in that location, or the failure of the T-POD to record the click. Finally, although feeding events can be identified through click analysis, there will be some error associated with our ability to identify feeding events. We can estimate these errors using statistical state space model in which the observed clicks are assumed to be dependent on the activity state of the individuals emitting them, a valid assumption (Hastie et al. 2006), which is recorded with error (see Part III). We can use this sampling technique to collect data to parameterise the behavioural effects of disturbances and parameterise the state space model described in part I to infer time series of energy allocation and condition for females.

Inferring body condition from photogrammetry

Photogrammetry is a photographic method in which we try to estimate the size of objects from their image in a photo. Photogrammetry has previously been used with large whales, principally to infer calf growth rate (Whitehead & Payne 1981). Recent advances in digital photography means that such techniques can now be extended to smaller dolphins. The body length and fin morphometry of bottlenose dolphins have been reliably estimated in Fiordland, New Zealand (Rowe et al. 2010). We have now trialled this sampling technique in the Moray Firth and can reliably deploy it during photo-identification sampling. Our approach, as in New Zealand, relies on using parallel laser pointers to display a known 'scale' on the animal when the photograph is taken. Using this scale we can measure the distance between the blowhole and the dorsal fin which is linearly related to total body length. The relationship between both measures is known from necropsies of stranded animals. It may in future also be possible to estimate the "plumpness" of individuals, and therefore time series of body condition indices for individuals (see part I), by using a third laser pointer to define the curvature of the back of the animal. We can therefore use this sampling technique to inform the PhysDem model (Figure 2.1). Specifically, we can use these data to parameterise the calf growth sub-model and therefore infer the energetic demand on female driving her energy allocation needs. We can also test whether we can develop a reliable body condition index for adults to parameterise the adult energy allocation to survival sub-model. This will also help infer the energy allocation process.

Demography from photo-ID data

Finally, we can use traditional photo-identification sampling techniques to inform both the demographic model (Figure 2.1) and the movement parameters in the state space model simulations

(see part I). These data can be used to estimate survival rate, population abundance, and calf survival.

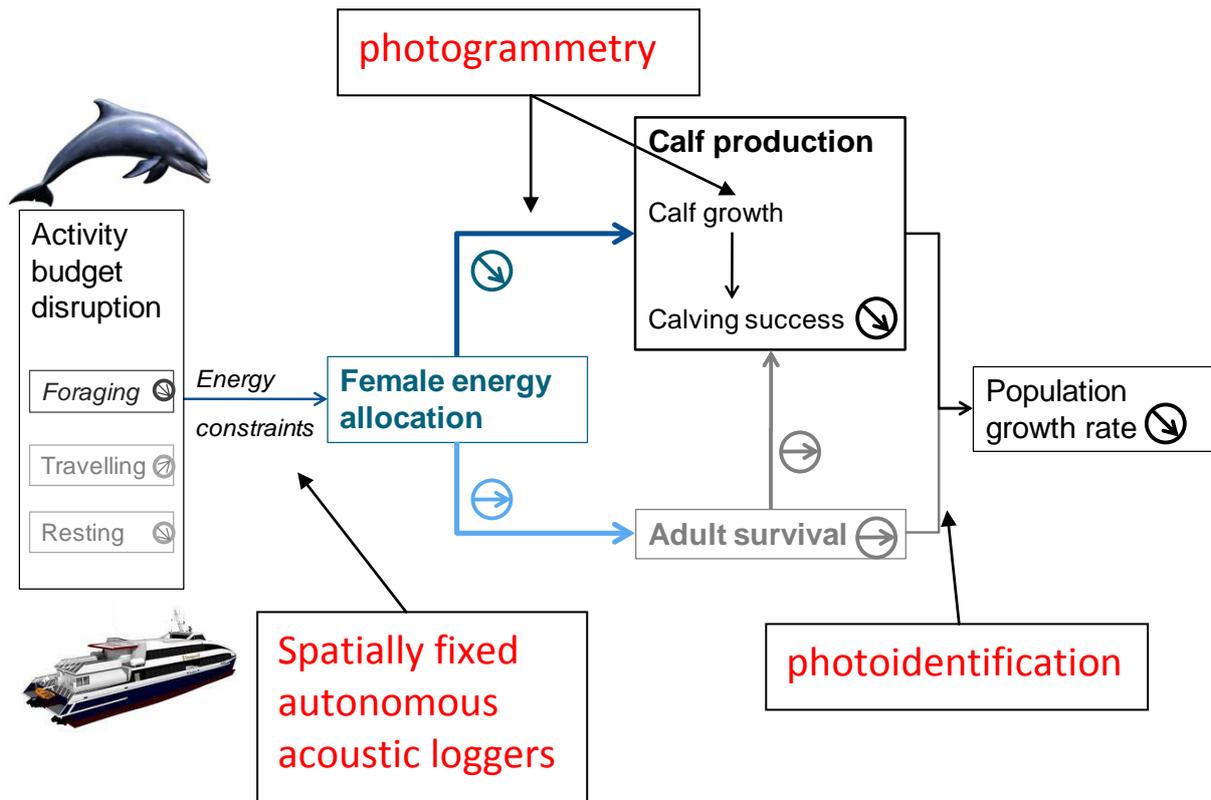


Figure 2.1. Proposed data and field sampling techniques to inform mechanistic links of the model

DATA COLLECTED IN THE MORAY FIRTH

Autonomous acoustic loggers

T-PODs and the newer C-PODs have been deployed in the Moray Firth by the University of Aberdeen at numerous locations over the past 5 years (Figure 2.2). Some stations, such as the Sutors, have been sampled almost continuously over that period, while others have only received focussed sampling over a period of months in response to particular contractual demands (figure 2.3). The data is held by the University of Aberdeen Lighthouse Field Station under various contractual agreements. The advantage of PODs is their ability to pre-process acoustic data and to only retain key parameters, saving a lot of post-processing time. This also means that they can record dolphin detections continuously, so there is no need to set sampling periods to save onboard memory. However, it may be preferable to shift autonomous acoustic logging to another recording system such as EARs (Lammers et al. 2008) for two reasons. First, such devices record the whole sound environment and therefore we could use not only on clicks but also other dolphin vocalisations to infer behaviour (and discriminate between species in more offshore locations). Secondly, such a system would also record the presence of anthropogenic activities (boat noise, pile-driving, etc.) and we would therefore have a fully-autonomous sampling system that would record not only dolphin variables but relevant covariates as well.

Photo-identification

The goal of photo-identification is to estimate the probability of encountering known individuals in time and space. Those individuals are known because they can be recognised from marks that are visible in photographs. The University of Aberdeen has been collecting photo-identification data since 1989 in the inner Moray Firth, averaging around 15-20 sampling sessions every summer from May to September. From 2001 this information has included a digital record of the exact location both of each photo-identification events and survey effort. From 2001 to 2009 290 sampling trips were undertaken recording 2614 capture events of 95 individually marked individuals (Figure 2.3).

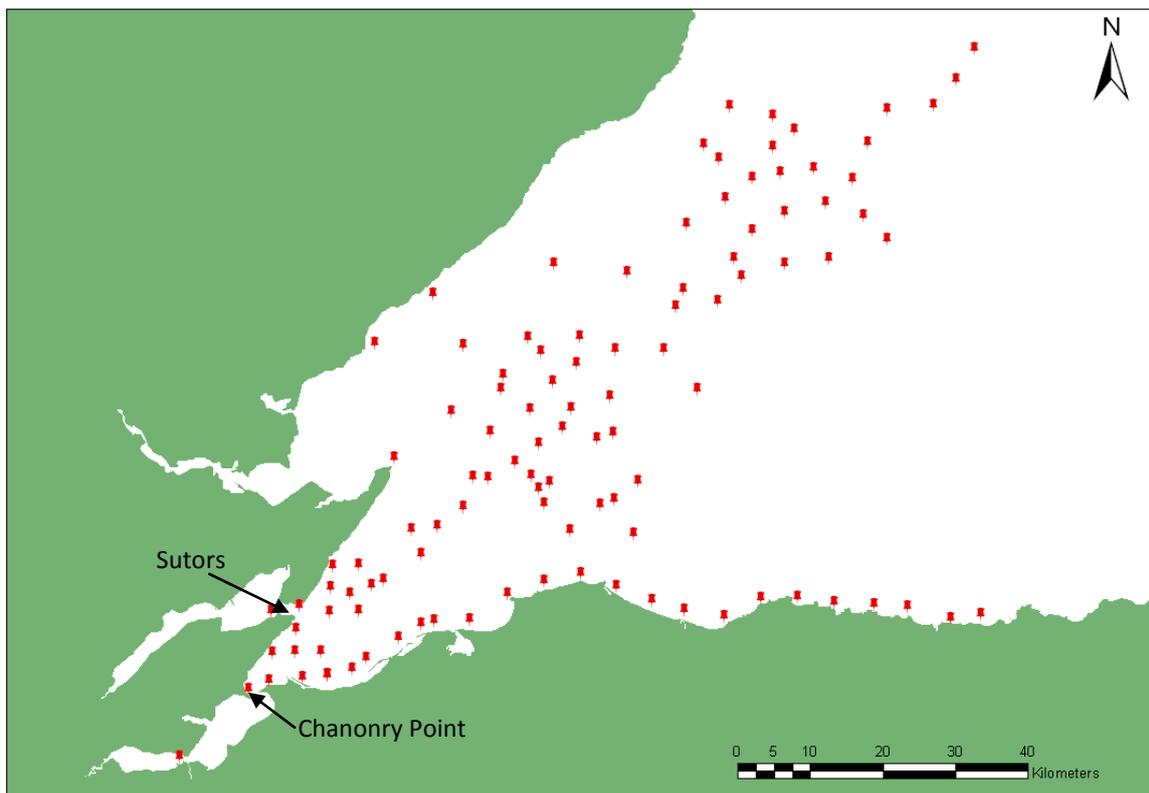


Figure 2.2 Location of stations where TPODs and CPODs have been deployed since 2005.

Photogrammetry

This sampling technique has been trialled in the Moray Firth and is now deployed regularly during photo-identification sampling effort. However, we currently lack enough samples to use this data to inform models of calf growth, or variation in adult body condition (Figure 2.3). This element of the model is crucial and therefore sampling this data should become a top priority.

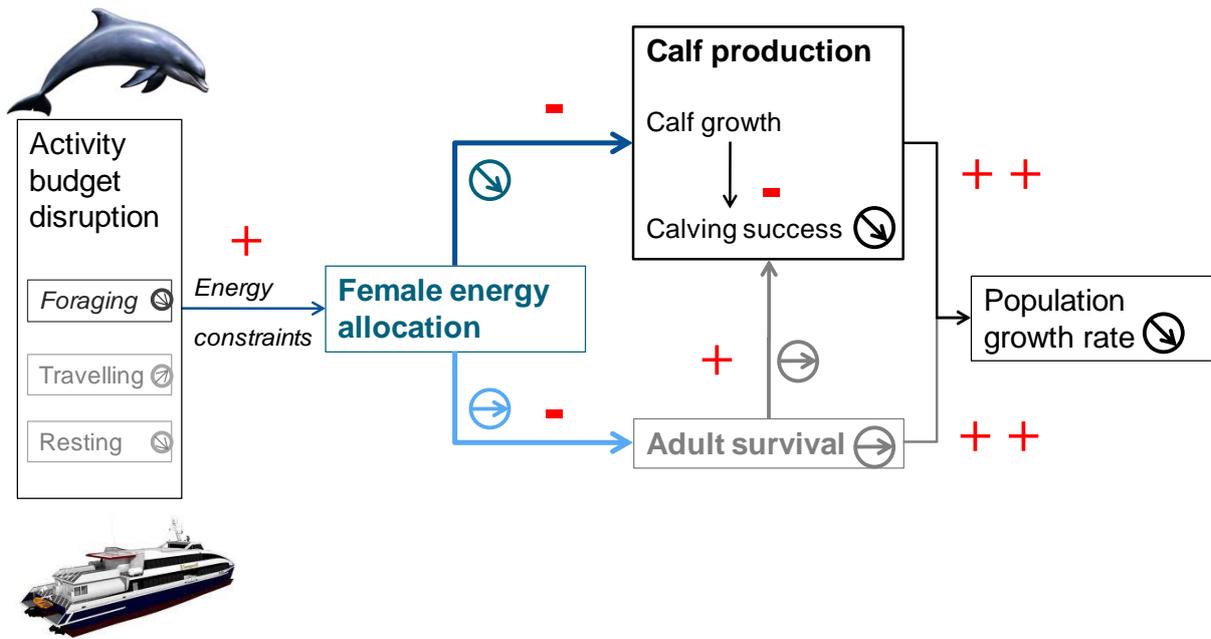


Figure 2.3. Data availability to instigate parameter estimation for each link: (-) insufficient, (+): sufficient for preliminary studies, (++): mature dataset

PART III – An observation model to infer dolphin behaviour using data from Automated Porpoise Detectors (T-PODs)

CONCEPTUAL BACKGROUND

Dolphins use echolocation clicks to navigate and to detect objects in their environment. Echolocation clicks are projected from the dolphin's head in a highly directional beam (Richardson et al. 1995). The beam width of the click trains emitted by bottlenose dolphins ranges from 10 to 11.7° at an angle 5° above the body axis (Richardson et al. 1995). The rate at which clicks are emitted by individual dolphins depends on the distance between the dolphin and the object it is targeting. When travelling, dolphins tend to emit regular echolocation clicks that allow them to perceive their environment tens of meters ahead of them. Clicks are emitted at a faster rate when a specific object, such as a prey, is targeted. However, the time elapsed between two clicks is still dependent on the distance between the dolphin and the object because the dolphin needs to receive and process the information contained in the echo of the first click before emitting a new one. The inter-click interval (ICI) therefore tends to correspond to the time it takes sound to travel from a dolphin to an object and back (the echo processing time is negligible). This mechanism leads dolphins to produce two types of click trains (bouts of clicks). The first type is composed of clicks produced at regular, well-spaced intervals, and corresponds to bouts of clicks produced when dolphins are travelling. The second type is composed of rapidly emitted clicks that are called feeding buzzes. These click trains are emitted as a dolphin homes on a prey, hence just before prey capture. Therefore, if we are able to recognise feeding buzzes, from their inter-click interval characteristics, we could infer time series of relative feeding success, as the number of feeding buzzes should be related to the number of prey captured. Interestingly, the amount of echolocation clicks produced by dolphin schools is not dependent on the number of dolphins present in the school (Dawson 1991, Götz et al. 2006). Individuals are able to eavesdrop on others and therefore the echoes of returning clicks can be received not only by the dolphin that emitted them but also by all others in the school. Therefore echolocation clicks can provide a 'school-wide' measure of activity state.

Preliminary work shows that we can use time series of echolocation clicks time detected using PODs to infer the activity state of bottlenose dolphin schools in the NE Scotland population (Powell 2008). In particular, we can infer physiologically important states such as foraging and how those are affected by boat interactions (Powell 2008). The directionality of the dolphin's echolocation beam makes it difficult to record all click trains produced by an echolocating dolphin in the wild. Since the dolphin and its prey move in three dimensional space relative to one another the click train could be emitted in any direction. In order for the click train to be logged by the T-Pod the dolphin's head must be facing directly towards the hydrophone. Therefore, a relatively large proportion of click trains will not be picked up by the T-Pod. A significantly larger proportion of shorter ICI clicks are recorded in the five minutes before the observation of foraging behaviour compared with randomly selected times from the same encounter indicates, suggesting that this may be used to identify episodes of feeding (Powell 2008). This work also confirms that, like bats, dolphins emit a buzz of clicks with short ICIs at the end of a prey capture (DeRuiter et al. 2009, Aguilar de Soto et al. 2008, Madsen et al. 2005, Miller et al. 2004, Au 1993). T-Pods are capable of detecting and distinguishing these trains. The likelihood of detecting these buzzes is not influenced by environmental parameters and hence the proportion of buzzes detected can be compared through time.

We develop here an observational model to infer activity state time series from echolocation click time series detected on PODs and assess the influence of boat presence. This model will then be used to inform the observation component of the BehPhys model (Figure 1.2).

METHODS

A T-Pod was deployed from 26 March- 8 July 2008 at the entrance of Aberdeen Harbour and from 15 April – 14 June 2005 off South Sutors in the Cromarty Firth. These deployments were coupled with visual observations during which dolphin presence, behaviour, and boat presence were recorded. The timing of visual and TPOD data were synchronised. For the Sutors study, 28 visual samples were recorded during this period, each lasting on average 163 minutes. During this period 35 boat interactions were observed lasting on average 17 minutes (range: 5-84min). Here we defined boat interactions as loosely as possible in order to match the needs of our current state space model (parts I, III, IV). It is a conservative definition of interaction based on spatial co-occurrence (both boat and dolphins were present in the study area). We recorded 55 visual samples at the entrance of Aberdeen harbour lasting on average 128 minutes. We observed 118 boat interactions lasting on average 14 minutes (range: 5-145min.).

The T-POD consists of a hydrophone, an analogue processor and a digital timing/logging system. It has six programmable channels; each channel is set to look for sounds in a given frequency range. Once in the water, the pod scans each channel sequentially for 9.3s out of every minute. To identify cetacean clicks the pod compares the output of two bandpass filters, one of which is set to the frequency range of the clicks of the species of interest and the other set to a reference level. When there is sufficient difference in detection between the two bandpass filters a click will be logged to a resolution of 10 μ s. Previous research has indicated that the range of detection for an individual T-Pod is approximately 1 km for bottlenose dolphins (Bailey et al. 2010a). The software analyses the clicks logged and utilises a detection algorithm to identify click trains. These click trains are then classified based on the likelihood of their being produced by a cetacean (Table 3.1). For all subsequent analysis only trains classified as 'Cet-hi' or 'Cet-Lo' were used, as previous work has verified these as being reliably produced by cetaceans (Bailey et al. 2010a). Given the click details produced by the T-Pod software, the inter-click interval can be calculated for every click recorded. The ICI varied from very short time periods (20 μ s) to much longer ones (>10 minutes) and the data is multimodal. Analyses were carried out on the natural log-transformed ICIs to help understand this multimodality.

Table 3.1. T-Pod software click train classification categories (www.chelonia.co.uk, 2008)

Train classification	Description
Cet-Hi	Train with a high probability of being produced by a cetacean.
Cet-Lo	Less distinctive trains that are still likely to have come from a cetacean, particularly if there are Cet-Hi detections as well.
Cet-All	All cetacean detections, both Cet-Hi and Cet-Lo.
Doubtful Trains	Often these are cetacean trains, but are sometimes unreliable.
Very Doubtful Trains	Less likely cetacean trains and are more likely to arise from boat sonar or chance sequences from random sources.

Sutors and Aberdeen Harbour: two foraging hotspots.

Both the Sutors and the entrance of Aberdeen Harbour are known to be foraging hotspots for the NE Scotland bottlenose dolphin population (Hastie et al. 2006, Powell 2008). Dolphins tend to feed mid-water at the Sutors (Hastie et al. 2004) whereas they tend to feed close to the surface at Aberdeen harbour and seem to use the tidal front created by the freshwater flow of the Dee River to aid in

prey capture in the same way as they do at Chanonry Point and at the mouth of the Ness River in Inverness (Mendes et al. 2002, Bailey and Thompson 2010). Therefore sound exposure caused by boat interactions during a prey capture event will differ at these two locations. In addition, boat presence is expected in Aberdeen harbour as boats enter and leave the harbour on a regular basis. Bottlenose dolphins started to use the harbour more frequently recently. Boats have always been present as a constant covariate in this recently established foraging hotspot. Because boat traffic is more predictable and has always been a factor attributable to the Aberdeen site, we would expect that it would cause less of a perceived risk to dolphins. We can therefore anticipate that boat type and boat predictability will influence risk perception of boats by dolphins (Lima and Zöllner 1996), and therefore any observable 'boat effect' on the population should vary spatially. We would expect to not see any overall effects in Aberdeen. At both study sites dolphins are well within the POD's range of detection when present.

MODELLING APPROACH

The goal of this analysis was to translate time series of inter-click intervals (ICI) resulting from clicks detected on TPODs into time series of the hidden activity state in which individuals present in the vicinity of TPODs were during the duration of the deployment. From the literature and exploration of the data we defined four possible observations that could result in inter-click intervals of observable durations:

1. Very short ICIs associated with a feeding buzz (F: performed when the animal is homing on a prey right before capture)
2. Short ICIs between regular clicks (R: performed when dolphins are not feeding and primarily travelling)
3. Inter-train intervals (ITI: time that elapses between two bouts of click emission)
4. Inter-visit intervals (IVI: time that elapses between two visits to the area by dolphins)

We know that click detection on TPODs occur with error. Moreover, the four hidden states resulting in these observations can produce possible ICI of which the duration can overlap. For example, the ICI for a long ITI could also result from a short IVI. We therefore modelled the ICI time series samples using a hidden Markov modelling approach (HMM, Figure 3.1).

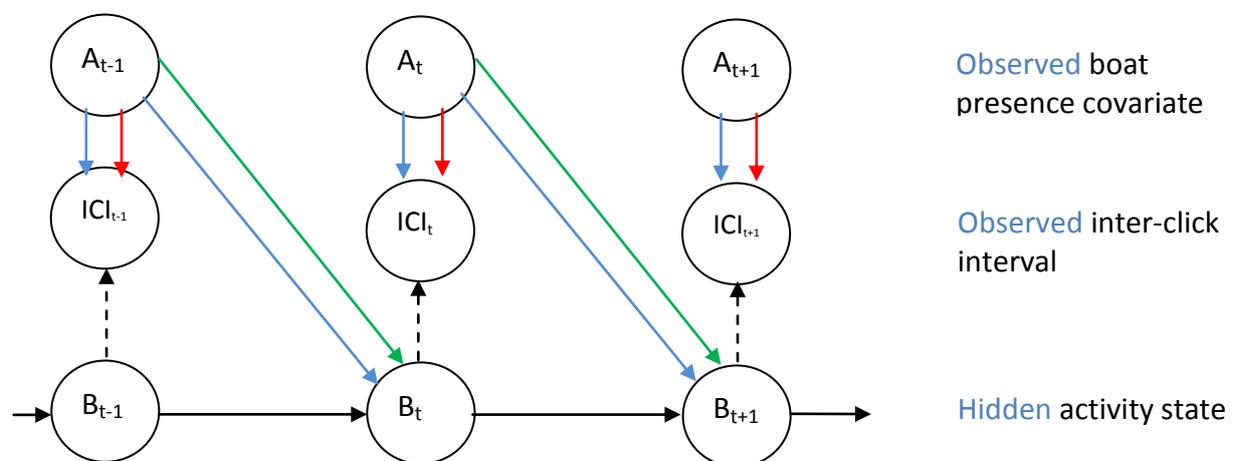


Figure 3.1. A graphical representation of the hidden Markov models fitted to the Sutors and Aberdeen harbour TPOD data. The boat presence covariate was recorded visually. We tested four contrasting

hypotheses (see text) that are represented by the different arrow colours. The null model is only composed of the black arrow, and those are present for all models.

In these models, we assumed that the activity state was unknown before the detection of each ICI because of the potential for gaps in detections due to the directionality of echolocation clicks. We restricted the TPOD data to the visual samples during which dolphins were detected. Therefore, we fitted a hidden process as the mixture of three log-normal distributions (F, R, and ITI). Indeed, data exploration shows that ICI distribution in these restricted samples did not overlap with detected ICI for IVI in year-long deployment (Figure 3.3). We used the year-long deployments to define the initial values for means and standard deviations of the ICIs representing the four hidden states. Each visual sample, lasting typically 3 hours, was considered as a replicate sample of the hidden Markov process we determined. Models were fitted to the data to estimate *parameters which were assumed not to change between samples* (no sample random effect). In addition to the mixture model described above (represented by the solid dash lines in Figure 3.1), the HMM was also composed of a transition intensity matrix which directed the probability that dolphins would be in activity state F,R, or ITI, given that they were in one of those states at the previous time step (solid black lines in Figure 3.1). We provided vague initial values for those parameters. We fitted four contrasting models to the ICI time series corresponding to four alternative hypotheses:

1. No boat influence: ICI is only related to the hidden activity state and activity state at time t only depends on activity state at time $t-1$.
2. Boats influence activity transition probabilities (activity state disruption hypothesis): ICI is only related to the hidden activity state and activity state at time t depends on activity state at time $t-1$ and boat presence at time $t-1$ (Figure 3.1, green).
3. Boats influence ICIs (echolocation abilities disruption hypothesis): ICI is related to the hidden activity state and boat presence at time t and activity state at time t only depends on activity state at time $t-1$ (Figure 3.1, red).
4. Boats influence both activity transition probabilities and ICIs (a combination of both 2 and 3): ICI is related to the hidden activity state and boat presence at time t and activity state at time t depends on activity state at time $t-1$ and boat presence at time $t-1$ (Figure 3.1, blue).

Models were implemented in R (version 2.13.0) using the package `msm` (version (Jackson 2011)). We used a Newton-type algorithm for the optimisation of the likelihood function (package `nlm`). We selected the best fitting model on the basis of the Akaike Information Criteria. We assumed that the initial state (at $t=0$) was ITI. We changed initial values a number of times to assess the influence of initial conditions on the estimation procedure, and to ensure that we were not fitting to local maximum. This had little effects on the fitted models and did not change the results of the model selection.

RESULTS

Consistency across deployments

If ICI can be used reliably to infer behaviour we would expect the same ICI modes for F and R to emerge at multiple sites in the Moray Firth and F to occur more often during the summer season. To test this, we explored ICI time series for three year-long deployments at three locations (Figure 3.2). Those modes were consistent across the three sites and between the four seasons (Figure 3.3). From this we could infer initial values for ICI means and standard deviations for F, R, and ITI to be used in the HMM for the two deployments during which we had visual observation of boat presence.

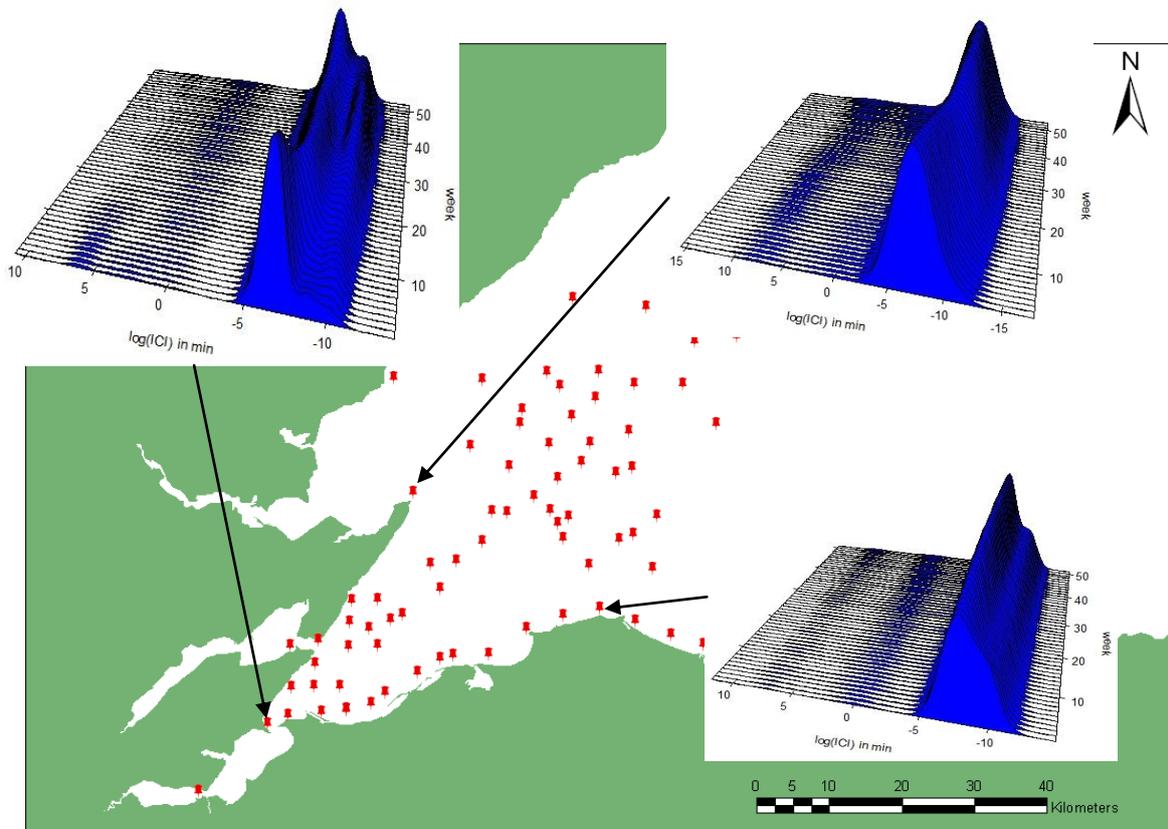
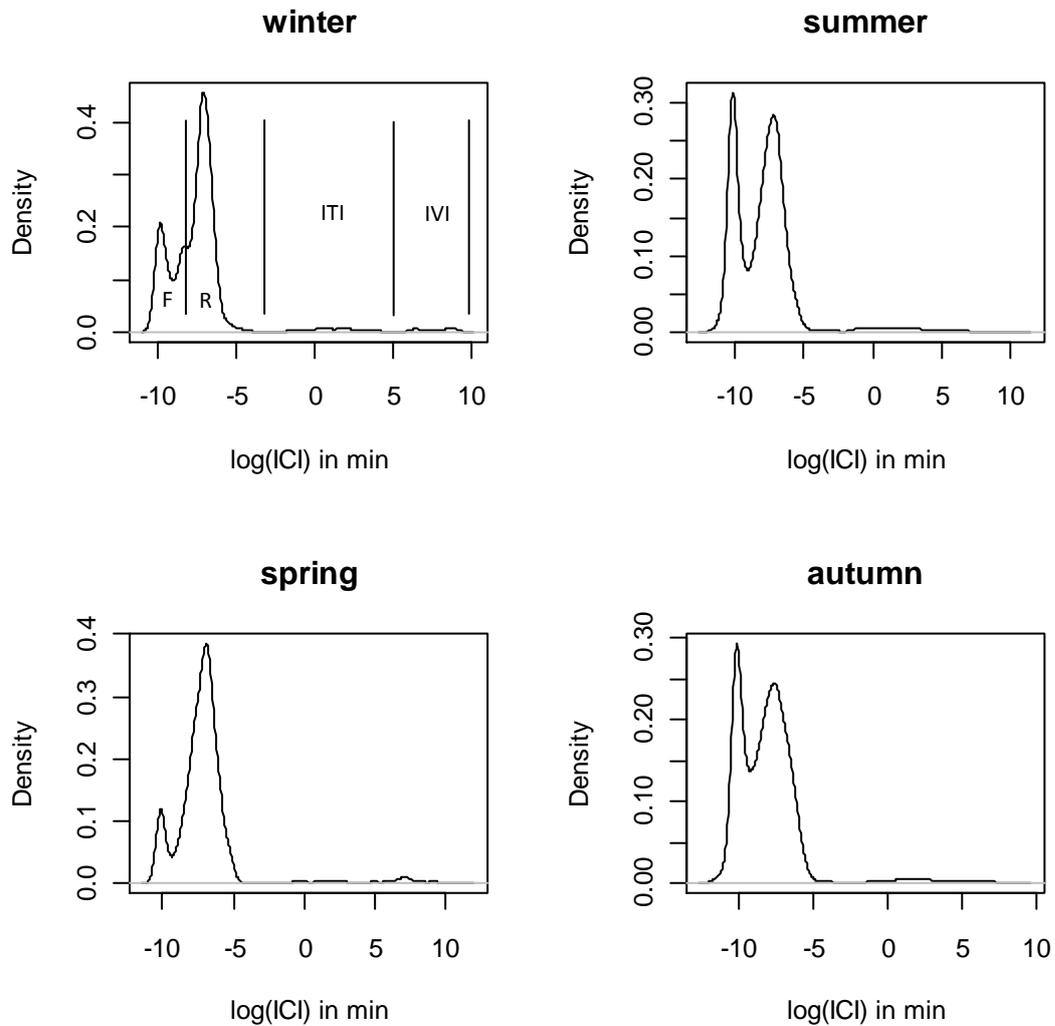


Figure 3.2. Density distribution of the natural log of inter-click intervals (ICI) in min detected on T-PODs deployed at three locations in the Moray Firth (conditional kernel density estimates over 52 weeks, 52 density distribution plots, from 1 January 2007 to 31 December 2007). Chanonry Point is a known foraging hotspot, while Tarbat Ness and Lossiemouth are not heavily used by dolphins where they are assumed to only pass by.

Besides their use for the inference of boat effects on behaviour, these time series can also be used to infer the spatial ecology of the population. We can also use the Viterbi algorithm (Jackson 2011) to translate the ICI time series into time series of information on activity state time series. This means we can then infer the amount of time dolphin spend in an area when they visit it, how long it was since the site was last visited and what the foraging success of dolphin schools were for each visit (Figure 3.3). However, this is a substantial undertaking that was deemed outside the remit of this current work. Instead, we focussed on the immediate needs to determine boat effects.

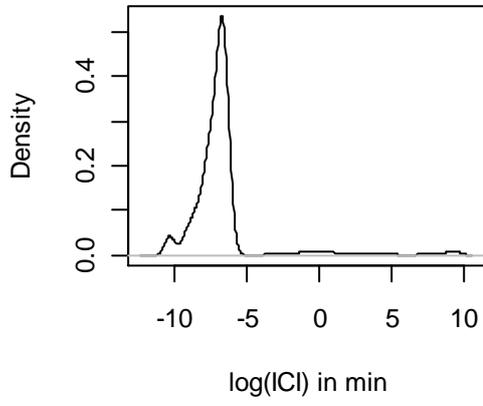
Figure 3.3. The relative density distribution of $\log_e(\text{ICI})$ at the three locations shown in Figure 3.2 for year-long deployments in 2007 showing the inter-site and intra-site consistency in ICI modes corresponding to the 4 processes identified (F: foraging buzzes, R: regular clicks, ITI: inter-click train interval, IVI: inter-visit interval). (A) Chanonry Point, (B) Tarbat Ness, (C) Lossiemouth. These are relative density distribution plots; hence we cannot interpret the difference in densities around the modes between graphs but can interpret the relative difference of densities around modes within graphs.

(A) CHANONRY POINT

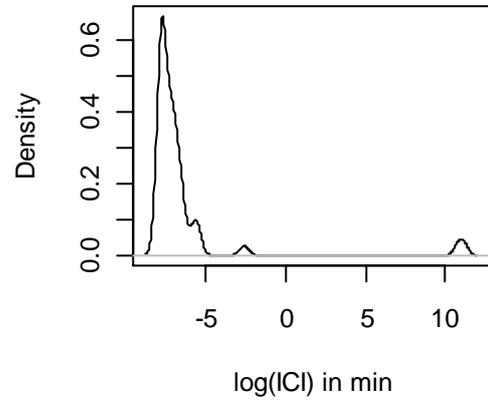


(B) Tarbat Ness

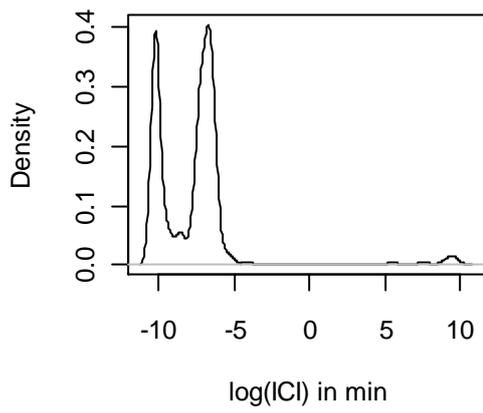
winter



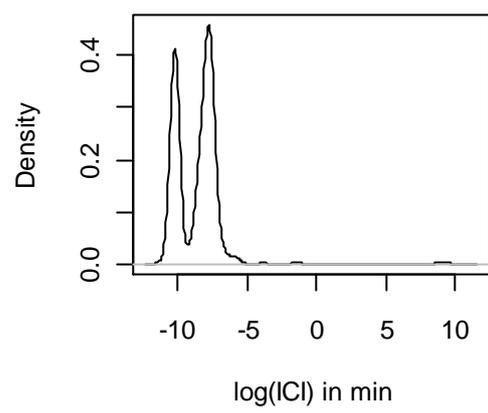
summer



spring

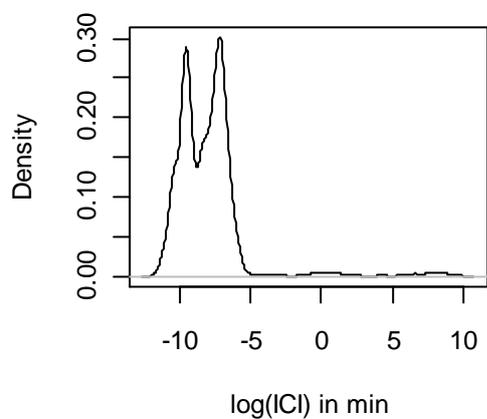


autumn

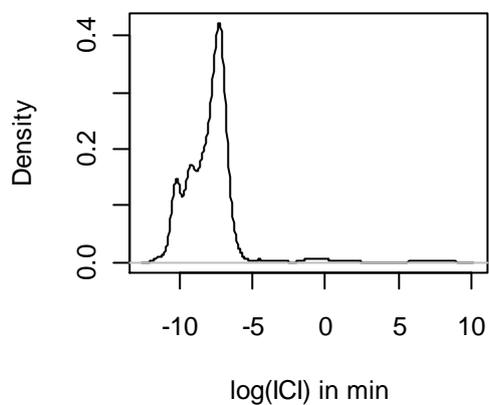


(C) Lossiemouth

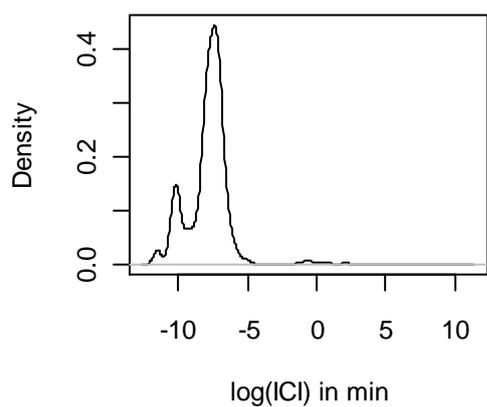
winter



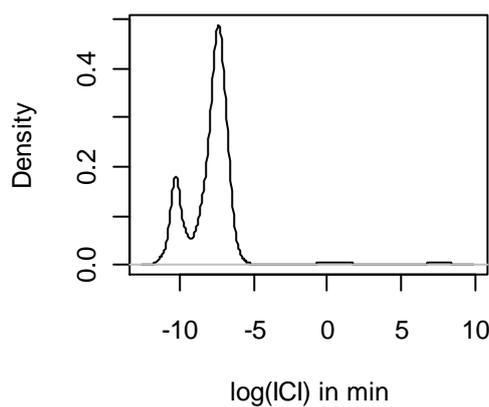
summer



spring



autumn



Boat effect

Models that considered an effect of boat presence on the emission of ICI from a given state alone did not converge adequately (Tables 3.2 and 3.3). Diagnostics of this issue showed that it was most probably caused by an erroneous hypothesis formulation. Hence, as expected biologically, the hypothesis that dolphins performed different ICI when in a given state depending on boat presence was very unlikely. The best fitting model at the Sutors included an effect of boat presence on both the characteristics of ICI emitted when dolphins are in the three activity states and the transition probabilities between activity states (Table 3.2, Figure 3.4).

Table 3.2 Summary information for the four contrasting models fitted to the Sutors data. Summary statistics (mean and standard deviation) for the three hidden process are given on a \log_e scale ($\log_e(\text{ICI})$ in minutes). *model discussed in the text, the effects described are similar for the next best model.

Model	AIC	ITI	R	F
Null	16973	-0.58 (2.607)	-6.78 (0.517)	-8.15 (0.741)
Boat effect on transitions	16983	-0.58 (2.606)	-6.78 (0.517)	-8.15 (0.741)
Boat effect on ICI	Hessian matrix is not positive definite			
Boat effect on ICI and transitions	16833	-0.73 (2.712)	-6.82 (0.501)	-8.17 (0.752)
Boat effect on ICI (ITI and R only)	Hessian matrix is not positive definite			
Boat effect on ICI (ITI,R) and transitions	16831*	-0.75 (2.721)	-6.82 (0.500)	-8.17 (0.751)

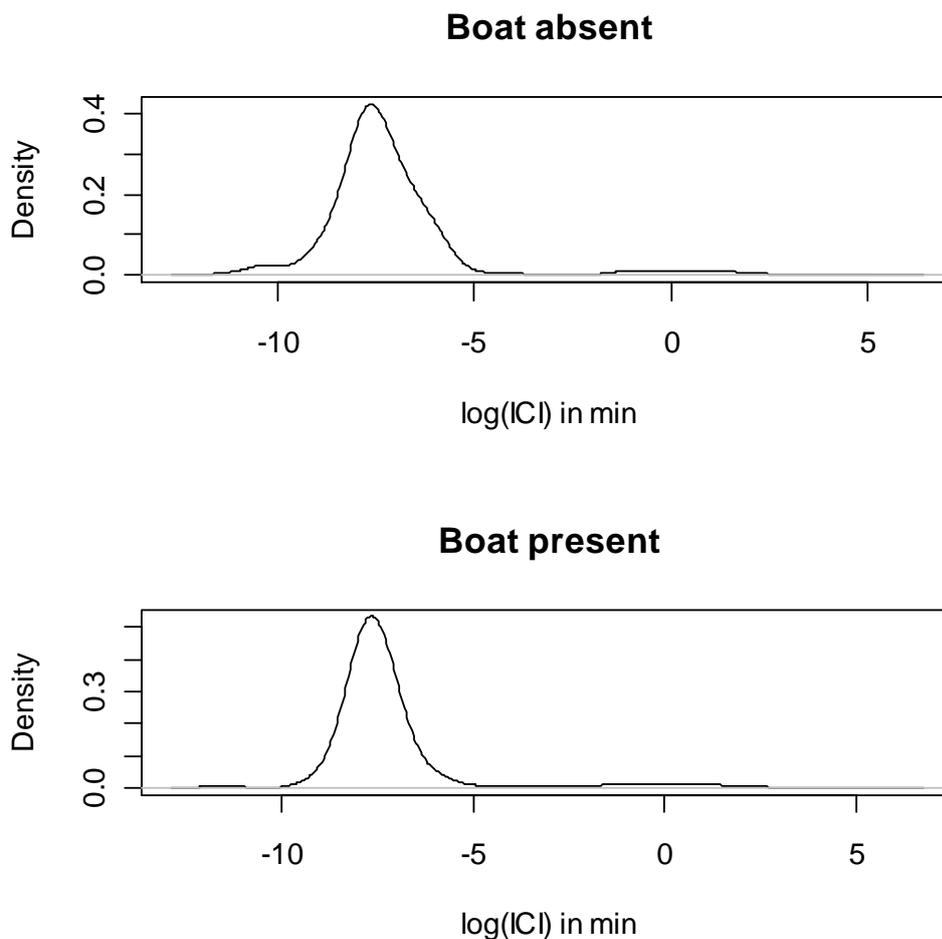


Figure 3.4. The relative density distribution of $\log_e(\text{ICI})$ at the Sutors depending on boat presence

The presence of boats at the Sutors decreased the time that elapsed between click trains; however this effect was not significant (Effect on the mean ICI for ITI, boat parameter: -1.1; 95% confidence interval:-2.743 – 0.577). It significantly decreased the time elapsed between two regular clicks (Effect on the mean ICI for R, boat parameter: -0.51; 95% confidence interval:-0.596 – -0.416). Using the transition probability matrix of the HMM and the estimated effect of boat presence on each transition probability, we can calculate how much time dolphins would typically spend in each state over a given period with and without boat present. We estimate the expected total length of stay in each set of states for 60 minutes. Dolphins spent less time performing foraging buzzes when boats were present (15.9 minutes v. 9.8 minutes), therefore we can infer from this model that boat presence decreases foraging success by 30-40% in the type of foraging context the Sutors offer.

The best fitting model at Aberdeen harbour included an effect of boat presence on both the characteristics of ICI emitted when dolphins are in the three activity states and the transition probabilities between activity states (Table 3.3, Figure 3.5).

Table 3.3 Summary information for the four contrasting models fitted to the Aberdeen data. Summary statistics (mean and standard deviation) for the three hidden process are given on a \log_e scale ($\log_e(\text{ICI})$ in minutes). *model discussed in the text, the effects described are similar for the next best model.

Model	AIC	ITI	R	F
Null	45833	0.70 (2.398)	-6.95 (0.593)	-9.41 (1.106)
Boat effect on ICI	Hessian matrix is not positive definite			
Boat effect on transitions	Hessian matrix is not positive definite			
Boat effect on ICI and transitions	45690*	0.68 (2.383)	-6.99 (0.605)	-9.44 (1.095)

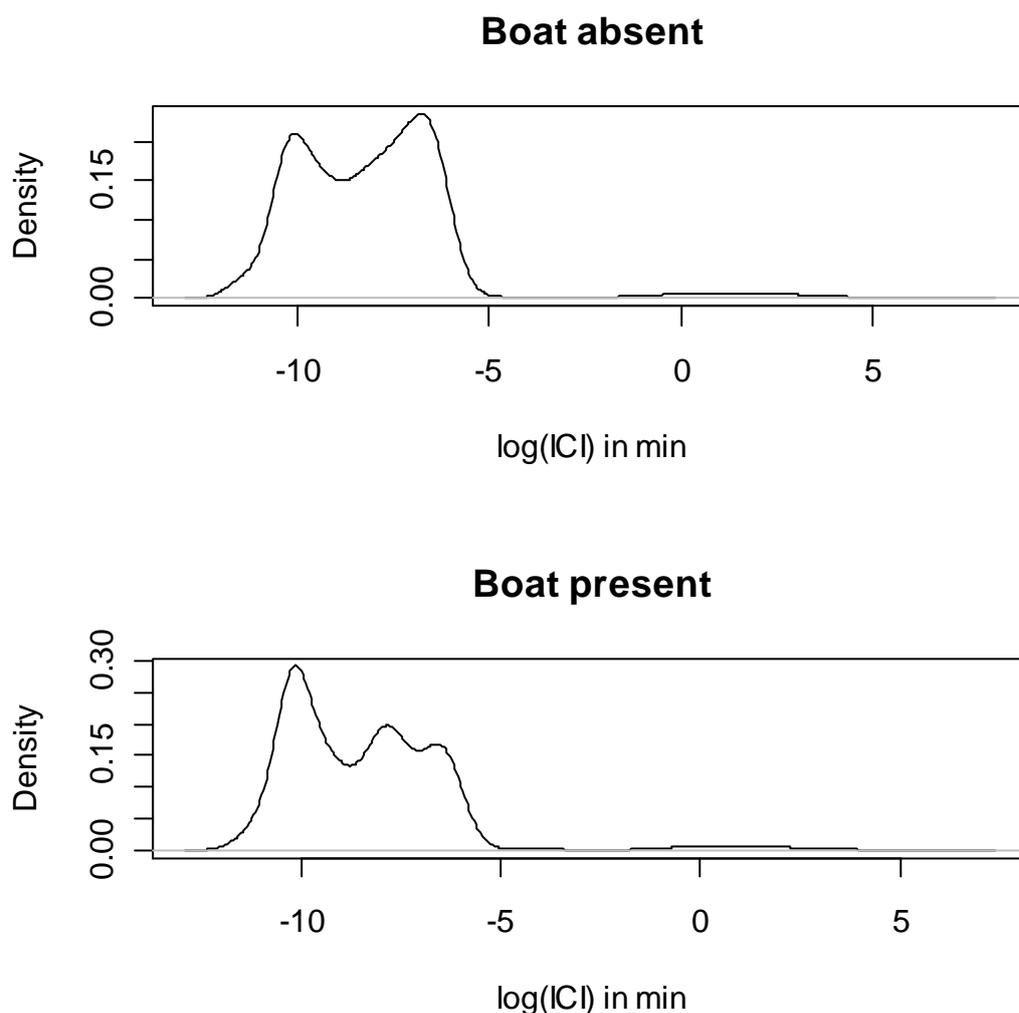


Figure 3.5. The relative density distribution of $\log_e(\text{ICI})$ at Aberdeen harbour depending on boat presence

Boat presence at Aberdeen harbour significantly decreased the time that elapsed between click trains; (Effect on the mean ICI for ITI, boat parameter: -0.65; 95% confidence interval:-1.079 – -0.215). It also significantly decreased the time that elapsed between two buzz clicks (Effect on the mean ICI for F, boat parameter: -0.15; 95% confidence interval:-0.196 – -0.096). Using the transition probability matrix of the HMM and the estimated effect of boat presence on each transition probability, we can calculate how much time dolphins would typically spend in each state over a given period with and without the presence of boat. We estimate the expected total length of stay in each set of states for 60 minutes. Dolphins spent similar time performing foraging buzzes when boats were present and when they are not (18 minutes v. 22 minutes).

CONCLUSIONS

Foraging disruption caused by boat presence has been observed at a number of locations with a number of species (e.g., killer whales: Williams et al. 2006, common dolphins: Stockin et al. 2008). We need more samples to develop more precise estimates of the observed foraging disruption

effect and determine whether it is affected by environmental features. Results at the Sutors show that boat presence can cause substantial disruption to foraging success. Results at the entrance of Aberdeen harbour show that this effect is not spatially fixed and that it probably depends on the risk that dolphins perceive from the presence of boats in a given area (Beale and Monaghan 2004, Lima and Zöllner 1996). In addition, the ecology of this bottlenose dolphin population is tightly linked to salmon availability which is a pulse food source (Lusseau et al. 2004). Therefore the ability to compensate for any foraging disruption will vary depending on the timing of the salmon runs and whether the disruption takes place during a salmon rich or a salmon poor period. The effect on ICI emission at each state points to some changes to the way the environment is perceived, dolphins echolocating more often (shorter click train intervals) and concentrating on object at a shorter range (shorter ICI for R and F respectively at both locations) when boats are present. This supports the hypothesis that boat presence reduces the active space of cetaceans (the perimeter they can sense, Miller 2006) given the small spatial scale (tens of meters) in which dolphins and boats are concentrated in the harbour.

These analyses show that we can use time series of ICIs detected when dolphins are present in the vicinity of acoustic loggers to infer the activity of dolphins. This demonstrates that the sampling technique can be used to inform the BehPhys state space model.

PART IV – A predictive model of the way boats use the area of the Moray Firth

OVERVIEW

We developed here a model to predict the density of boats in the Moray Firth based on the way boats behaved departing from all harbours in the Firth. The modelling described here provides spatio-temporal predictions of boat-traffic given various data sources and development scenarios. The boat model described here is intended to give predicted boat usage at 1km×1km grid cell resolution for a selected time period. It is also intended to allow predictions on the basis of speculated future scenarios where the location and composition of future ports, new commercial traffic or individual vessels may be inserted.

This document provides the following for the Moray Firth Boat Model V0.2 (MF Boat Model V0.2):

1. A description of the calculation process underpinning the models.
2. A high-level description of the code developed. Note the code is currently programmed in the statistical computing environment R. There is, as yet, no agreed graphical user interface(GUI) but the program is amenable to this.
3. A description of the inputs required to the model and the outputs.
4. A series of outputs for several development scenarios as requested.

What the model provides

The boat “model” is a framework and set of software tools that help construct simulations for many sources of boat traffic in the Moray Firth. Conceptually, sources of vessels within the Moray Firth are modelled to produce a layer (consisting of 6496 1km×1km cells) of boat activity in the Moray Firth. For the scenarios offered in this report a layer for each source of vessels is produced for each of 365 days. The sources of vessels can be existing, such as Inverness Marina, or speculated, such as a new marina or future increases to commercial traffic.

For example, the recreational vessels resident in the Inverness Marina are modelled as five classes of vessel based on length (David & Latimer, 2010a), where the composition of vessels in the Marina is known from previous surveys (David & Latimer, 2008, Richard Robinson Consulting (MFP), 2009). Vessels within the same class are treated as having similar behaviours, which are described by sets of parameters and statistical distributions. The parameters are estimated from previous studies or recent boat tracking studies, depending on the information available. The vessel movements are simulated on a daily basis for 1 year. In the Inverness Marina example here, 365 layers (comprising 6496 grid cells) are simulated for each of the five vessel classes. Additional layers are/can be added for individual tour operators and other commercial traffic.

The model currently provides tools for:

- Calculating the *geodesic* distances throughout the Moray Firth i.e. distances between points from paths that go around land.
- Specifying general paths for vessel activity e.g. speculative new routes for commercial vessels.

- Specifying general areas of vessel operation e.g. a tour vessel that is expected/known to operate in a restricted area of the Moray Firth.
- Specifying different classes of vessels that contain vessels with broadly similar behaviours.
- Associating these classes of vessels to known or speculated sources of vessels.
- Sampling vessels from sources and simulating their activity on a daily basis i.e. once the parameters for the various sources are defined, layers can be produced for any point of the year, or for multiple years.
- Storing and accumulating these different layers of vessel activities.
- Varying the activity of the vessels through time at a source or vessel class level e.g. a particular port might have strong seasonal trends in the numbers of vessels taking to sea.

The model is not intended to accurately predict individual boat trips – no model can do this, except for exceptional cases like regular ferries. It is instead intended to give estimates of average behaviour and uncertainty to allow general statements.

It has also been constructed to be easily adaptable to:

- New data.
- Changing assumptions.
- The addition of new sources of vessels.

DATA AND MODEL DEVELOPMENT

The following outlines the rationale and calculation process used to give estimated vessel activity within the Moray Firth. The program operates under varying levels of assumption depending on the data available. The program therefore forms a framework that will benefit from increasing data of improving quality.

Model formulation

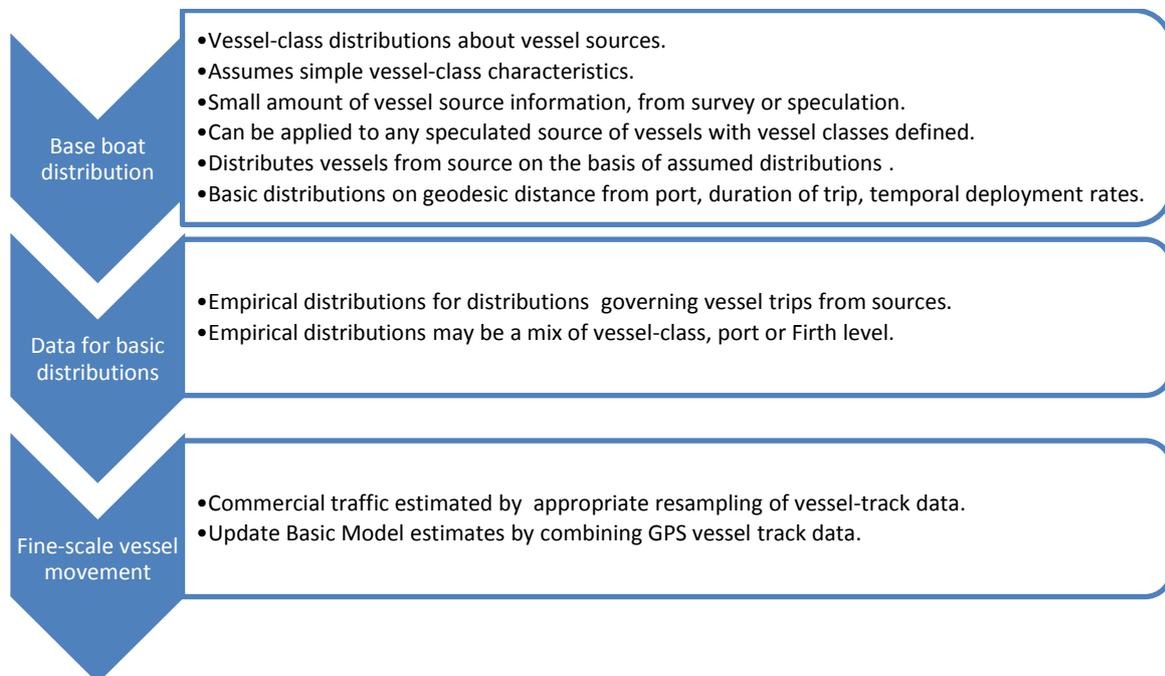
There are several input/output requirements for the model. At a basic level, predicted densities for any 1km grid-cell at any timepoint(s) can be requested. There are caveats on the feasibility of such a request. In particular the spatial resolution has been fixed at the outset of this project – similarly there will be practical constraints on the temporal scope.

The models here seek to provide predictions of the number of vessel-hours/km²/day, generally referred to from this point as *vessel occupation*. The day unit here is nominal and could be redefined as weeks, months etc. Day may seem a relatively fine-scale unit to use, however estimates can be generated as daily averages for a month or season in keeping with the amount of useful data coverage. Using day as a level of reporting averages over day-level factors such as tide-cycles and their relationship with vessel activity.

Conceptually the model produces, for each 1km² grid-cell, a distribution of the number of vessel-hours per day. This can be generated for specific ports, vessels, time periods, or averages over these

groups. The measure can be further decomposed to the vessel hours that are transiting hours or those hours that are stationary.

The model operates at several levels depending on the level of data supplied to it. The components of the model are outlined here, starting with the most data-sparse/assumption-laden level of modelling and moving to the data-rich layers, as indicated below.



Basic Distribution models

Previous work on this problem¹ has used relatively little data explicit to the Moray Firth, therefore some extrapolation from other regions and a series of assumptions to generate predicted densities has been carried out. Recommendations were made at that time for the collection of more detailed boat movement data within the Firth, and some has been subsequently gathered.

The data collected will not apply to all desired applications of the model and has some shortcomings – in light of this, the current modelling exercise retains a refined version of previous models, which offers predictions in most situations, even where data is sparse. Assumptions are necessarily used to bridge shortfalls in data.

This is the least-desirable level to be using, but is necessary for predictions, particularly in the case of projections for where data is non-existent. We describe this model layer in brief.

The base boat distribution model assumes that vessel occupation is a function of distance from the vessel's port and characteristics of the vessel class in question. Previous modelling sought to predict the expected number of vessels within a cell, for some vaguely specified time frame, interpretable as an instantaneous snapshot for some peak usage time. We retain a simplistic approach here, but now focus here on estimating the amount of usage in terms of vessel minutes within the grid-cells.

¹ WPCL boat survey (David & Latimer 2010b); Donovan *et. al.* 2009

Distribution based on distance from port

In the absence of other data, the vessel occupation of a particular class of vessel is assumed to be uniform with respect to distance from port. The particular class of vessel has assumed constraints on the maximum travel distance, the values for which are drawn from the WPCL Boat Survey (David & Latimer 2010b).

Complications arise as the distances from port are not necessarily straight-line distances, necessitating calculation of geodesic distances about the land-mask. Relatedly, the vessels are constrained in 2-dimensions due to land meaning that, while the distribution is uniform with distance from port, the resulting 2-dimensional distribution is complex. An example of a geodesic distance matrix is given in Figure 4.1. This allows definition of the distribution with respect to distance from port, the final distribution of vessels accounts for the constraint of land.

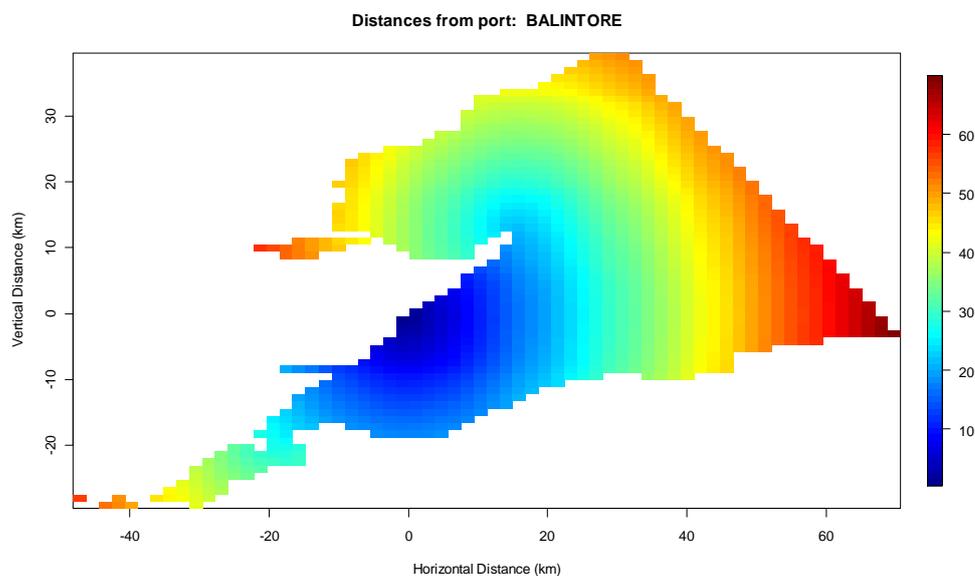


Figure 4.1. example geodesic distances in km calculated for the Balintore port.

Another feature of the complex topology is that, while the distribution with respect to distance is simple, the 2-dimensional extension of this becomes interesting with land constraints. For example, while vessels might be assumed equally likely to occupy cells at a distance d from the port, the numbers of these cells available for occupation varies with d given the land constraints. In practice this means narrow channels will be more heavily utilised, all other things being equal.

The calculation process is as follows:

1. Geodesic distance matrices are calculated for every port and vessel source of interest in the Firth.
2. The cells distances are binned into groups of similar distances from source.
3. Basic calculations are made from this using distributions governing transit speeds, static periods etc.

We expand now for our specific case where assumed distributions are applied for distance-from-source, transit times & static periods.

Transit and stasis times

The simple distance-from-port approach requires calculation for the 2-dimensional area of the Moray Firth. In the extension of this, further account of the land-mask is required, such that the density of vessels is altered in line with the area of water available at some distance d for the port and vessel-class in question. Put plainly, bottlenecks in the Firth will have higher densities of vessels predicted, even assuming uniform distribution with respect to distance from port.

The very basic MFBM uses assumed distributions on the distance travelled from port, and the amount of time spent on the water (the basic parameters are part of the vessel class data contained within the Boat Survey). More refined versions, where there is data to support them, use estimates from the data for the distributions, or empirical distributions – examples of which are given in Figure 4.2 for one vessel class.

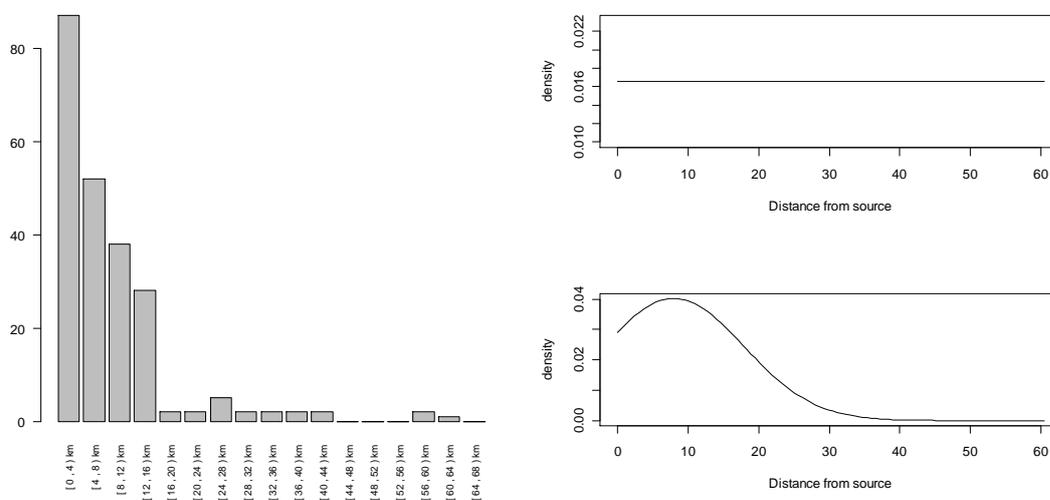


Figure 4.2. empirical distributions of distances from port [left] simple parametric models [right]

Distributions for the time spent from port are similarly generated, with (correlated) bivariate versions used where data supports it.

Extending the simple vessel distributions temporally

Inclusion of a simple temporal component can be achieved by temporal distributions of probability of deployment. Estimates for this are drawn from various survey data sources. Two temporal scales are reasonable given current and foreseeable data: a coarse scale at seasonal/monthly level, and a daily cycle that can be referenced by tide-state and day-light. The default position is to assume a constant underlying rate of vessel deployment throughout the year.

MODEL IMPLEMENTATION

The Moray Firth Boat Model (MFBM) has been coded entirely in the R statistical programming environment (R Core Development Team, 2010). This is a free, open source language, specifically

designed for statistical programming and probably now the most widely used tool for statistical analysis.

R function sets

The MFBM (v 0.2) consists of dozens of bespoke R functions that implement the methods indicated previously and a series of associated tools. These are not specifically described here for brevity.

Inputs/outputs

We outline here the sets of data and parameters that are generally used in calculating vessel occupation under the MFBM.

Vessel class definitions

There are currently 7 vessel classes associated with ports in the Moray Firth, although an arbitrary number can be created. However, generally only 5 of these are filled for existing ports in line with the compositional data from port surveys. It is necessary that there be an estimate of the numbers of different classes of vessels within each port to perform the basic distribution modelling. These classes are also broadly represented in the vessel movement data (Figure 4.20 & Figure 4.21).

These can be arbitrarily increased to include other classes that data exists for, or for which a specification can be made. Specifically the classes currently contain:

- CLASSNAME – vessel class name e.g. vesselClass1
- CLASSDESCRIPTOR – text description of the characteristics of the class e.g. length
- NOMINALUPPERDIST – the maximum distance that this class of vessel will reasonably travel from its source. Not a true upper bound on travel distance, but one that generally applies for the majority of vessels of this class.
- NOMINALUPPERDURATION – the maximum length of time that a vessel of this class will reasonably spend away from its source. Not a true upper bound, but one that generally applies for the majority of vessels of this class.
- PROPORTIONPOWER – the proportion of this vessel class that is powered (as opposed to sail). The current classes are based on length, so sail/power could be accounted for here if required. Currently no distinction is made between sailing or power vessels.
- DISTANDSTASISDISTRIBUTION – the probability distribution that dictates the realisations of distance from port and duration of stops. Several options have been included and can be expanded arbitrarily. Currently the distributions are bivariate Uniform, mixes of Uniform and Normal, bivariate Normal, and empirical (from pooled vessel class data). Parameters can be drawn from nominalUpperDist and nominalUpperDuration.
- TEMPORALDEPLOYMENT – potentially a day-level distribution for the proportion of vessels that deploy (probability of deployment) throughout a year. Currently a uniform or empirical distribution. This can also be controlled at the port-level, or Firth-level if more appropriate.

Port-level

There are currently 34 point sources of vessels specified for the MFBM. These consist of ports, harbours, marinas, moorings, piers etc, identified with the Moray Firth from boat survey data. These sources have varying amounts of survey data to serve as parameters for the MFBM. The port-level parameters potentially utilised are:

- VESSEL_TOTAL_NUMBER – the total number of vessels thought to be resident at the source.

- PERCENT_POWER – the percentage of power vessels estimated within the source, as opposed to sail.
- PORT LOCATION – the coordinates of the source, in metres UTM.
- DISTRIBUTION OF VESSEL CLASSES – the numbers or proportion of vessels in the source that fall into the vessel classes characterised.
- TEMPORAL DEPLOYMENT RATE—a day-level distribution for the proportion of vessels that deploy (probability of deployment) throughout a year. This can be a uniform or empirical distribution and can also be controlled at the Firth-level if more appropriate.
- PORT-CENTRIC GEODESIC DISTANCES – each of the sources with known coordinates have geodesic distances calculated to each grid-cell within the inner Moray Firth. This permits calculation of the distributions of vessels with respect to distance from source port.
- Arbitrary numbers of additional vessel sources with these details can be added. Note the MFBM has a source of data giving all inter-cell geodesic distances within the inner Firth.

Firth-level

- REFERENCE SET OF GRID-CELLS – the centre-points for all cells of interest within the Firth i.e. all 1km×1km sea based cells.
- BATHYMETRY DATA – the set of bathymetry measurements for all of the reference set of grid-cells.
- GEODESIC DISTANCE MATRIX – a set of all inter-cell distances where cells are connected by shortest paths via sea-based cells i.e. shortest distances connecting cells without crossing land.

Individual vessel level

The MFBM has a set of tools that allow the drawing of polygons or waypoints that can restrict the vessel activity for particular sources of vessels. For example:

- Commercial traffic may follow narrow avenues in/out of the Moray Firth. These are represented as a series of waypoints (drawn using the way-point tool or from estimated from data) and a random component allowing some deviation.
- A tour operator may expect to be active in a specific region of the Moray Firth. A bounding polygon can be drawn, which will constrain vessel movements within the MFBM simulations.

Interface options

Currently the MFBM is coded entirely in R. The control of some parameters/features is by directly altering the arguments to the component R functions. Additional parameters/settings are provided from tables within Comma-Separated-Value (CSV) files. Datasets are similarly read to the program as CSV files.

The program is largely inaccessible without capabilities in R. The simplest means of allowing use by an R-naïve user group is either by:

- i. Running R scripts with all parameters altered via CSV templates – editable within Excel, or

- ii. linking R to Excel via the RExcel and associated packages. Excel templates could be created that would perform all calculations in R via calls from Visual Basic macros.

SCENARIOS USING THE MF BOAT MODEL (V0.2)

The following are a series of scenarios requested by SNH (*pers. comm.* D. Lusseau & B.Leyshon).

1. Scenario 1: There will be a new offshore renewables fabrication facility developed at Nigg in the Cromarty Firth. This could result in an additional 100, 200 or 400 extra vessel movements in the Firth each year. The vessels would comprise barges and other large commercial vessels. Two variants are considered where the vessel movements are:
 - a. At a roughly even rate throughout the year.
 - b. Predominantly over summer months.

2. Scenario 2: The Whiteness Marina site will be used for a renewables fabrication facility serviced by 100, 200, and 400 vessel movements. The vessels would comprise of large commercial vessels. Two variants are considered where the vessel movements are:
 - a. At a roughly even rate throughout the year.
 - b. Predominantly over summer months.

3. Scenario 3: There is a 5%, 10% and 20% increase in leisure craft up to 10m arising from promotion and development of the Caledonian Canal.

4. Scenario 4: A tour boat operator based at Inverness operating a 10m RIB.

5. Scenario 5: Two new commercial dolphin watching operators based at the new marina in Inverness. They will be deploying ribs, one will work the Beaully Firth and the Inverness Firth and the other will work along the Rosemarkie to Shandwick Coast.

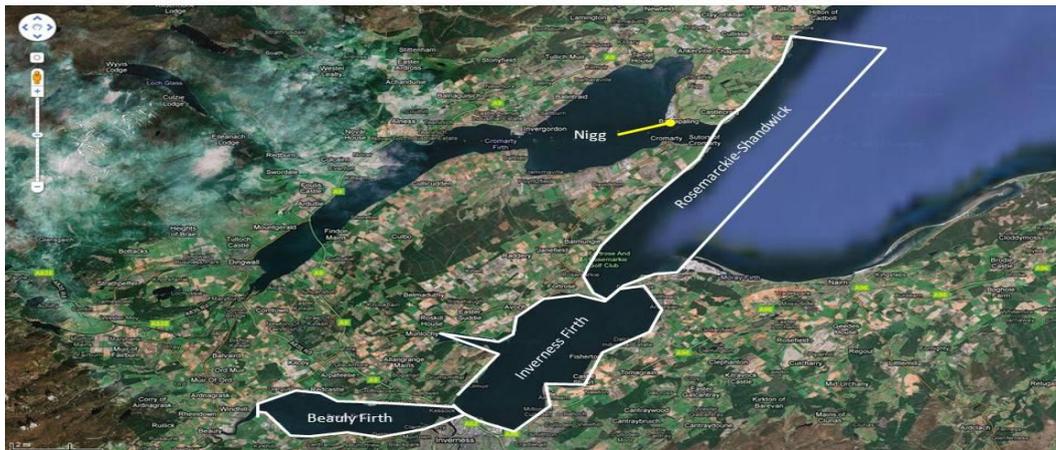


Figure 4.3. Regions within the inner Moray Firth relating to the scenarios of changing usage.

The boat model consists of many layers covering different vessel types and sources, both existing and projected. These layers are generated for the inner Moray Firth at 1km×1km resolution down to a day-level, and are combined as required for scenarios. The models have a random element (they are simulations) and the results presented here are for a simulated year. The outputs for these scenarios are detailed in the following sections.

Distribution of the resident recreational vessels

In *all* the following scenarios a layer of vessel activity is included for the recreational vessels resident in the Moray Firth. These are relatively well studied, with information available from boat surveys (David & Latimer 2008, David *et. al.* 2010a,b) as well as GPS & visual-observer tracking studies (David & Latimer, 2010a,b).

There are up to 33 potential sources of recreational vessels considered within this layer, including harbours, marinas, piers & moorings. *It is assumed these are effectively all the current sources of resident recreational vessels in the Moray Firth.*

The recreation vessels are modelled as 5 separate classes of vessels based on length: ≤5m, >5m and ≤8m, >8m and <10m, >10m and ≤25m and >25m. The choice of vessel classification has been dictated by previous boat surveys where counts were conducted within these classes. *It is assumed here that vessels within these classes have a broadly similar behaviour, particularly in terms of the distance they tend to travel from their port and the amount of time they spend away from their port.* The behaviour of these classes is estimated by pooling the GPS data for each class (David & Latimer, 2010b), combined with broad observations of their behaviour in the boat surveys.

Viewing the model as a series of layers, the resident recreational vessel population is created from (up to) 5 vessel-class layers from (up to) 33 vessel sources on a per-day basis. Daily simulations of vessel usage are created from these, where the sources of the vessels deploy vessels at a rate according to an annual distribution. *It is simply assumed here to be generally 3% with a peak of 5% over the summer months of June/July/August (Figure 4.4) – this is broadly consistent with some available estimates (David & Latimer, 2010a) which note specific deployment rates of 5.4% and 3.3% for Inverness Marina during summer².*

² At specific times; the deployment rate over a day is not known.

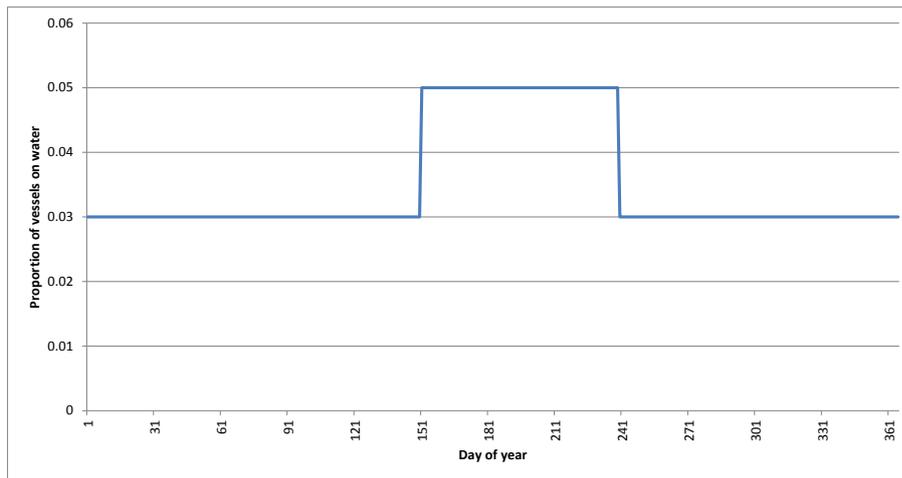


Figure 4.4. Assumed deployment rate throughout the year for all modelled sources of recreational vessels resident in the Moray Firth.

SCENARIO 1 – INCREASED TRAFFIC ABOUT NIGG

The following scenario has been proposed for investigation:

“There will be a new offshore renewables fabrication facility developed at Nigg in the Cromarty Firth. This could result in an additional 100, 200 or 400 extra vessel movements in the Firth each year. The vessels would comprise barges and other large commercial vessels.”

The Moray Firth Boat Model (MFBM) was consequently run for 4 annual scenarios consisting of the current usage and the 3 scenarios of increased commercial traffic. Additionally the summer months were considered where $\frac{1}{2}$ the commercial traffic occurs in June/July/August.

Model inputs for the Nigg scenario

Some primary assumptions and inputs to the model were as follows:

- The current number of sailings to/from Nigg is 70 per annum³, in keeping with the recently collected AIS (Automatic Information System which tracks vessel movement) data.
- The existing commercial vessels follow a well-defined route indicated by AIS records.
- The recreational activity follows the patterns described above.
- An additional 100, 200 and 400 commercial sailings to/from Nigg per annum (i.e. 170, 270 and 470 including current rates).
- The additional sailings are spread roughly evenly throughout the year and follow paths similar to previous AIS recordings.

³David, J.A. & Latimer, M.R. (2010b). Moray Firth Vessel database.

- Commercial vessels only transit – they move to/from Nigg without pause and travel at rates similar to previous AIS records.

Additionally scenarios were run with the following modification:

- ½ the sailings occur roughly evenly during June/July/August, with the remainder being roughly evenly spread throughout the remaining months.

Model outputs

The distributions of vessel activity for all ports and vessel classes were generated for the Moray Firth, for a 365 day period. Each of the 1km×1km grid cells therefore had a distribution of usage (vessel –hours) for an entire year. This accumulates usage from recreational vessel sources and the commercial traffic specific to Nigg. The amount of output, in its entirety, is substantial, being the accumulation of distributions for: 5 vessel-classes within 28 ports for 6,496 grid cells over 365 days. For greatest contrast, we compare here the current assumed baseline level 70 sailings per annum with an additional 400 sailings. A small number of pertinent summaries are given here.

	Commercial sailings to/from Nigg			
Annual sailings	70	170	270	470
Annual number of vessel-hours	78	207	347	569
Mean change (vessel-mins) from activity	0.14	0.37	0.62	1
Central 95% of changes in cell means (vessel-mins) from activity	0.03 to 0.8	0.04 to 1.9	0.09 to 2.6	0.3 to 4.6
Peak change in a cell mean	1.5	4.0	7.2	11.2
Number of 1kmx1km cells affected	90	92	92	92
Peak change (vessel-mins) over all cells and days	24	36	48	60
Median change (vessel-mins) over all cells and days	12	12	12	12

The model estimates that the current commercial traffic of 70 sailings to/from Nigg contributes approximately 78 hours of traffic annually to the inner Moray Firth⁴. An increase to 470 sailings gives approximately 569 hours of traffic annually to the inner Moray Firth. There is similarly a 7-fold increase in the average commercial vessel-hours associated with Nigg.

The effect of the increased commercial traffic to Nigg is imperceptible against current usage when taking a Firth-wide view of vessel usage (Figure 4.6 & Figure 4.7). Taking a focussed view on the cells that occasionally make up the commercial route to/from Nigg, there is a general increase, but it is on average small (less than one minute/day). However, the average daily increase was up to 11 minutes for the most heavily utilised cell within the commercial traffic route.

⁴ The AIS data does not extend over the entire Moray Firth.

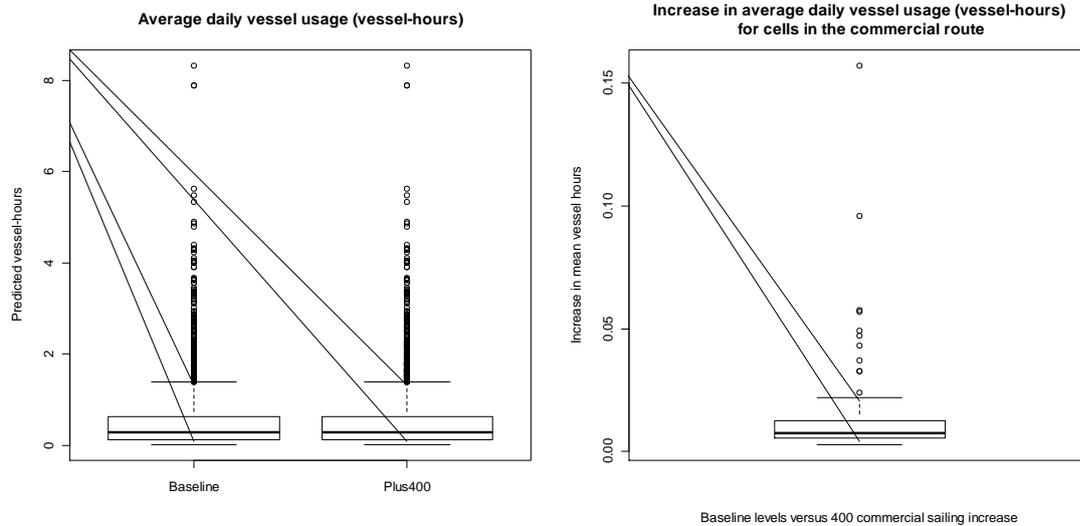


Figure 4.5. comparisons of scenarios in terms of average daily vessel occupation for [left] all utilised cells in the Moray Firth [right] only cells in the Nigg commercial traffic route.

The model outputs over the entire Moray Firth are plotted below, providing predicted average daily usage over the year (Figure 4.6) for current usage, and when the number of commercial sailings is increased to 470 (Figure 4.7).

These are similarly repeated where approximately $\frac{1}{2}$ the sailings are conducted in the months June/July/August. Figure 4.8 & Figure 4.9 present the summer average for the estimated current level of 70 sailings and for the projected 470 respectively.



Figure 4.6. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period including the current pool of recreational vessels and 70 commercial sailings to Nigg.

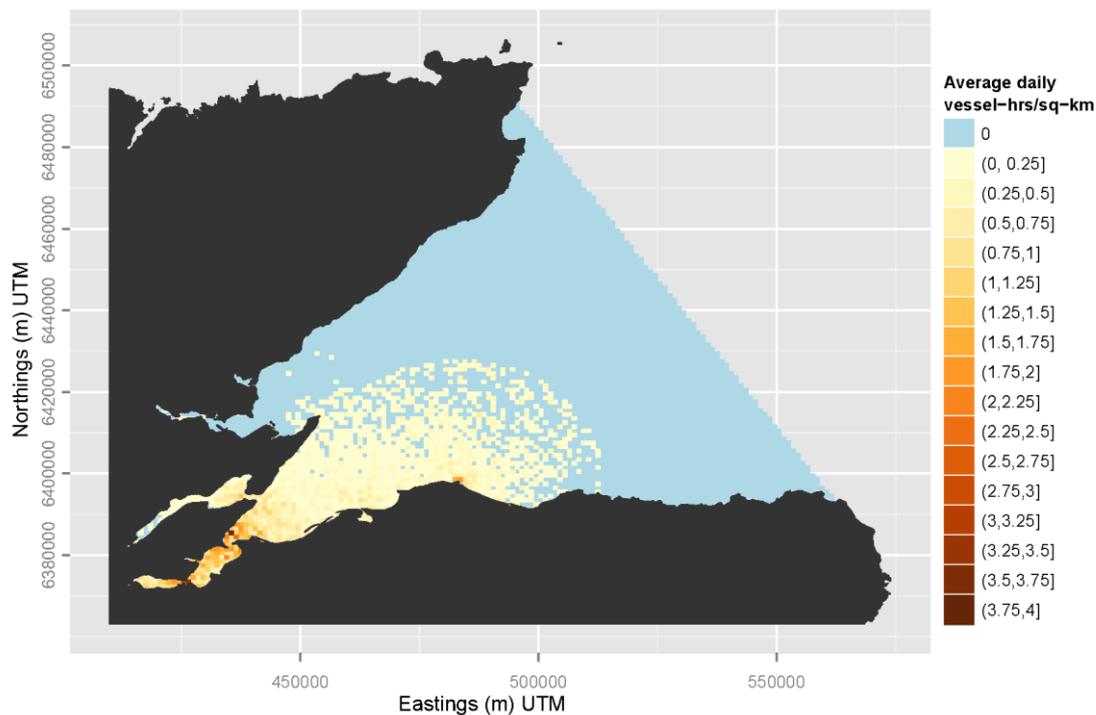


Figure 4.7.The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period including the current pool of recreational vessels and 470 commercial sailings to Nigg (an additional 400).

To explore the effect of concentrating the commercial traffic into summer, the following summaries are over the summer months only⁵. The model estimates that the current commercial traffic of 70 sailings to/from Nigg contributes approximately 48 hours of traffic over the summer months to the inner Moray Firth⁶. An increase to 470 sailings contributes approximately 273 hours of traffic to the inner Moray Firth over the same period. There is similarly an almost 6-fold increase in the average commercial vessel-hours associated with Nigg.

	Commercial sailings to/from Nigg (1/2 concentrated over summer)			
	70	170	270	470
Annual sailings	70	170	270	470
Annual number of vessel-hours	48	104	135	273
Mean change (vessel-mins) from activity	0.47	0.8	1	2
Central 95% of changes in cell means (vessel-mins) from activity	0.13 to 2	0.13 to 3.1	0.13 to 4.7	0.6 to 9.6
Peak change in a cell mean	3.5	9.7	10.8	22.8
Number of 1kmx1km cells affected	68	87	92	92
Peak change (vessel-mins) over all cells and days	24	48	48	60
Median change (vessel-mins) over all cells and days	12	12	12	12

⁵ The effect of seasonal fluctuations is less apparent if averaging over the full year.

⁶ The AIS data does not extend over the entire Moray Firth.

The effect of the increased commercial traffic to Nigg is again almost imperceptible against current usage, when taking a Firth-wide view of vessel occupation. Taking a focussed view of the cells that occasionally make up the commercial route to/from Nigg, there is a general increase of approximately 2 minutes over summer. However, the average daily increase was up to 20 minutes for the most heavily utilised cell within the commercial traffic route.

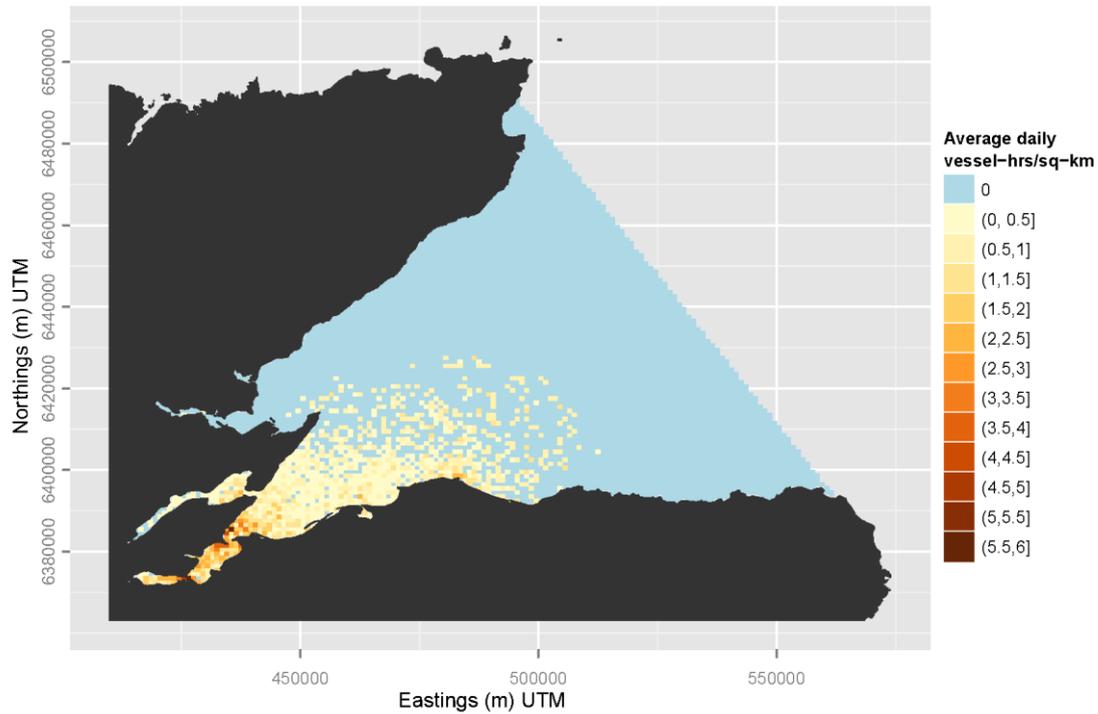


Figure 4.8. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a summer period including the current pool of recreational vessels and 70 commercial sailings to Nigg. One half of the total commercial traffic occurs during the summer months.

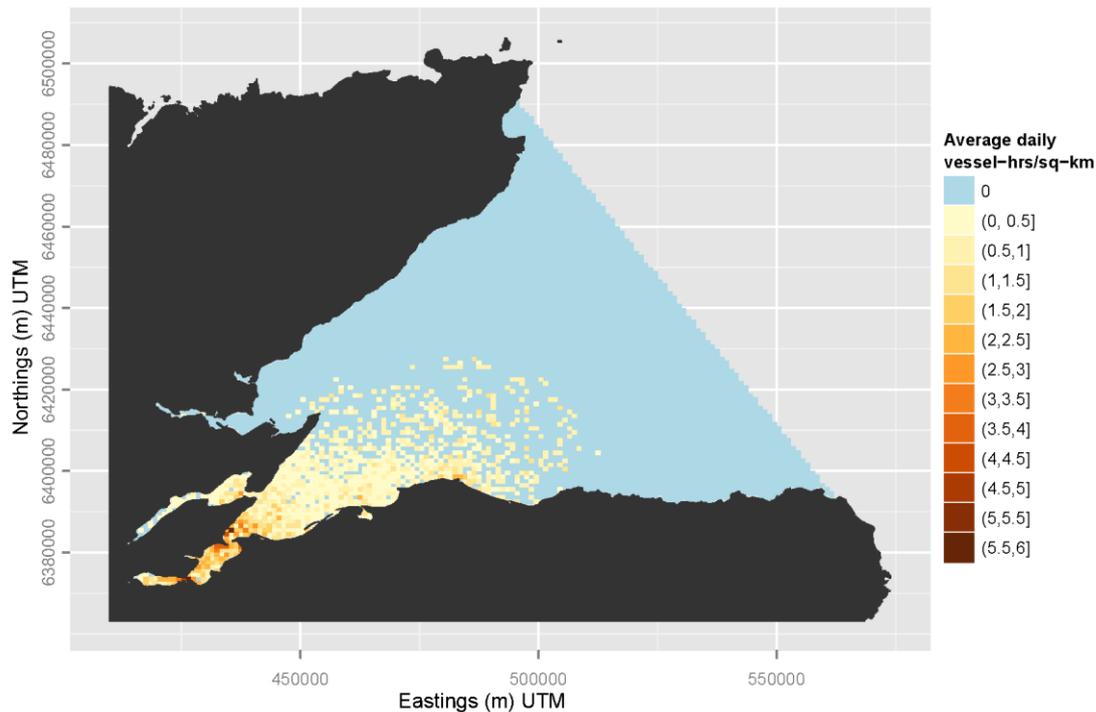


Figure 4.9. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a summer period including the current pool of recreational vessels and 470 commercial sailings to Nigg (an additional 400). One half of the total commercial traffic occurs during the summer months.

Summary of scenario 1 Model runs

There is little appreciable change to the usage of the Moray Firth with the increase in the commercial traffic to Nigg under this scenario. This is under the assumed model and the current choice of metric.

With the maximum increase of 400 additional sailings, daily usage is generally only increased by 1-2 minutes within the commonly transited cells (ie. about the commercial traffic route). The average daily increase can be as high as approximately 10 minutes for cells more heavily utilised by commercial traffic. This increase can be further as high as 20 minutes over the summer months if there was a markedly greater frequency of sailings at that time of the year. These are relatively small compared to usage by smaller local vessels which is typically in the order of hours for accessible cells.

There are approximately 90-100 cells (1km × 1km) within the inner Moray Firth that are traversed by commercial vessels associated with Nigg⁷. *The model assumes that any future increases in commercial traffic to/from Nigg will operate along similar paths to those already operating.*

Both seasonal and constant rates of sailings have been considered in the commercial traffic to Nigg. The number of commercial vessel trips have been permitted to fluctuate in a random way day-to-day, but the underlying rate is either constant or with a marked seasonality that has ½ of the sailings occur during summer. Even assuming the higher number of annual commercial sailings to Nigg (470) and a summer bias, the number of transits is typically 3 transits per day. Under this assumption the commercial vessels will only occupy a cell for a matter of minutes per day whilst transiting.

⁷ Based on AIS and visual observer data

SCENARIO 2 – WHITENESS AS A RENEWABLES FACILITY

The following scenario has been proposed for investigation which mirrors that of Nigg:

“There will be a new offshore renewables fabrication facility developed at Whiteness. This could result in an additional 100, 200 or 400 extra vessel movements in the Firth each year. The vessels would comprise barges and other large commercial vessels.”

The Whiteness proposal differs from Nigg particularly as there are currently no commercial vessels servicing the site.

The MFBM was consequently run for 4 annual scenarios consisting of the current usage and the 3 scenarios of increased commercial traffic. Additionally the summer months were considered separately assuming ½ the commercial traffic occurs in June/July/August (as in Figure 4.4).

Model inputs for the Whiteness scenario

Some primary assumptions and inputs to the model were as follows:

- The current number of sailings to/from Whiteness is 0 per annum.
- The commercial vessels follow a fairly-well defined route, entering the Moray Firth at similar points to those that service Nigg.
- The commercial vessels make a generally direct path to Whiteness upon entering the Moray Firth.
- The recreational activity follows the patterns described above.
- 100, 200 and 400 commercial sailings to/from Whiteness per annum.
- The commercial sailings are spread roughly evenly throughout the year.
- Commercial vessels only transit – they move to/from Whiteness without pause and travel at rates similar to previous AIS records.

Whiteness as a commercial destination with summer activity peak

- As above, but ½ the sailings occur roughly evenly during June/July/August, with the remainder being roughly evenly spread throughout the remaining months.

Model outputs

The distributions of vessel activity for all ports and vessel classes were generated for the Moray Firth, for a 365 day period. Each of the 1km×1km grid cells therefore had a distribution of usage (vessel –hours) for an entire year. This accumulates usage from recreational vessel sources, commercial traffic specific to Nigg and any speculated commercial sailings to/from Whiteness.

For greatest contrast, we compare here the current assumed baseline level of recreational activity with 70 sailings per annum to Nigg, to the same with an additional 400 sailings annually to Whiteness. A small number of pertinent summaries are given here.

	Commercial sailings added to Whiteness		
	100	200	400
Additional annual sailings	100	200	400
Annual number of vessel-hours added	200	400	800
Mean change (vessel-mins) from added activity	0.1	0.17	0.3
Central 95% of changes in cell means (vessel-mins) from added activity	0.03 to 0.36	0.03 to 0.6	0.03 to 1.2
Peak change in a cell mean (vessel-mins)	3.3	6.6	13.2
Number of 1kmx1km cells affected	304	397	423
Peak change (vessel-mins) over all cells and days	36	60	60
Median change (vessel-mins) over all cells and days	12	12	12

The model estimates that the additional commercial traffic of 400 sailings to/from Whiteness contributes approximately 800 hours of traffic annually to the inner Moray Firth⁸.

The effect of the new commercial traffic to Whiteness is perceptible against current usage when taking a Firth-wide view of vessel usage (Figure 4.6 & Figure 4.7). The sailings to Whiteness are across areas with relatively low levels of vessel activity.

Within the commercial sailing routes to Whiteness there was an estimated average daily increase of approximately 0.3 minutes per grid-cell per day. However, the average daily increase was up to 13 minutes for the most heavily utilised cell(s) within the commercial traffic route.

The model outputs over the entire Moray Firth are plotted below, providing predicted average daily usage over the year (Figure 4.6) for current usage, and when the number of commercial sailings to Whiteness is set to 400 (Figure 4.7).

These are similarly repeated where approximately ½ the sailings are conducted in the months June/July/August. Figure 4.8 & Figure 4.9 present the summer average for the estimated current level of recreational/commercial sailings and for the projected 400 Whiteness sailings respectively.

⁸ The AIS data does not extend over the entire Moray Firth.

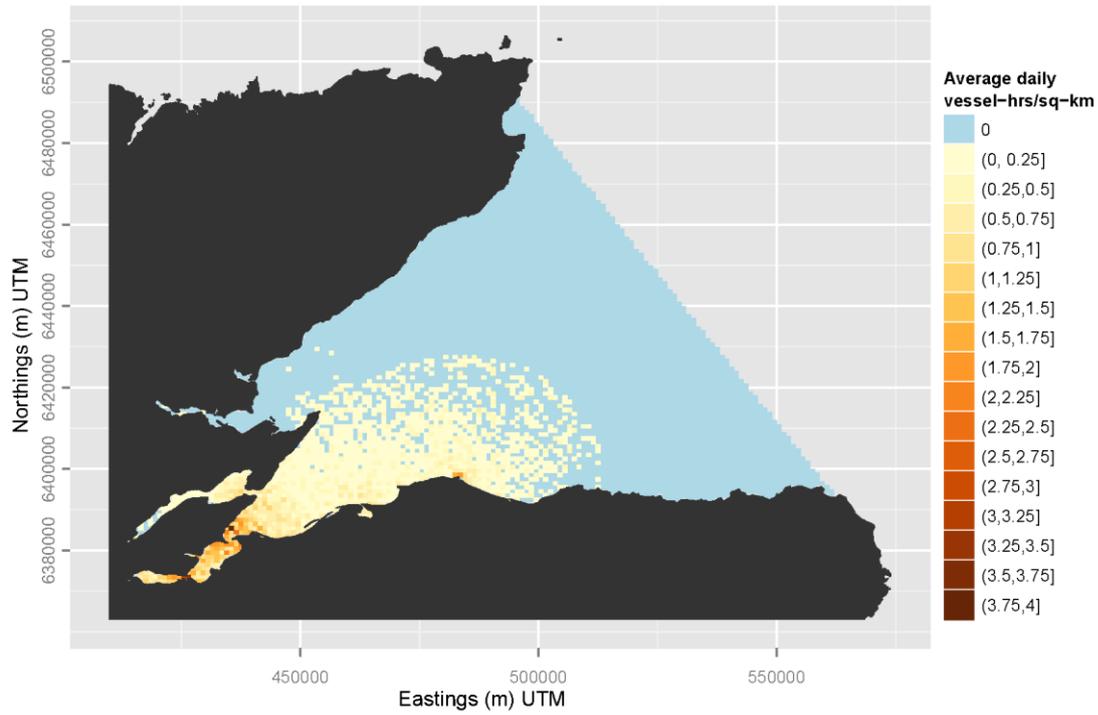


Figure 4.10. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period including the current pool of recreational vessels and 70 commercial sailings to Nigg.

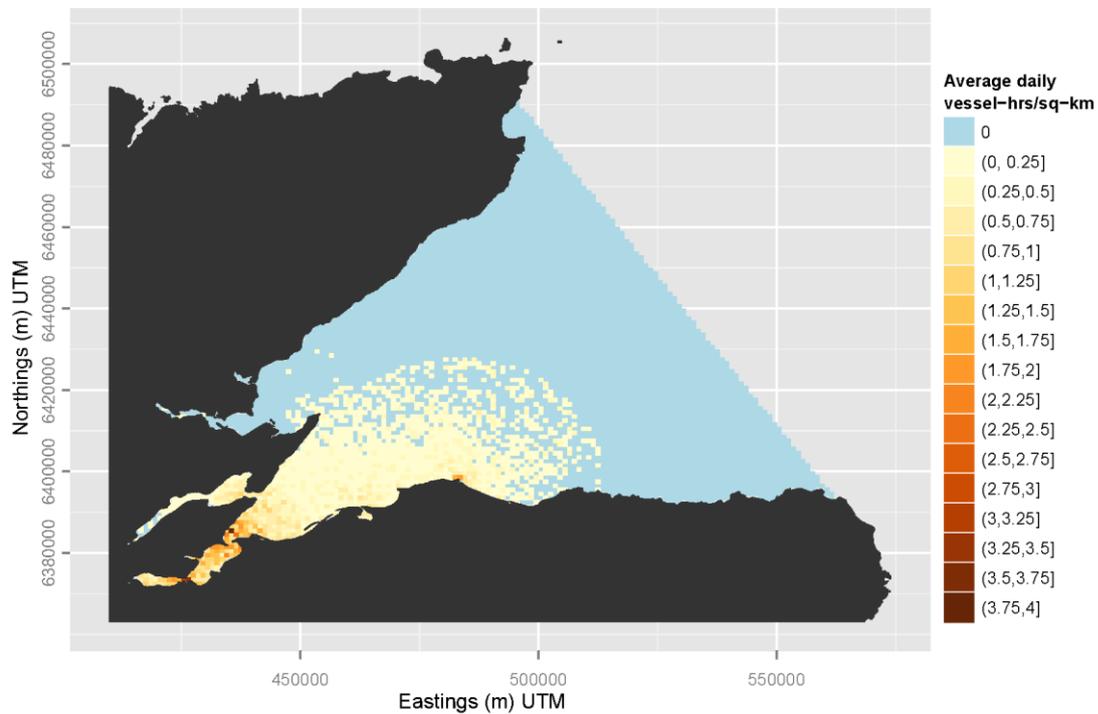


Figure 4.11. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period including the current pool of recreational vessels, 70 commercial sailings to Nigg and a further 400 commercial sailings to Whiteness.

To explore the effect of concentrating the commercial traffic into summer, the following summaries are over the summer months only⁹.

	Commercial sailings added to Whiteness		
Additional annual sailings	100	200	400
Annual number of vessel-hours added	94	210	422
Mean change (vessel-mins) from added activity	0.27	0.44	0.74
Central 95% of changes in cell means (vessel-mins) from added activity	0.13 to 0.8	0.13 to 1.46	0.13 to 2.7
Peak change in a cell mean (vessel-mins)	6.3	14	28.1
Number of 1kmx1km cells affected	234	322	382
Peak change (vessel-mins) over all cells and days	24	60	132
Median change (vessel-mins) over all cells and days	12	12	12

The model estimates that the increase of 400 sailings to Whiteness contributes approximately 422 hours of traffic to the inner Moray Firth over the summer period.

The effect of the increased commercial traffic to Whiteness is perceptible against current usage, when taking a Firth-wide view of vessel occupation (Figure 4.12 & Figure 4.13).

Within the commercial travel routes to Whiteness there is an estimated average daily increase of approximately 1 minute per grid-cell per day over the summer months. However, the average daily increase was approximately 28 minutes for the most heavily utilised cell within the commercial traffic route (the cell the Whiteness site is in).

⁹ The effect of seasonal fluctuations is less apparent if averaging over the full year.



Figure 4.12. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a summer period including the current pool of recreational vessels and 70 commercial sailings to Nigg. One half of the total commercial traffic occurs during the summer months.

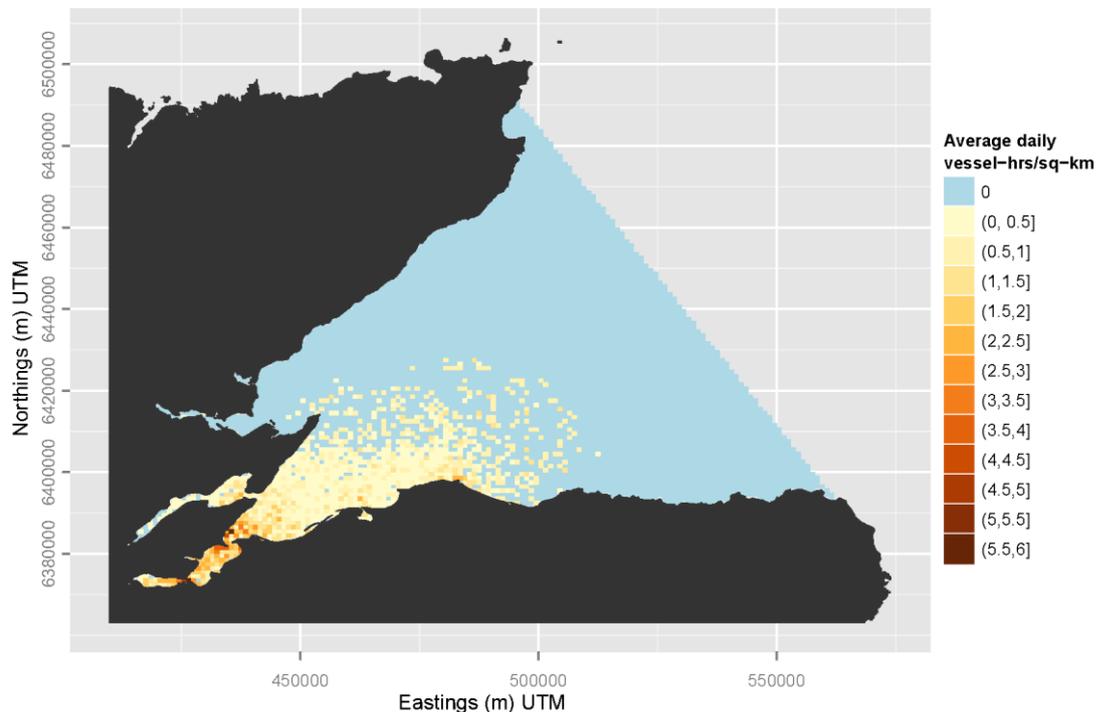


Figure 4.13. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a summer period including the current pool of recreational vessels, 70 annual commercial sailings to Nigg and 400 annual commercial sailings to Whiteness. One half of the total commercial traffic occurs during the summer months.

Summary of scenario 2 Model runs

There is little appreciable change to the usage of the Moray Firth with the increase in the commercial traffic to Whiteness under this scenario. This is under the assumed model and the current choice of metric.

With the maximum increase of 400 additional sailings, daily usage is generally only increased by 1-2 minutes within the commonly transited cells (ie. about the commercial traffic route). The average daily increase can be as high as approximately 10 minutes for cells more heavily utilised by commercial traffic. This increase can be further as high as 20 minutes over the summer months if there was a markedly greater frequency of sailings at that time of the year. These are relatively small compared to usage by smaller local vessels which is typically in the order of hours for accessible cells.

Both seasonal and constant rates of sailings have been considered in the commercial traffic to Nigg. The number of commercial vessel trips have been permitted to fluctuate in a random way day-to-day, but the underlying rate is either constant or with a marked seasonality that has ½ of the sailings occur during summer. Even assuming the higher number of annual commercial sailings to Nigg (470) and a summer bias, the number of transits is typically 3 transits per day. Under this assumption the commercial vessels will only occupy a cell for a matter of minutes per day whilst transiting.

SCENARIO 3 – INCREASED CALEDONIAN CANAL VESSELS

The following scenario has been proposed for investigation:

“There is a 5%, 10% and 20% increase in leisure craft up to 10m arising from promotion and development of the Caledonian Canal.”

The MFBM was consequently run for 4 annual scenarios consisting of the current usage and the 3 scenarios of increased leisure craft.

Model inputs for the increasing caledonian canal traffic

It is unclear what characteristics should be attributed to new vessels arising from promotion of the Caledonian Canal. For example, how long such new vessels would reside in the Firth, whether they are located or travel in specific areas and what their activity rates are relative to Moray Firth resident vessels. There are specific examples available (David & Latimer, 2010a,b) but these are too limited to provide a comprehensive view. It was agreed that general increases to the Moray Firth boat population would be a suitable approximation for the Caledonian Canal contribution (B. Leyshon, *pers. comm.* 2011).

There are several estimates of the total traffic in/out of the Caledonian Canal. However there is little information on the composition of the transiting vessels – in particular the length classes which are used in modelling the resident population or generally <10m as asked for in the scenario.

Some primary assumptions and parameters provided to the model were as follows:

- It was assumed that 750 vessels <10m are added to the Moray Firth boat population annually due to the Caledonian Canal. No distinction was made with respect to direction of travel through the canal, simply that the Moray Firth vessel pool would increase to this extent. The figure is approximately ½ of the 2008 vessel movements through the

Clachnaharry sealock (Richard Robinson Consulting (MFP), 2009). The numbers of movements to/from the Caledonian Canal were similar in 2010 (David & Latimer, 2010a).

- The new vessels have been assumed to reside *pro rata* across existing vessel sources i.e. have been distributed throughout the Moray Firth where recreational vessels reside.
- The characteristics of the increased traffic are assumed in line with current Moray Firth vessels <10m. In particular their travel distances, durations and direction of travel.
- The rate of sailing for vessels derived from the Caledonian Canal is assumed to be on average one movement every two days – this is a purely contrived figure and portrays any visiting craft as much more active than the resident population.
- The addition of vessels associated with the Caledonian Canal was seasonally distributed, in line with that of 2008 movements (Richard Robinson Consulting, 2009) as indicated in Figure 4.14.

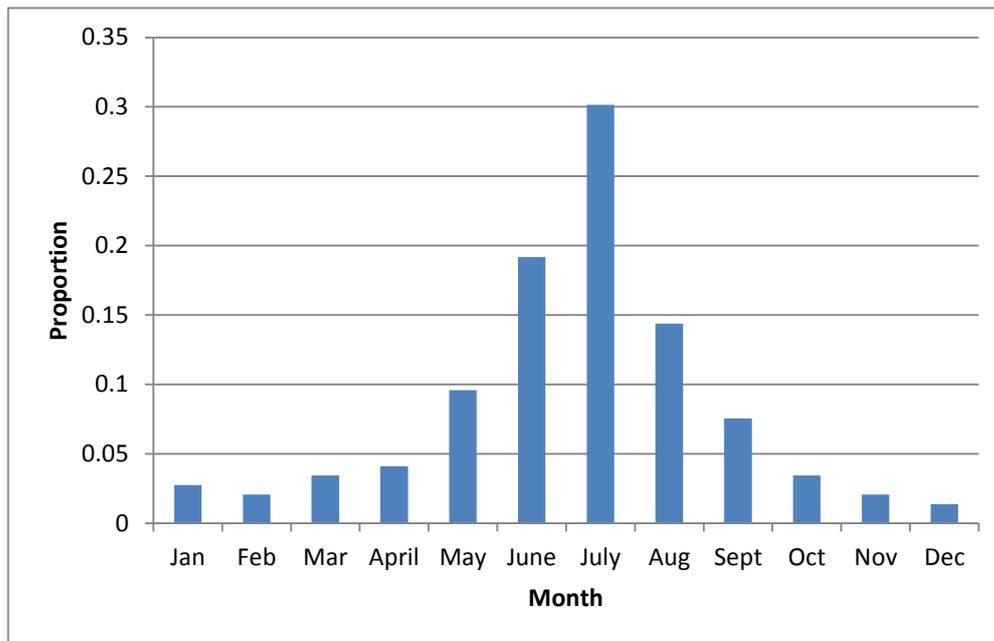


Figure 4.14. The annual distribution of vessels added to the Moray Firth population as a result of the Caledonian Canal.

Model outputs

The distributions of vessel activity for all ports and vessel classes were generated for the Moray Firth, for a 365 day period. Each of the 1km×1km grid cells therefore had a distribution of usage (vessel–hours) for an entire year. This accumulates usage from sources of recreational vessels along with general increases due to promotion of the Caledonian Canal. A small number of pertinent summaries are given here and we only compare the current Moray Firth vessel occupation (including current Caledonian Canal contributions) with the most extreme 20% increase requested.

	Increases to Caledonian Canal traffic <10m		
Percentage increase	5	10	20
Increase in annual number of vessel-hours	1473	3363	9201
Mean change (vessel-mins) from increased activity	0.167	0.261	0.757
Peak change in a cell mean	25	20	32
Number of 1kmx1km cells affected	1339	1368	1409

The effect of the increased vessel numbers was a general increase when taking a Firth-wide view of vessel occupation (Figure 4.15 & Figure 4.16) – with the day-to-day variability being marked. Increasing the Caledonian Canal contribution by 20% added an estimated additional 9200 hours use to the Moray Firth. This equated to an average increase of approximately 1.2 vessel-minutes per day over all cells utilised by vessels. However, increases in the average usage for specific cells could be as high as 0.5 vessel hours per day.

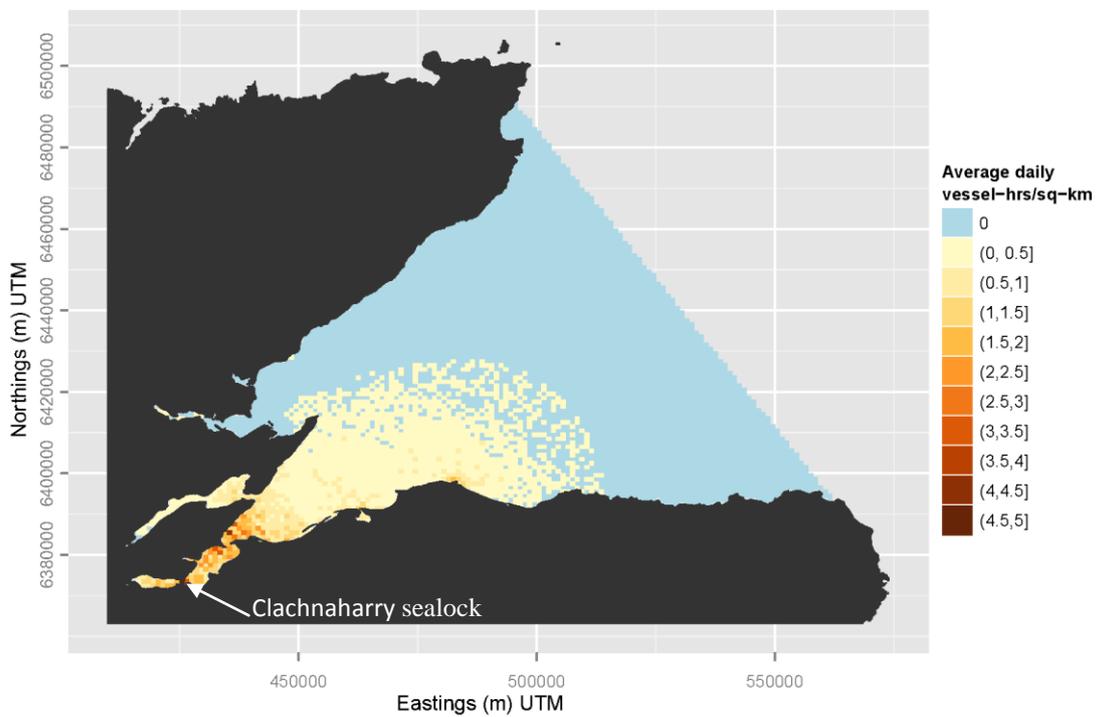


Figure 4.15. The predicted average daily vessel-hours for all cells within the Moray Firth, The averages are calculated over a realisation of a one year period assuming current vessel levels.

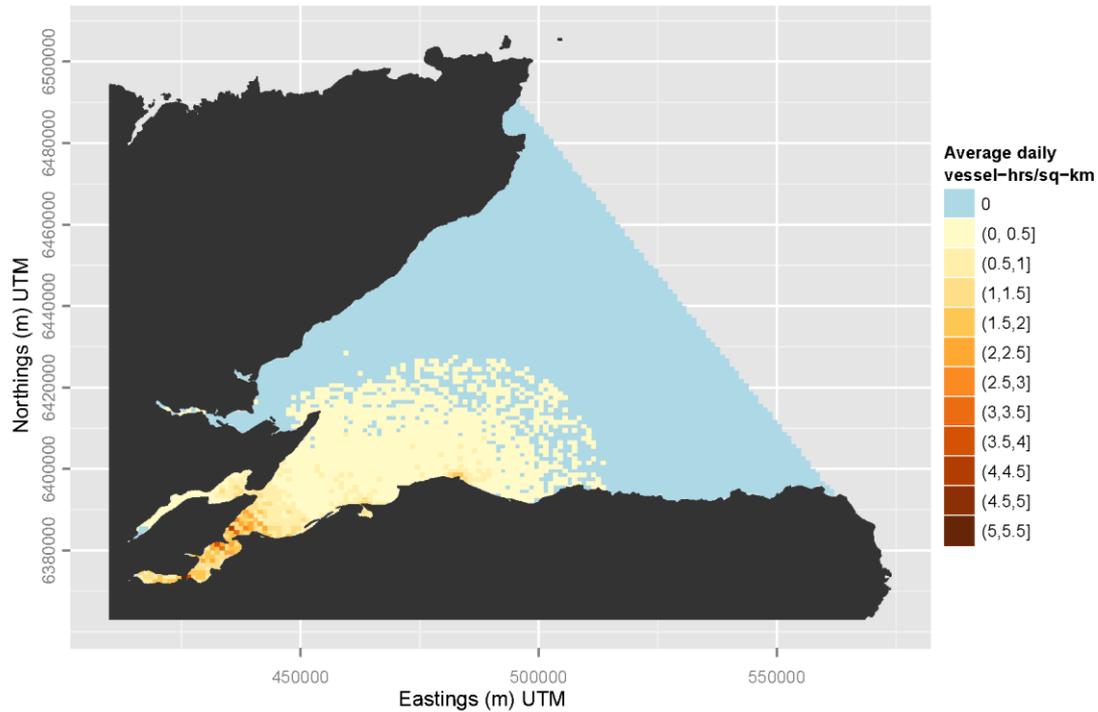


Figure 4.16. The predicted average daily vessel-hours for all cells within the Moray Firth, The averages are calculated over a realisation of a one year period, assuming a 20% increase in <10m leisure vessels.

Summary of scenario 3 Model runs

There was a small change in average usage of the Moray Firth with the increase in Caledonian Canal leisure vessels under the most extreme of these scenarios. This is under the assumed model and the current choice of metric.

With the maximum speculated increase of 20% in <10m leisure vessels, daily usage is only increased by approximately 1.2 minutes across all the cells utilised by vessels, however variability across the entire system is substantial.

The speculated increases in vessels are constrained to the <10m vessel classes. These, by their vessel-class specifications, are shorter-range/shorter-duration vessels. As a result, the increases will be most marked about immediate vicinity of the sources of the vessels. The broader view of the Moray Firth will be less affected as the numbers of longer-range vessels remains constant.

SCENARIO 4 – SINGLE TOUR OPERATOR ADDITION TO INVERNESS

The following scenario has been proposed for investigation:

“A new tour boat in Inverness”

Further information was sought from the operator (B. Leyshon *pers. comm.*, 2011) leading to the following general inputs for the model. It is assumed:

- The vessel is a 10 Meter RIB.
- The vessel travels at 0-15 knots.
- There are up to 4 journeys per day, with an average of 3.
- The trip durations are up to 1 1/2 hours.
- The trips are conducted within the following area (pink polygon, Figure 4.17) and the trip will not be more than 30km from the home port. The operator description of the area of operation was “from Inverness to the North Sea”.

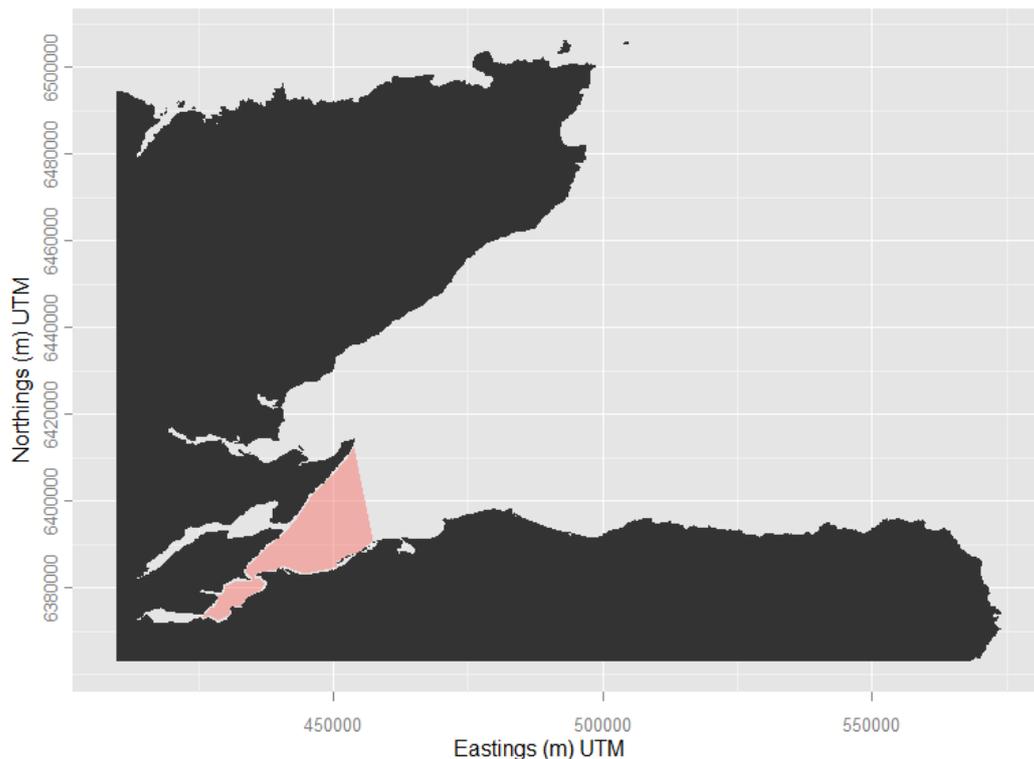


Figure 4.17. Bounding polygon for the tour boat operations

Model outputs

The distributions of current vessel activity were generated for the Moray Firth, for a 365 day period. Each of the 1km×1km grid cells therefore had a distribution of usage (vessel –hours) for an entire year. This accumulates usage from main sources of commercial and recreation vessels to which the speculative tour operations are added. A small number of pertinent summaries are given here.

	Tour vessel
Annual number of vessel-hours	1092
Mean change (vessel-mins) from activity	1
Central 95% of changes in cell means (vessel-mins) from activity	0.16 to 3.1
Peak change in a cell mean (vessel-mins)	6.9
Number of 1kmx1km cells affected	180
Peak change (vessel-mins) over all cells and days	120
Median change (vessel-mins) over all cells and days	60

The effect of the introduced tour vessel was a very small increase in usage when taking a Firth-wide view of vessel occupation – with the day-to-day variability being marked. The tour contributed an estimated 1092 hours use to the Moray Firth over the course of the year against a background of >150,000 hours. This equated to an average increase of approximately 1 vessel-minute within the area of operations of the tour vessel. However, increases in the average usage for specific cells in this area could be as high as 7 vessel-minutes per day.

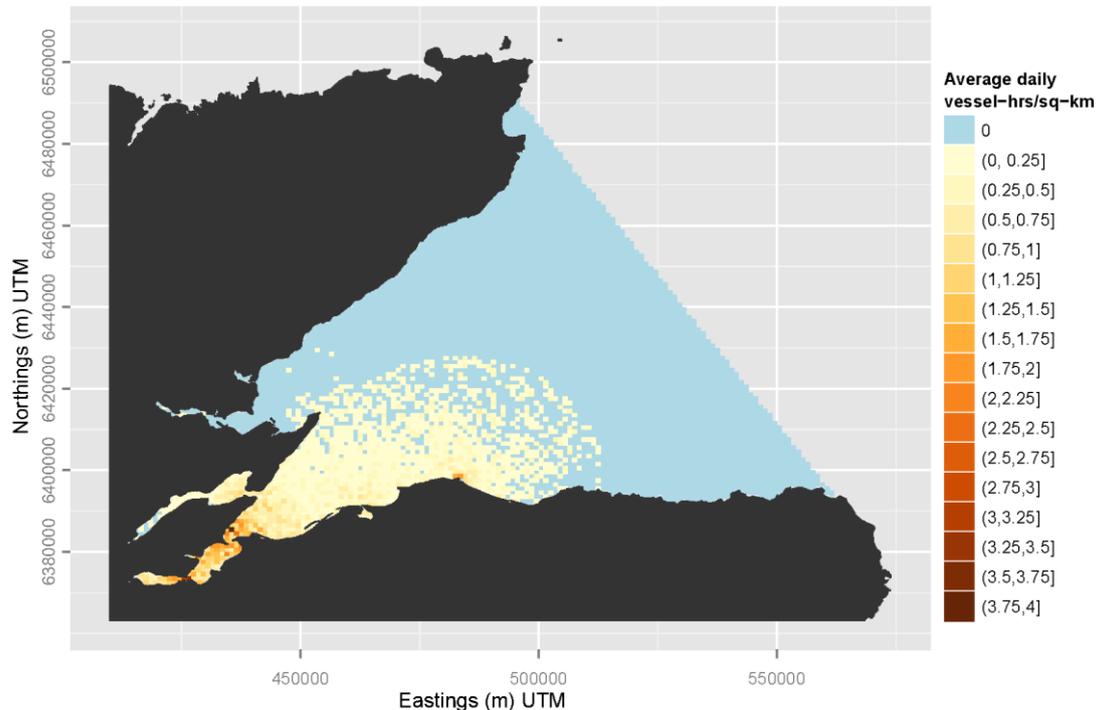


Figure 4.18. The predicted average daily vessel-hours for all cells within the Moray Firth under current usage. The averages are calculated over a realisation of a one year period.



Figure 4.19. The predicted average daily vessel-hours for all cells within the Moray Firth. The averages are calculated over a realisation of a one year period, assuming an additional tour vessel as described.

Summary of scenario outputs

The inclusion of an additional tour vessel adds little against the background of the estimated current usage. Within the area of operation of the tour vessel, we estimate that the average annual usage increases by much less than a vessel-minute per 1km×1km grid-cell. The average increase can be as high as approximately 6 vessel minutes. This is qualitatively imperceptible when considering the pattern of average annual usage (Figure 4.18 & Figure 4.19) where average usage can be in the order of hours.

ADDITIONAL SCENARIOS

The following additional scenario was also proposed for investigation:

“Two new commercial dolphin watching operators want to start business based at the new marina in Inverness. They will be deploying ribs, one will work the Beaully Firth and the Inverness Firth and the other will work along the Rosemarkie to Shandwick Coast.”

This scenario is similar to the individual tour boat operator and requires very specific information about the projected activity. The operators in question were approached several times for specifics (B. Leyshon *pers. comm.*) but these were not forthcoming. If details about vessel use and regularity of service are provided in the future, an additional layer can be added to the outputs.

DISCUSSION OF THE MFBM

The MFBM presented here attempts to provide general answers to a very complex problem. It offers framework and tools for specifying and accumulating many models for the large number of existing (or speculated) sources of vessels in the Moray Firth.

There are many improvements that can be made, but note that no model will be able to provide accurate predictions of vessel activity at fine scales of space or time. We discuss briefly here the current MFBM implementation, some particular limitations, cautions about its results, probable sensitivities and future developments.

Assumptions

There are a number of assumptions inherent, but not apparent, in the MFBM formulation. This is inevitable given the paucity of data relative to the complexity of the problem. Several assumptions are discussed in turn.

The model currently treats all vessels and time spent in the MFBM equally – simply calculating the amount of time that vessels occupy particular cells. Most importantly for these scenarios there is no distinction made between time spent transiting cells or whether the vessel is static. This is also inconsistent between types of vessels – the commercial traffic is treated as continually moving when not along-side its destination. This is certainly not true. Conversely, a significant amount of the recreational traffic contribution is likely to be time spent static in the Moray Firth. Time spent stationary and time spent moving could be accounted for separately in future, if the distinction can be usefully applied to dolphin impacts.

Similarly no particular distinction is drawn between vessel types e.g. large commercial vessels or small sailing vessels all contribute in the same way to the number of vessel-hours across the Moray Firth. Again a differential accounting could be made if some quantitative distinction can be drawn.

The current view of vessel occupancy in the Moray Firth from the MFBM assumes (effectively) all the traffic is accounted for. There are likely to be other sources, but it seems reasonable that the vast majority has been identified through the several previous studies of boat traffic.

Traffic generated by the Caledonian Canal is poorly characterised. The assumptions used here reflect this lack of information. The behaviour of Caledonian Canal vessels is likely to be markedly different to the resident population, and there are some observations that testify to this (David & Latimer, 2010b), but not enough to draw a general rule.

All vessels are assumed to act independently of one another (beyond common drivers like deployment rates). This is certainly not true as vessels are likely to consciously cluster or spread out depending on situation. For example commercial traffic is likely to be scheduled rather than approaching their destination at random times.

Data

There are a number of data sources that have been used to parameterise the MFBM. These have their own biases and limitations. Some examples are discussed here.

Deployment rates from the sources of recreational vessels is a key parameter. A doubling of a deployment rate is roughly equivalent to doubling the number of vessels. This has been previously identified as a sensitivity (Donovan *et. al.* 2009) and some data has been subsequently collected (David & Latimer, 2010a). There is great flexibility in the MFBM for variable deployment rates by vessel type, port, time, but it is unlikely these will ever be well supported by data.

Seasonally varying deployment rates have been applied to both commercial and recreational vessels in the scenarios. The deployment rates for recreational vessels has been set to 3%-5% in keeping with some published figures. However such estimates are for specific times on a few qualitatively selected days. It is not clear how an instantaneous figure of 5% ought to be scaled up to a daily deployment rate, although it will certainly be larger. There are also indications that rates between ports are highly variable with a deployment of 16.7% noted for North Kessock. The currently used rates seem likely to be underestimates.

The existing and speculated commercial traffic has its paths dictated in large part by AIS measurements. However the AIS recordings do not begin until well within the Moray Firth. Using the current database, commercial movements in the outer parts of the Firth have not been modelled. This is of probably of little importance however, as the recreational traffic is very sparse in these regions, so vessel occupancy will be very low regardless.

Sensitivities

It is clear that the resident recreational vessels of the Moray Firth make up the vast majority of vessel occupancy. Therefore it is assumptions relating to these that the results will be most sensitive. The deployment rates are still one of the most important parameters in this regard. Currently all ports and vessel classes are treated the same, although some seasonality is included. There are small amounts of data available on these rates and have been used accordingly.

The specific port and vessel-class movement patterns are also likely to be influential. Currently the GPS data is pooled to parameterise distributions of vessels from their ports. The specific GPS tracks offer detailed information for some classes and ports, but coverage is not extensive. There are a large number of visual observations, but these rarely ascertain the port of origin. As indicated below, there is still much that can be gleaned from the GPS data in particular and research into this is intended.

Unlike previous models, a temporal component is now implicit in the results. As a consequence, the motion of boats is integral to all simulation results, which makes a distinction possible between time spent moving and time spent static. Should these be treated separately, then the outcomes may be markedly different.

Improvements

We have presented model results from a single realised year. Under this model, there is very large variability in vessel occupation of the Firth on a day-to-day basis, which tends to obscure systematic alterations of the numbers of vessels. This reflective of the true state of vessel movement in the Firth, where numbers and types of vessels deploying each day vary, the areas they travel to vary, the times spent on the water vary. As a result a specific cell may see low levels of activity through time, punctuated by chance usage by several vessels – which is more marked than an underlying small percentage increases in vessel numbers.

Ideally a large number of simulated years would be run, which would collectively give a better picture of the distribution of vessels in the Moray Firth. The amount of information being created by the MFBM is currently very large and multiple years can quickly outstrip the resources of quite powerful computers. Some future optimisation of how the MFBM handles data would be useful. It is however the periphery of the vessel distributions that is most affected, so not essential.

We see future improvements of the MFBM as being largely conducted as an independent research topic. Specifically:

- The code will need to be more robust for wider use, in particular with a view to be used as components in any future GUI.

- Additional data of the form found within the Moray Firth Vessel Database (David & Latimer, 2010b) needs to be automatically ingested by the MFBM.

- Further research is required for fully balancing vessel track data, in particular GPS, against patterns given by the current simulations.

APPENDICES

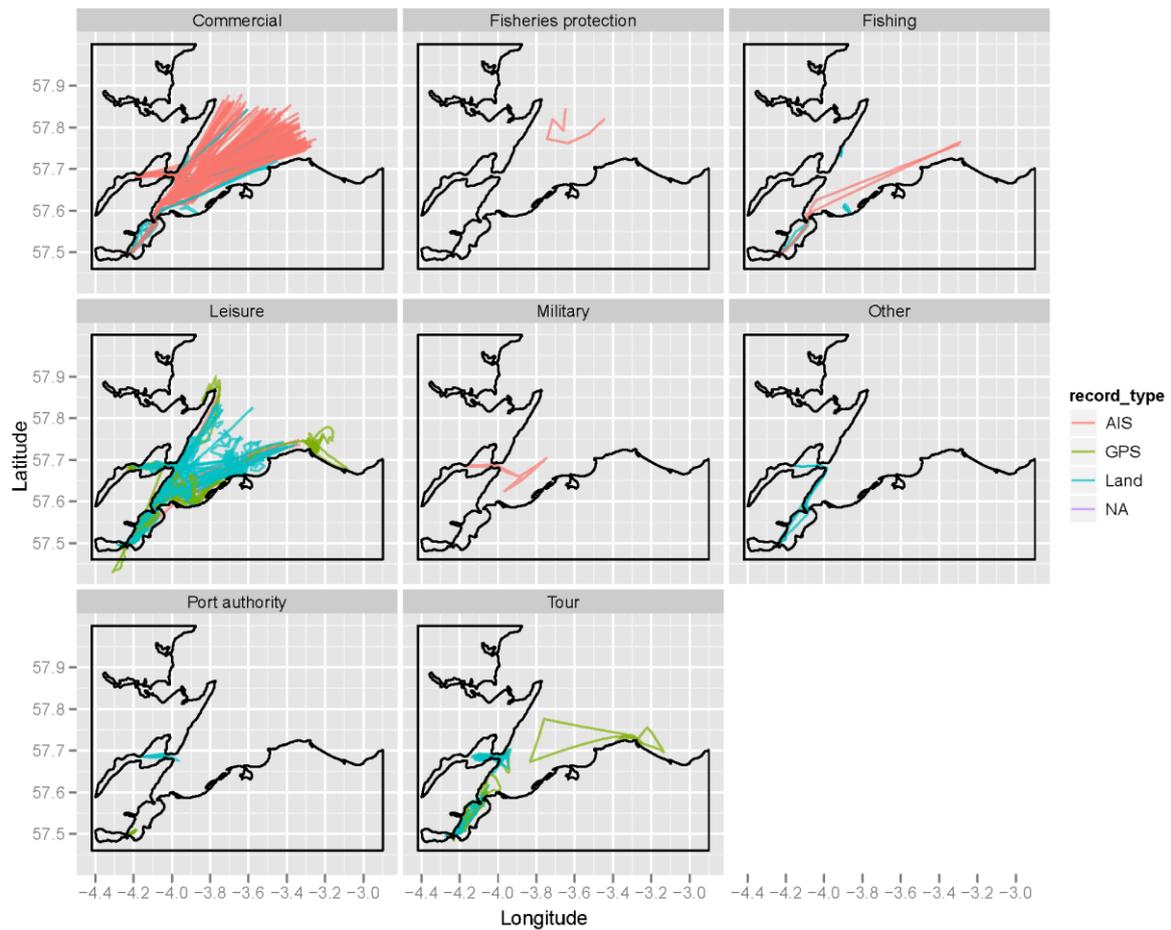


Figure 4.20. examples of the vessel movement data available to the modelling process (based on David & Latimer, 2010b).

port	port_style	vessel_total_number	percent_sail	percent_power	HWS_window	Notes	<=5	>Sto8	>
Avoch	Harbour	36	80	20	2		8	15	12
Balintore	Harbour	26	20	80	2	includes 10 from slip	12	12	2
Banff	Marina	92	50	50	4				
Brora	Quay Wall	1	100	0					
Buckie	Harbour	0							
Burghead	Harbour	20				Commercial			
Caledonian Canal	Link	1231				Clachnaharry Sea Lock			
Caley	Marina	80	20	80					
Cromarty	Harbour	28	70	30	4	14 on harbour pontoons, 14 on moorings:	12	12	2
Cullen	Harbour	18	70	30	3				
Findhorn	Moorings	73				Sum of marina and bay	2	34	27
Findhorn Bay	Moorings	57	90	10	2		2	22	23
Findhorn Marina	Marina	16	50	50	2		0	12	4
Findochty	Harbour	85	60	40	3				
Fortrose	Harbour	40	80	20		20 on moorings	20	8	7
Golspie	Pier	4	0	100	3				
Helmsdale	Harbour	27	50	50	4				
Hopeman	Harbour	65	50	50	2				
Invergordon	Moorings	8	80	20		includes 4 commercial	3	4	1
Inverness Harbour	Harbour	5					1	1	0
Inverness Marina	Marina	149					0	8	52
Lossiemouth	Marina	93	90	10	3		0	15	15
Lybster	Harbour	4							
Macduff	Harbour	0							
Nairn	Harbour	76	70	30	2		2	59	15
Nigg	Pier	10				Launched from slip	10	0	0
North Kessock	Moorings	18					15	2	1
Portgordon	Harbour	5	10	90	3				
Portknockie	Harbour	26	20	80	4				
Portmahomack	Harbour	24	20	80	3				
Portsoy	Harbour	5	10	90					
Rosemarkie	Moorings	19				Assume mobile pool of 15	15	2	2

Figure 4.21. example of the port-level data available to the modelling process. (screen capture from David & Latimer, 2010b)

PART V – A descriptive model of the way dolphins use the Moray Firth

CONCEPTUAL BACKGROUND

As we have shown in the previous sections, behavioural disturbances act at the level of the individual. In order to understand the proportion of the dolphin population that may be affected by a given activity in the Moray Firth we need to understand how individuals are distributed throughout their habitat. In addition, since individuals have the ability to move away from undesirable situations, we need to understand the ranging patterns of individuals to assess the proportion of the home range of each individual affected by a given human activity. The greater the proportion of the home range of an individual is affected, the less opportunity that individual has to compensate for this habitat degradation, because the area that is available to carry out essential behavioural activities is reduced. We therefore need to understand how individual dolphins are distributed in the Moray Firth and what their ranging pattern is.

METHODS

We focussed here on describing the way individuals use the Moray Firth given the sampling effort available. From 2001 to 2009, the University of Aberdeen carried out photo-identification trips in the Moray Firth to capture the presence of individual dolphins using natural markings (Table 5.1). The goal of the model we used was to describe the observed variation in the likelihood to detect individual dolphins in the area as opposed to trying to predict the presence of dolphins (as we did above for the distribution of boats).

Table 5.1 Summary of yearly sampling effort and photographic capture history

Year	Sampling occasions	Encounters	Number of individuals captured	Number of captures
2001	29	54	48	254
2002	24	60	47	248
2003	24	57	45	200
2004	21	46	52	166
2005	19	56	43	177
2006	30	60	45	292
2007	34	71	47	407
2008	30	68	40	315
2009	39	105	57	555

We used a spatially explicit mark-recapture modelling approach to estimate the density of dolphins in the studied area (Borchers and Efford 2008). While this sampling approach is regularly used to estimate population abundance, it has only been recently extended to estimate density. This technique uses spatial information about where “captures” of individuals took place to estimate where the activity centre for each individual is located (Royle et al. 2009). An activity centre is best described as the location where we are more likely to encounter a given individual and it therefore measures the home range of individuals. Once the position of the activity centres has been determined, we can then derive a density estimate for the whole study area by simply measuring the density of activity centres. Such a modelling approach is useful to our study for three reasons:

1. We can obtain a measure of the variation in density of the studied population and an indirect measure of the average range that individuals cover. As with other mark-recapture models, we can account for the 'unmarked' individuals in the population and therefore estimate the density of the 'true' population.
2. We can use the estimated spatial probability distribution of the position of activity centres to estimate the home range of individuals. This probabilistic estimation is more precise and more accurate than classical measures of home range and its probabilistic nature makes the prediction of boat traffic exposure easier, and because it is a direct measure of the probability that an individual can be found at a given location in space.
3. At this stage, we are using the approach in a descriptive manner at this stage, but spatially explicit mark-recapture density models can be extended to estimate the influence of covariates (such as measures of habitat quality) on the distribution of activity centres. Hence, they can be used in a predictive manner once the appropriate covariates have been identified.

The goal of this model construction is twofold. First, it will help us assess the proportion of individuals in the population that would be affected by an increase in activities in a given area of the Moray Firth. Second, we can derive home range sizes from it and therefore assess the proportion of a given home range that will be affected by changes in boat distribution. This modelling approach requires that the history of photographic captures of individuals be spatially explicit. We therefore overlaid a 1km x 1km grid over the study area and defined each grid cell as a photographic 'trap'. The grid was defined to match the grid used in the boat model in order to be able to assess the consequences of changes in boat distribution. Each boat trip was defined as a sampling occasion. We recorded the 'traps' visited during that occasion and the identity of individuals we captured at each of these traps. This provided a spatially explicit capture history from which we could estimate the likelihood to capture an individual i . *This modelling approach assumes that the capture probability of individual i at trap j is directly influenced by the distance between trap j and the activity centre for individual i .* This intuitively makes sense: we are less likely to observe individuals in locations where they spend less time and vice-versa. Therefore given the capture history of individual i over all traps in the study area, we can essentially triangulate the activity centre for i . More importantly, we can therefore directly estimate the probability that the activity centre is located at any given (x,y) coordinates. This spatial probability distribution function provides a direct measure of the home range of an individual.

One of the assumptions of this type of models is that the population of which the density we are trying to estimate is closed to immigration and emigration. Previous modelling studies (Wilson et al. 1999) show that this assumption is met within a year for the Moray Firth bottlenose dolphin population. Therefore we fitted a model to each year of the photoidentification mark-recapture sampling dataset. *We assumed that the likelihood to photographically capture individual dolphins was not affected by the sampling regime, a safe assumption in this population (Wilson et al. 1999).*

We used a Bayesian approach to estimate the model parameters for two reasons. Firstly, it offers a more flexible framework to retrieve the probability distribution of activity centres. Secondly, it allows more control on what can be defined as suitable habitat for dolphins (where the activity centres can be located). Trivially, this ensures that we can exclude all the land as 'unsuitable' habitat in our map of the Moray Firth. In addition, we were conservative in our prior estimation of suitable habitat and only allowed any grid cell visited at least once (+ a 500m buffer around that cell) during the multiannual sampling period to be defined as suitable habitat. This conservative definition for the prior distribution of habitat meant that we did not extrapolate to unknown areas, even though this modelling approach should provide good extrapolation abilities over the short spatial range we

have here. *It also meant that we restricted near shore habitat in the outer Moray Firth as suitable habitat, an assumption that is appropriate given what we know of bottlenose dolphin distribution in the area.* We also assumed that our ability to detect dolphins in a grid cell decayed following a half-normal distribution over a 500m range. This again is an appropriate assumption given our sampling technique. We used a Monte Carlo Markov Chain (MCMC) simulation algorithm to estimate the parameters of the models given our data (Royle et al. 2009). We iterated the fitting process 50,000 times and discarded the first 1000 iterations to ensure that the parameters estimates were not influenced by the random initial conditions set by the MCM algorithm. This iterative approach informs not only the mean estimate for each parameter of the model, but provides also an estimation of the distribution around that mean given our samples. The model was implemented in R (version 2.12.0 -64bit) using the `SPACECAP` (version 1.0.1) package (Royle et al. 2009). We report here on three parameters of the model that are biologically relevant to our question: D , the density of individuals in the study area (in individuals/100km²); N , the total number of individuals in the populations; and σ , a measure of the mean ranging of individuals in the population.

Another advantage of this approach is that it models the true population, accounting for the fact that individuals that are marked are the observed state of a hidden process which is the ranging dynamics of the total population (marked + unmarked individuals). So not only are we able to infer the activity centres of photographically distinguishable (marked) individuals, but we are also at the same time estimating the activity centres of unmarked individuals. To estimate N from m marked individuals we augment the model with $N-m$ unmarked individuals. We set the prior augmentation rate using estimates of marked to unmarked ratio of photographed individuals during photoidentification occasions. This prior rate estimate is only used to start the fitting process and the posterior distribution of N results from the values of the rate estimated at each MCMC iteration.

RESULTS

We only had time to fit Bayesian models to most of the years for which we had data (2001-2007) because we spent some time trying a frequentist approach. Given that this is a descriptive model fitting exercise, this did not limit our ability to make inferences about individual ranging patterns and therefore did not influence the conclusions we can draw from this analysis. The whole dataset will be used in the future when moving to a predictive modelling framework.

Density estimation

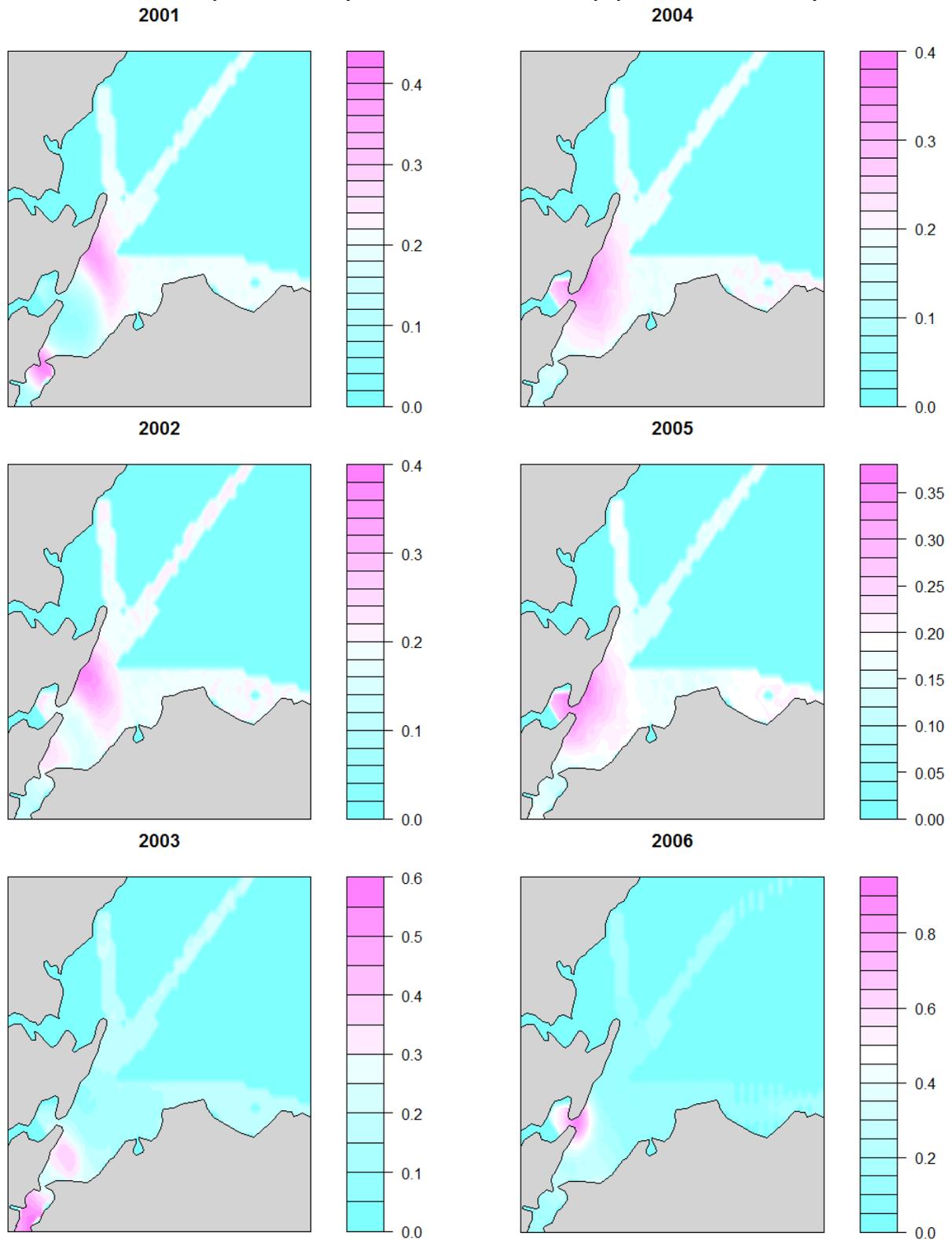
The posterior density estimates in the study area were relatively constant over the study period (Table 5.2). The estimated bottlenose dolphin abundance were also comparable with previously reported estimates obtained using other methods (Thompson et al. 2010). In contrast, the spatial distribution of posterior probability distribution of activity centres changed drastically every year and this was reflected in the variation in σ (Figure 5.1, Table 5.2). The standard error for σ is a measure of how different σ estimates are between individuals and in some years the variation is doubled (Table 5.2).

Table 5.2. Posterior means of D , N , and σ and their associated standard errors (in parentheses) and 95% confidence intervals (in brackets)

YEAR	D (individuals/100km²)	N (individuals)	σ
2001	16.9 (1.78) [13.8-19.9]	107.6 (11.34) [88-127]	4.57 (0.85) [3.06-6.26]
2002	16.5 (2.11) [12.8-20.1]	105.4 (13.48) [82-128]	6.45 (2.38) [3.22-11.31]
2003	16.5 (1.76) [13.5-19.6]	105.12 (11.25) [86-125]	4.00 (0.82) [2.59-5.55]
2004	19.0 (1.55) [15.7-20.7]	121.1 (9.89) [100-132]	5.77 (2.56) [2.05-10.93]
2005	13.9 (2.13) [9.9-17.9]	88.6 (13.56) [63-114]	5.83 (2.18) [2.59-10.26]
2006	11.7 (1.19) [9.6-14.1]	74.5 (7.57) [60-89]	2.90 (0.43) [2.16-3.75]
2007	9.83 (0.69) [8.46-11.13]	62.7 (4.43) [53-70]	8.80 (1.25) [6.50-11.24]

Most individuals use most of the study area every year; however there was year-to-year variation in the density of distributions (Figure 5.1 and 5.2). The ranging patterns of individuals changed from year-to-year (Figure 5.3) regardless of sex or reproductive status. This variability was not caused by changes in sampling effort as it occurred even within the area (inner Moray Firth) that was sampled regularly every year. We need more gender information to start looking more systematically into differences in ranging patterns between age/sex classes.

Figure 5.1. Contour maps of predicted usage individuals make of the surveyed area in a given year. Values represent the sum over all individuals of the probability that a given coordinate (X,Y) is an activity centre for an individual. The measure of the probability of an activity centre position represents a measure of the spatial variation in habitat use for an individual. Hence, the cumulative measure presented here provides a measure of the overall spatial variability in which individuals of the population use the Moray Firth.



2007

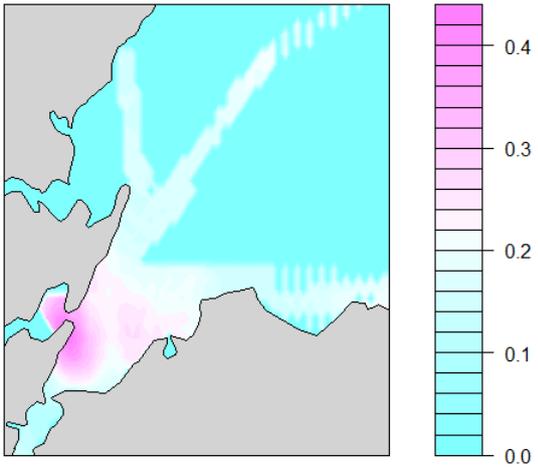
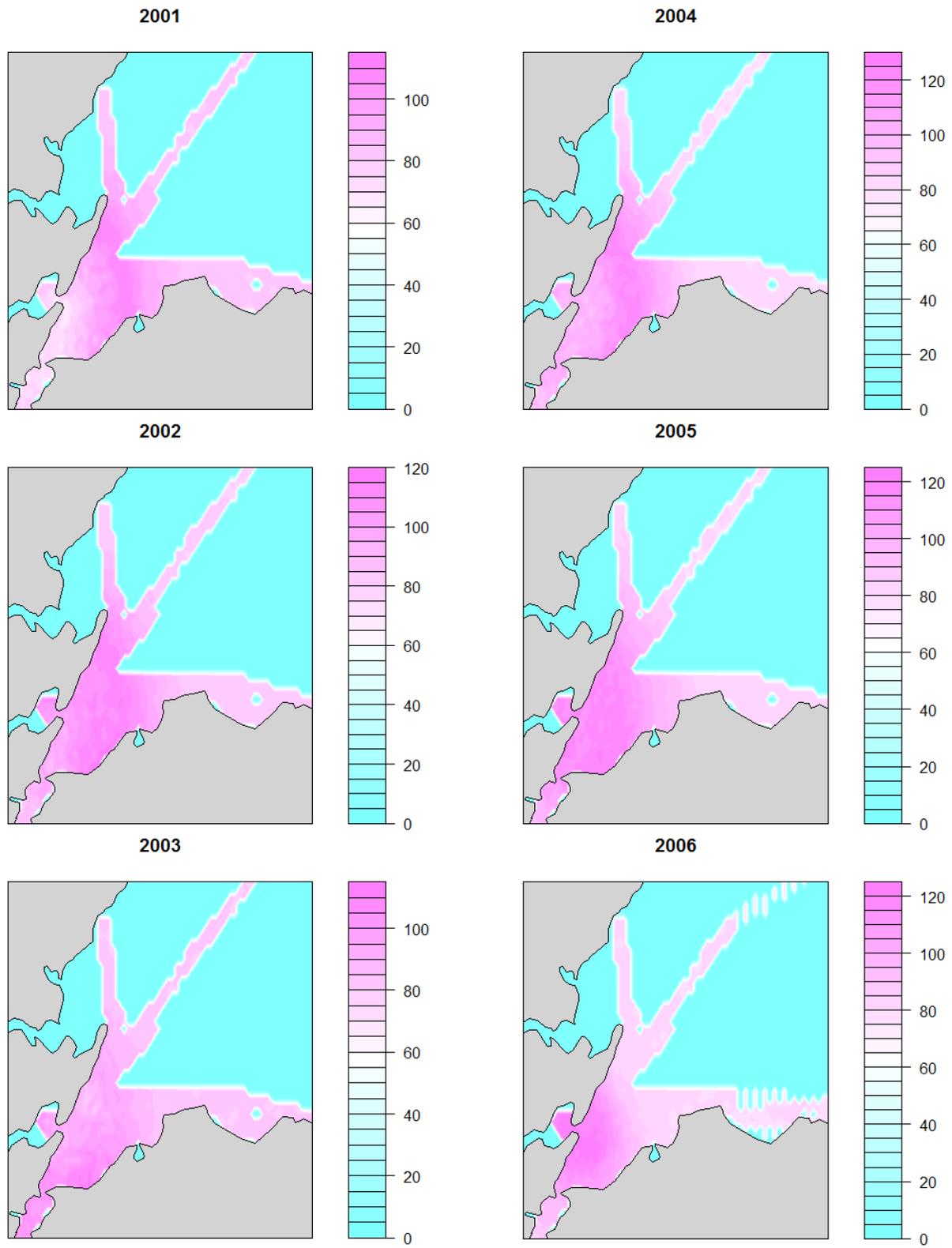


Figure 5.2. Contour maps of predicted number of individuals that can be found in the surveyed area in a given year. Contours represent the number of individuals whose activity centre has been estimated to be located at the given coordinates at least once.



2007

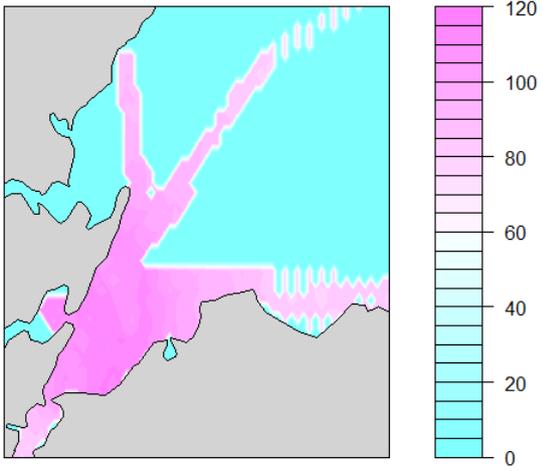
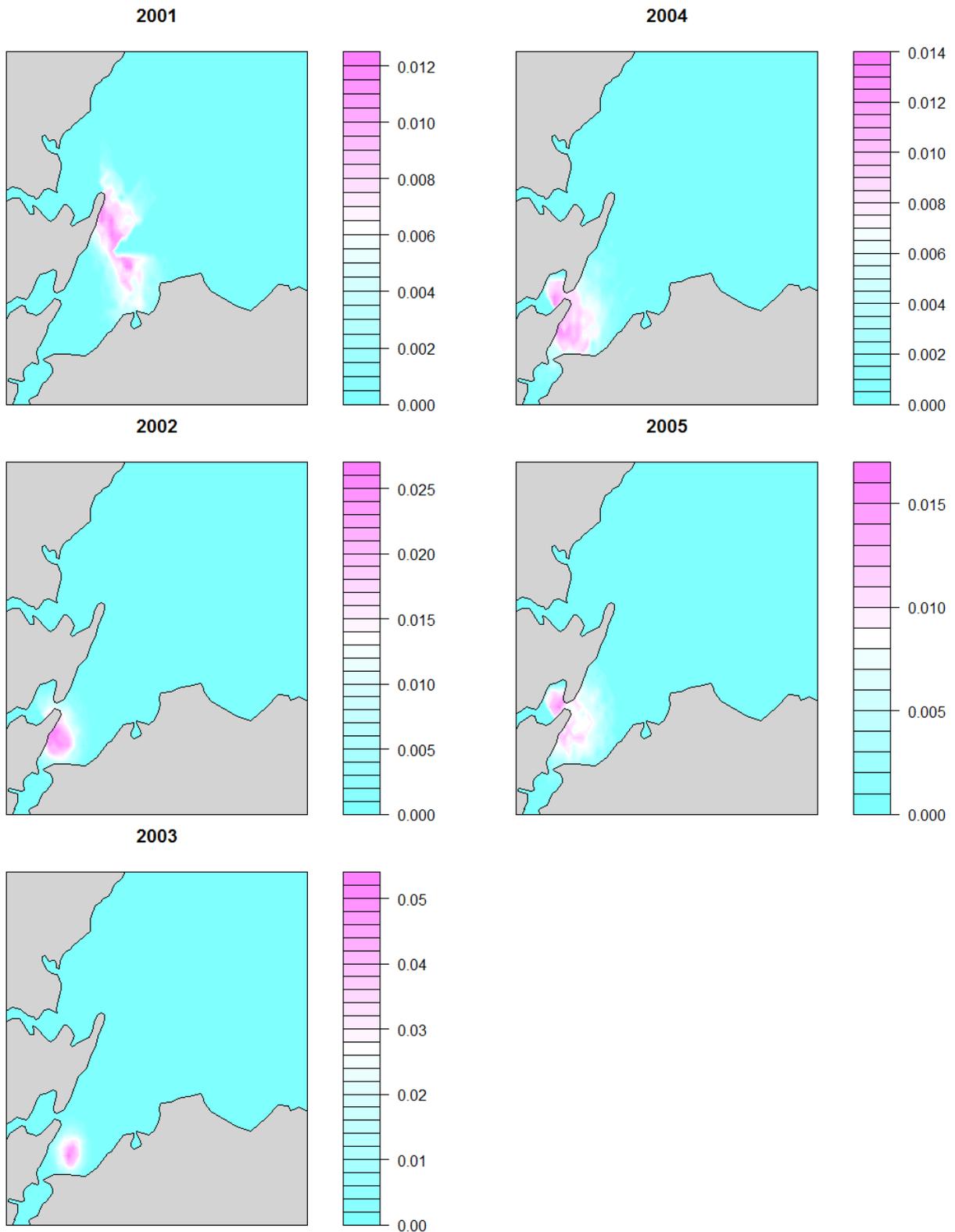
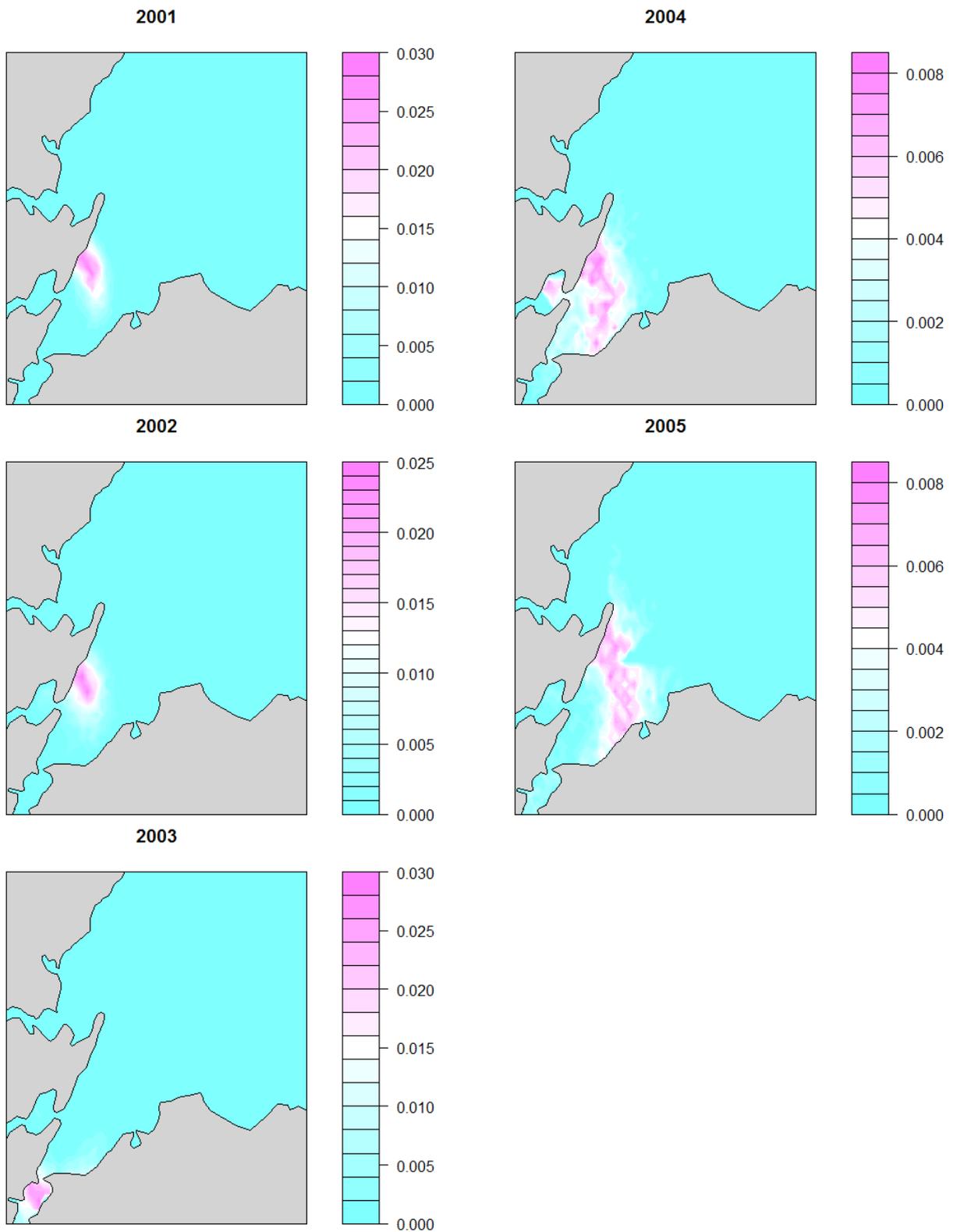


Figure 5.3. Inter-annual variation in the posterior probability of the position of activity centres for selected individuals. This posterior probability distribution can be thought of as a measure of the home range of the individuals (the probability to encounter a given individual in the Moray Firth).

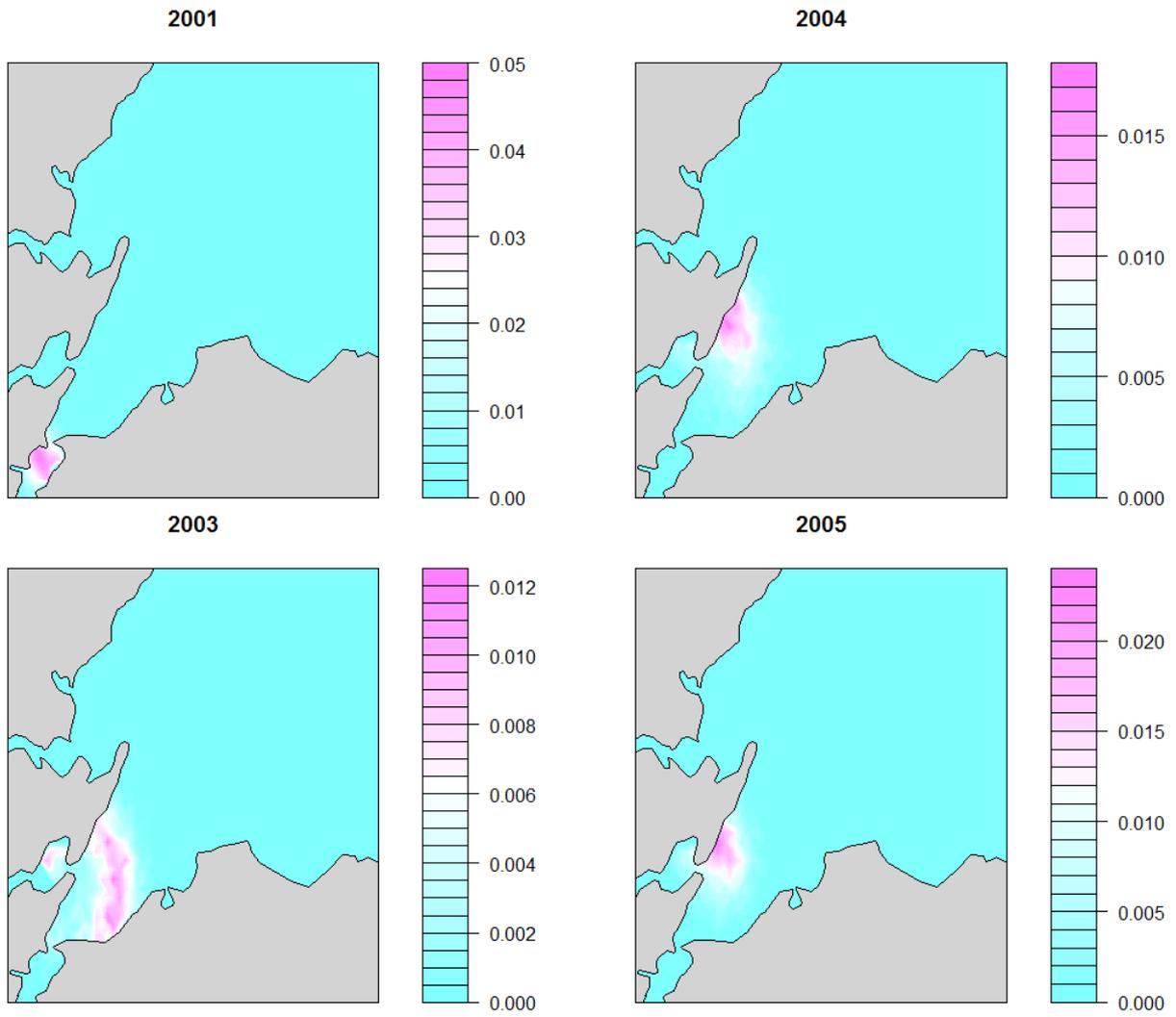
(A) Inter-annual variation in the home range of individual #31, a female that calved in 2001



(B) Inter-annual variation in the home range of individual #8, a male



(C) Inter-annual variation in the home range of individual #11, a female with no known calving over the study period and not photographically captured in 2002



Boat exposure scenarios

The large year-to-year variability in ranging patterns of individuals means that we cannot use this descriptive model to infer increase in boat exposure for a given year in the future given predicted future boat coverage of the area. However, we can still predict how much more time individuals would have spent exposed to boats in the past given the predicted added boat traffic. We used the predictions emerging from the modelled scenarios in Part IV and estimated how much more time boats would spend on average per day for each grid cell which are our 'traps' for our spatially explicit mark-recapture dolphin density model. We therefore used two years (2003 and 2004) to consider exposure under two types of ranging pattern the population seems to display (as described by σ). Our probability distribution of activity centres gives us a direct measure of the likelihood that an individual will be located within a 1km^2 area. So we can simply measure the added exposure by multiplying this probability by the added exposure in that area, this will give the likelihood that an individual will be present in that 1km^2 area when the added boat traffic will also be present. For each scenario the mean (and associated variability between individuals) exposure (vessel-hours) for individual dolphins per year did not change drastically when considering scenarios at Nigg (Table 5.3). However, the variability between individuals changed between the two years. The exposure rate was more homogeneous between individuals when dolphins roamed more (2004, as inferred from σ), while it was more heterogeneous when their ranging was more restricted (Table 5.3). The difference is such that individuals using the affected area the most had a 50% increase in their exposure rate.

Table 5.3. The mean exposure (in vessel-hours) per year for an individual bottlenose dolphin from the Moray Firth population. Range values are 2.5% and 97.5% quantiles and with the associated standard deviation (sd) present the variability between individuals in exposure. Baseline corresponds to the baseline boat traffic (figure 4.3). Please see Part 4 for details for each of the scenarios described here (*refer to section 4 for explanations why the baseline for the Caledonia canal scenario differs from the others). Nigg and Whiteness +400 scenario is also a summer traffic scenario.

Year	Scenario	Mean	Sd	95% Range
2003	Nigg – Baseline	142.42	121.85	[47.4-399.2]
	Nigg + 100	142.49	121.86	[47.4-399.3]
	Nigg + 200	142.54	121.89	[47.4-399.3]
	Nigg + 400	142.67	121.92	[47.5-399.3]
2004	Nigg – Baseline	104.97	68.93	[45.4-303.7]
	Nigg + 100	105.09	69.01	[45.5-303.9]
	Nigg + 200	105.19	69.11	[45.5-304.1]
	Nigg + 400	105.41	69.27	[45.5-304.4]
2003	Caledonia – Baseline*	193.44	166.53	[63.6-529.8]
	Caledonia – +5%	196.68	169.91	[64.0-544.2]
	Caledonia – +10%	198.03	170.51	[65.0-544.9]
	Caledonia – +20%	202.20	172.96	[66.6-553.9]
2004	Caledonia – Baseline*	143.40	96.92	[61.1-426.5]
	Caledonia – +5%	145.46	98.41	[61.6-431.2]
	Caledonia – +10%	147.50	99.79	[62.3-434.2]
	Caledonia – +20%	150.78	100.75	[64.2-440.1]
2003	Whiteness – Baseline	142.42	121.85	[47.4-399.2]
	Whiteness +100	142.67	122.02	[47.5-399.8]
	Whiteness +200	142.93	122.2	[47.6-399.9]
	Whiteness +400	143.44	122.53	[47.8-400.1]
2004	Whiteness – Baseline	104.97	68.93	[45.4-303.7]
	Whiteness +100	105.19	69.08	[45.5-304.5]
	Whiteness +200	105.39	69.22	[45.6-305.2]
	Whiteness +400	105.83	69.52	[45.8-306.7]
2003	Nigg summer – Baseline	219.13	190.37	[73.3-653.4]
	Nigg summer +100	219.22	190.40	[73.3-653.4]
	Nigg summer +200	219.38	190.41	[73.4-653.4]
	Nigg summer +400	219.63	190.47	[73.6-653.4]
2004	Nigg summer – Baseline	155.77	98.09	[71.1-444.4]
	Nigg summer +100	155.93	98.21	[71.2-444.7]
	Nigg summer +200	156.21	98.41	[71.2-445.1]
	Nigg summer +400	156.65	98.68	[71.3-445.8]
2003	Whiteness summer – Base	219.13	190.37	[73.3-653.4]
	Whiteness summer +100	219.75	190.76	[73.5-653.6]
	Whiteness summer +200	220.02	190.92	[73.6-653.6]
	Whiteness summer +400	221.55	191.64	[74.2-653.9]
2004	Whiteness summer – Base	155.77	98.09	[71.1-444.4]
	Whiteness summer +100	156.28	98.45	[71.4-446.2]
	Whiteness summer +200	156.49	98.58	[71.5-447.0]
	Whiteness summer +400	157.37	99.18	[71.9-450.0]
2003	Nigg and Whiteness +400	221.55	191.64	[74.2-653.9]
2004	Nigg and Whiteness +400	158.24	99.76	[72.1-451.4]

2003	Inverness – Base	142.42	121.85	[47.4-399.2]
	Inverness – extra operator	144.20	124.16	[47.5-405.5]
2004	Inverness – Base	104.97	68.93	[45.4-303.7]
	Inverness – extra operator	105.88	69.96	[45.5-307.7]

We can also infer the spatial distribution of boat interactions (given the assumptions made in both models). In the same way as we summarise the exposure rate information above across individuals, we can do so across the position of the ‘traps’. This leads to the development of maps that can inform location where interactions are more likely to occur (Figures 5.4). We can see that the main difference between the two years is the substantial increase in interactions in the inner Moray Firth in 2003 when dolphins spend more time there (Figure 5.1) while exposure rate remains similar in over parts of the home range.

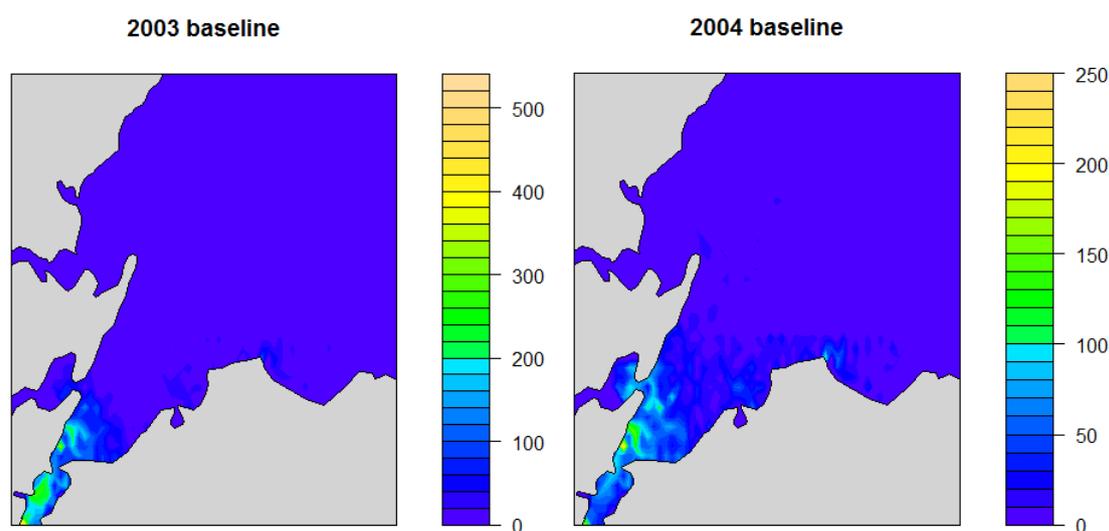


Figure 5.4. Spatial variation in exposure rate (vessel hours per year summed over all individual dolphins) under baseline scenario conditions for 2003 and 2004 (note the difference in scale between the two years).

CONCLUSIONS AND OUTLOOK

There is substantial inter-annual variability in the ranging of individuals in the area while density estimates did not change as much (Table 5.2). This is unsurprising as individuals will evolve in their home range in order to maximise the way they can exploit its resources. This inter-annual variability will limit the ability to predict change in dolphin distribution. However, we know that the schooling patterns of dolphins in this population correlates with large scale climatic indices (Lusseau et al. 2004) because those are linked to food availability. The winter North Atlantic Oscillation index is linked to summer salmon abundance in the rivers of the Moray Firth with 2 years of lag (Lusseau et al. 2004). It was proposed that poor winter conditions influenced overwintering survival of juvenile salmon in the rivers, leading to lower abundance of the resulting cohort returning as adults. In turn salmon abundance, hence summer food availability, influences the schooling pattern of dolphins in the Moray Firth, dolphin schools being larger when food is more abundant (Lusseau et al. 2004). Therefore, the winter NAO index, with 2 years of lag, is a good candidate covariate to incorporate in a spatially explicit mark-recapture predictive model of dolphin density, and its associated distribution of activity centres to explain the observed inter-annual variability in the present descriptive model. Indeed, we can see that the ranging measure of the density model is correlated to this climatic index ($\rho=0.74$), dolphins ranging more widely in expected poorer food condition years

(positive NAO index). Of course this climatic index is only correlated to dolphin ranging patterns; it does not cause changes in ranging. Prey abundance and distribution is the factor influence dolphin ranging but we currently lack any predictive model of at-sea salmon behaviour which would be a more desirable variable to include in dolphin distribution models.

This variability has a compounded effect on the exposure rate of individuals. Dolphins present in area with heavier boat traffic will be more exposed to disturbances when conditions are favourable because they roam less. As expected, any given non-touristic commercial activity will only raise exposure at a given 1km² area in the Moray Firth by a few minutes every day. However, we now have a framework to consider the compounded contribution of each potential activity to the overall boat traffic in the Moray Firth and therefore can:

1. Assess the overall exposure of dolphins to boat traffic
2. Define the relative contribution of each activity to the overall exposure

This latter advance is particularly important as our legal frameworks speak to minimising cumulative effects on wildlife population of conservation concerns. Here we now can estimate the contribution of each development proposal to this cumulative effect. It is particularly important to now focus on further developing the boat model to include boat behaviour. This component does not affect too much scenarios that involve boat traffic that has predictable homogeneous behaviour (e.g., shipping); but, as highlighted in part IV, it does influence the outcomes of scenarios in which traffic behaviour is more diverse (e.g., those involving recreational vessels).

PART VI – Synthesis

GENERAL MANAGEMENT GUIDANCE

Our preliminary analysis of the T-POD data indicates that boat interactions may disrupt the foraging of bottlenose dolphins at some sites in the Moray Firth. However, this effect was not evident in Aberdeen Harbour, and deserves further investigation with the much larger set of T-POD data available from the area. These results are consistent with the hypothesis that dolphins incorporate boat interactions as a risk factor in their landscape ecology (Lima and Zöllner 1996). Like other factors, boat interactions are considered risky when not predictable. It is therefore important at this stage, where we have little understanding of the maximum number of interactions that can cause site deterioration, to minimise interactions in locations known to be foraging hotspots where boat presence can be difficult to predict by dolphins (Hastie et al 2004). We now also know that the ranging patterns of individuals vary yearly most probably in relation to food availability. In years where ranging is limited, exposure rate for individuals ranging over heavily used area will increase, without boat traffic changing. Increased food availability may offer some scope for compensation of this increase in potential disturbance. However, we have no understanding at this stage of bottlenose dolphin's compensation abilities and therefore limitations in ranging can be perceived as increased potential for consequences of disturbances until proven otherwise.

Scenarios

The predicted increase in traffic proposed in the scenarios associated with wind farm developments at Nigg and Whiteness will lead to trivial increase in boat exposure in locations where dolphins are likely to be. However, these scenarios start to diverge at upper limits of simulated boat traffic, with Nigg resulting in smaller increase in exposure. It is therefore likely that, *if our model assumptions are correct*, those scenarios will not lead to population-level impacts because those appear to result in trivial increase in boat exposure of individuals. This is based on the assumption that boat vicinity elicits behavioural response, not boat acoustic characteristics, which is supported by other studies (Lusseau 2003a, Williams et al. 2011). If other factors, such as acoustic signal intensity, contributed to response elicitation, new predictions would have to be drawn. It is worth noting though that this is based on a descriptive model of dolphin density, not a predictive model. Moving the analysis in a predictive framework will improve our confidence in this conclusion.

Increases in boat traffic in the inner Moray Firth, such as the Caledonian channel scenario, led to more diverse exposure rates. Importantly, we see that the lack of discrimination in boat behaviour (boat static v transiting) limits our ability to predict exposure, even with this descriptive dolphin spatial model. Hence, increases in traffic can lead to predicted decreased exposure rate, which would not be the case (Table 5.3). We therefore need to now extend the boat model to distinguish between boat behaviours. This will become feasible as more GPS boat data becomes available and therefore this boat sampling effort needs to continue.

OUTLOOK

This report provides a framework to understand the population consequences of disturbances caused by human activities that interact with bottlenose dolphins in the Moray Firth. We also provide early evidence of the mechanisms involved in such effects and how to complement this research effort to achieve a management tool that can be used to simulate and predict the potential impact of planned additional activities. We have a clear roadmap of additional work needed for each component of this research tool needed to complete it (Figure 6.1).

Additional data collection

We need to focus additional sampling on three aspects:

1. *Continue the deployment of acoustic dolphin loggers and couple those with remote loggers that can systematically record boat presence.*

This can be achieved either by continuing the deployment of PODs and adding remote recorders, or simply migrating the whole remote acoustic logging sampling scheme to new devices that can record both dolphins and boats (at regular intervals). For example EARs are currently being deployed in a project looking at the population consequences of boat traffic on spinner dolphins in Hawaiian island to do this.

2. *Continue and expand the photogrammetry work*

This sampling technique can reliably infer variation in body condition of adults as well as growth rate of calves. Both parameters are key priority for the simulations as those are site-specific, especially for a population living at the extreme of the species range.

3. *Continue photo-identification work*

We now need to move from a descriptive dolphin-ranging model to a predictive approach. To do so we will require future sampling to test predictions and continue to inform the between-year variability in ranging patterns.

4. *Continue the deployment of GPS loggers on vessels using the Moray Firth*

This additional information will inform inter-annual variability in vessel distribution by vessel types.

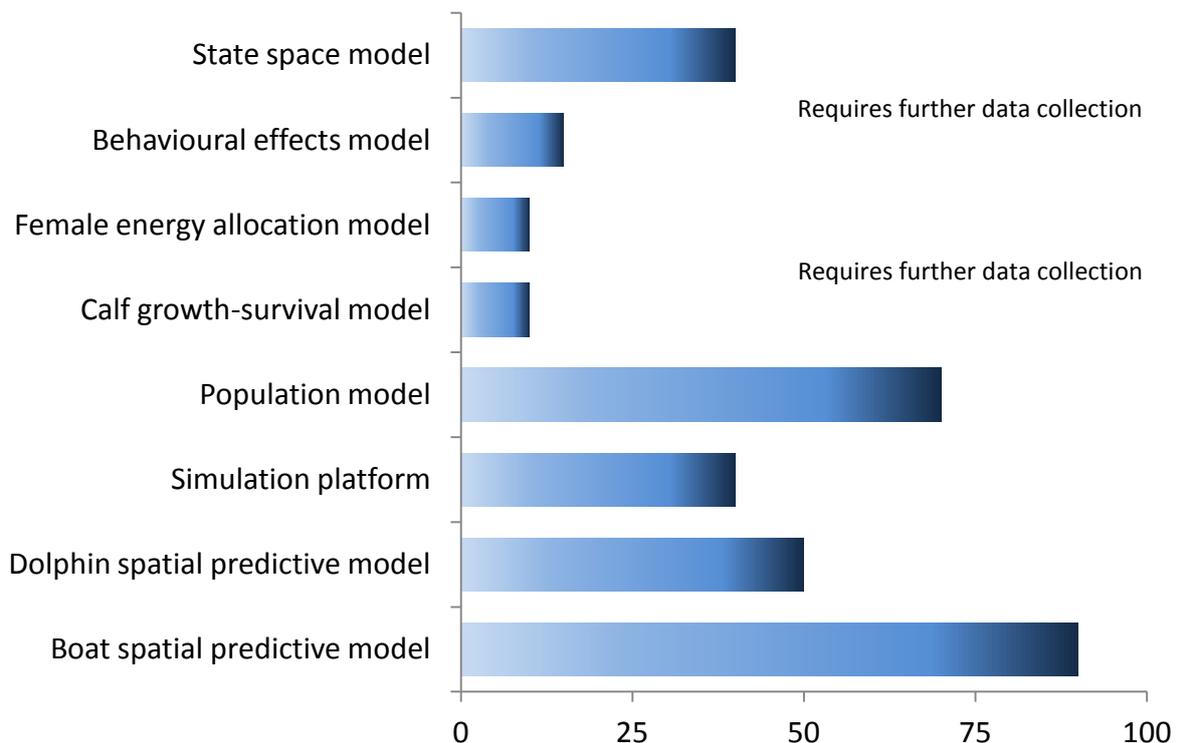


Figure 6.1. Progress made (percent completion) to date on all the components required to provide predictive scientific advice for the population consequences of disturbances on the Moray Firth bottlenose dolphin population.

Dolphin ranging models

We now need to move the dolphin modelling approach in a predictive framework. To do so we need to extend the modelling framework we used to cover spatially inhomogeneous processes, so that we can include spatial covariates, such as depth, oceanographic features or boat traffic, to explain the observed variability in ranging patterns. We also need to extend it so that it can incorporate yearly covariates, such as the winter NAO index, to explain yearly variations. Once these statistical developments have been established, we could then run forecasting scenarios similar to the example we gave here.

Simulation and parameter fitting

Fitting of the BehPhys state space model will require more data collection at this stage as we do not have enough samples in which we have time series of human activity covariates. Observed body condition indices will also improve the fitting process of this model. Deploying acoustic loggers for anthropogenic sounds (boat traffic or others) will speed up this process and will provide more detailed information about the characteristics of the disturbance (sound field).

Graphical User Interface (GUI)

One of the ultimate aims of this project is to produce a package that end-users can access. This will require a GUI as a front-end to the simulation model. Further software development, involving close communication with end-users, will be necessary to produce such an interface.

REFERENCES

- Acevedo-Gutiérrez, A. (2002) Interactions between marine predators: dolphin food intake is related to number of sharks. *Marine Ecology Progress Series*, **240**: 261-271.
- Aguilar de Soto, N., Johnson M.P., Madsen, P.T., Diaz, F., Dominguez, I., Brito, A. and Tyack, P.L. (2008) Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife. *Journal of Animal Ecology* **77**: 936-947.
- Au, W. W. L. 1993 *The sonar of dolphins*. New York: Springer.
- Bailey, H., Clay, G., Coates, E. A., Lusseau, D., Senior, B. and Thompson, P. M. (2010a) Using T-PODS to assess variations in the occurrence of coastal bottlenose dolphins and harbour porpoises. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**: 150-158.
- Bailey, H., Senior, B., Simmons, D., Rusin, J., Picken, G. and Thompson, P. M. (2010b) Assessing underwater noise levels during pile-driving at an offshore windfarm and its potential effects on marine mammals. *Marine Pollution Bulletin*, **60**: 888-897.
- Bailey, H. and Thompson, P. (2010) Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Marine Ecology Progress Series*, **418**: 223-233.
- Beale C.M. & Monaghan P. 2004 Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335-343.
- Bejder, L. (2005). Linking short and long-term effects of nature-based tourism on cetaceans. Unpublished PhD thesis, Dalhousie University, Halifax.
- Borchers, D. L. and Efford, M.G. (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* **64**:377-385.
- Brodie, P.F. (1975) Cetacean energetics, an overview of intraspecific size variation. *Ecology* **56**(1): 152-161.
- Connor, R. C., Wells, R. S., Mann, J., and Read, A. J. (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann, J., Conner, R. C., Tyack, P. L., and Whitehead, H. (eds.) *Cetacean societies*. University of Chicago Press, Chicago.
- Culloch, R. (2008) Bottlenose dolphins using coastal regions adjacent to a Special Area of Conservation in north-east Scotland. *Journal of the Marine Biological Association of the United Kingdom*, **88**: 1237-1243.
- Currey, R. J. C., Dawson, S. M., Slooten, E., Schneider, K., Lusseau, D., Boisseau, O. J., Haase, P. & Williams, J. A. (2008) Survival rates for a declining population of bottlenose dolphins in Doubtful Sound: an information theoretic approach to assessing the role of human impacts. *Aquatic Conservation-Marine and Freshwater Ecosystems* **19**, 658-670.
- David, J.A. (2006). An assessment of the potential impact of the proposed Whiteness Marina on populations of bottlenose dolphins and harbour porpoises in the Moray Firth. Report to Whiteness Property Company Ltd. 36pp. Unpublished.

- David, J.A. (2008). Start-up boat numbers at Whiteness Marina. Report to Whiteness Property Company Ltd. 22pp. Unpublished.
- David, J.A. & Latimer, M.R. (2008). Moray Firth boat survey conducted on Sunday 17th August 2008. Report to Whiteness Property Company Ltd. 3pp. Unpublished.
- David, J.A. & Latimer, M.R. (2009). Moray Firth boat surveys 2009 - the use of data to estimate numbers and densities of boats operating out of Whiteness Marina. Report to Whiteness Property Company Ltd. 26pp. Unpublished.
- David, J.A., Latimer, M.R. & David, C.G. (2010a). Boat survey conducted in the Moray Firth on 2 May 2010. Report to Scottish Natural Heritage. 20pp. Unpublished.
- David, J.A., Latimer, M.R. & David, C.G. (2010b). Boat survey conducted in the Moray Firth on 3 April 2010. Report to Scottish Natural Heritage. 20pp. Unpublished.
- David, J.A. & Latimer, M.R. (2010a). Vessel movements in the Moray Firth 2010. Report to Scottish Natural Heritage. 80pp. Unpublished.
- David, J.A. & Latimer, M.R. (2010b). Moray Firth Vessel database. <http://www.biomitor.org.uk/morayvessels/morayvessels.htm>
- DeRuiter, S.L., Bahr, A., Blanchet, M.-A., Hansen, S.F., Kristensen, J.H., Madsen, P.T., Tyack, P.L. and Wahlberg M. (2009) Acoustic behaviour of echolocating porpoises during prey capture. *Journal of Experimental Biology*, **212**: 3100-3107.
- Donovan, C., Mackenzie, M., & Hastie, G. (2009) Report to Scottish Natural Heritage: Analysis of at-sea distribution of vessels within the Moray Firth SAC. Unpublished.
- Dawson SM (1991) Clicks and communication: the behavioural and social contexts of Hector's dolphin vocalizations. *Ethology* 88:265-276
- Gibbs, M. T., Bowman, M. J., and Dietrich, D. E. (2001) Maintenance of near-surface stratification in Doubtful Sound, a New Zealand Fjord. *Estuarine, Coastal and Shelf Science*, **51**, 683-704.
- Götz T, Verfuss UK, Schnitzler HU (2006) 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biology Letters* 2:5-7
- Harding-Hill, R. (1993) *The Moray Firth review*. Scottish Natural Heritage, Edinburgh.
- Harwood J. & Stokes K. (2003) Coping with uncertainty in ecological advice: lessons from fisheries. *Trends in Ecology and Evolution*, **18**, 617-622.
- Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M. and Thompson, P. M. (2004) Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, **144**: 397-403.
- Hastie, G. D., Wilson, B. and Thompson, P. M. (2006) Diving deep in a foraging hotspot: acoustic insights into bottlenose dolphin dive depths and feeding behaviour. *Marine Biology*, **148**: 1181-1188.

- Higham, J.E.S., Bejder, L. and Lusseau, D. 2009. An integrated and adaptive management model to address the long-term sustainability of tourist interactions with cetaceans. *Environmental Conservation* 35(4): 294-302.
- International Whaling Commission (2006) Report of the Scientific Committee. *Journal of Cetacean Research and Management* pp 1-160.
- Jackson, C.H. (2011) Multi-State Models for Panel Data: The msm Package for R. *Journal of Statistical Software*, **38**(8), 1-28.
- Lammers, M.O., Brainard, R.E. and Au, W.W.L., Mooney, T.A. and Wong K. (2008) An Ecological Acoustic Recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *J. Acoust. Soc. Am.* 123:1720-1728
- Lima, S. L., and Zöllner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, 11, 131-135.
- Lockyer, C. (2007) All creatures great and smaller: a study in cetacean life history energetics. *Journal of the Marine Biological Association UK* 87: 1035-1045.
- Lusseau, D. (2003a) Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series*, **257**, 267-274.
- Lusseau, D. (2003b) The effects of tourism activities on bottlenose dolphins (*Tursiops* spp.) in Fiordland, New Zealand. PhD Thesis, University of Otago, Dunedin.
- Lusseau, D. (2003c) Effects of tour boats on the behaviour of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology*, **17**, 1785-1793.
- Lusseau, D. (2004) The hidden cost of tourism: Detecting long-term effects of tourism using behavioral information. *Ecology and Society*, **9**, 2.
- Lusseau, D. (2005) The state of the scenic cruise industry in Doubtful Sound in relation to a key natural resource: Bottlenose dolphins. In: Hall, M. and Boyd, S. (eds.) *Nature-based tourism in peripheral areas: Development or disaster?* Channelview Publications, London.
- Lusseau, D. (2006a) The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Marine Mammal Science*, **22**, 802-818.
- Lusseau, D. (2006b) Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand. *Behavioural Processes*, **73**, 257-265.
- Lusseau, D. and Bejder, L. (2007). The long-term consequences of short-term responses to disturbance: Experiences from whalewatching impact Assessment. *International Journal of Comparative Psychology*, **20**, 228-236.
- Lusseau, D., Bejder, L., Corkeron, P., Allen, S. and Higham J.E.S. (in revision) Learning from past mistakes: Regulating whalewatching as a consumptive activity. *Conservation Biology*

- Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., and Dawson, S. M. (2003) The bottlenose dolphin community of Doubtful Sound features a large proportion on long-lasting associations: Can geographic isolation explain this unique trait? *Behavioural Ecology and Sociobiology*, **54**, 396-405.
- Lusseau, D., Slooten, E., & Currey, R. J. C. (2006). Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tourism in Marine Environments*, **3**(2), 173-178.
- Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T. R., Hammond, P. S., and Thompson, P. M. (2004) Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters*, **7**, 1068-1076.
- Lusseau, D., New, L., Donovan, C., Cheney, B., Thompson, P.M., Hastie, G. & Harwood, J. (2011). The development of a framework to understand and predict the population consequences of disturbances for the Moray Firth bottlenose dolphin population. Scottish Natural Heritage Commissioned Report No. 94pp. Unpublished.
- Madsen, P. T., Johnson, M., Aguilar de Soto, N., Zimmer, W.M.X. & Tyack, P.L. (2005) Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *Journal of Experimental Biology*, **208**: 181-194.
- McFarland D.J. & Sibly R.M. (1975) The behavioural final common path. *Philosophical Transactions of the Royal Society of London Series B*, **270**: 265-293.
- Mendes, S., Turrell, W., Lütkebohle, T. & Thompson, P. (2002) Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series*, **239**: 221–229.
- Miller, P.J.O., Johnson, M.P. & Tyack, P.L. (2004) Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. *Proceedings of the Royal Society B* **271**: 2239-2247.
- Miller P.J.O. (2006) Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*. **192**: 449–459.
- National Research Council (2005) *Marine mammal populations and ocean noise: determining when noise causes biologically significant effects*. Washington, DC: US National Academy of Sciences.
- Perrin, W. F., Würsig, B., and Thewissen, J. G. M. (eds.) (2009). *Encyclopedia of Marine Mammals, Second Edition*. Academic Press, London. pp. 249-255.
- Powell, A. (2008) The foraging ecology of bottlenose dolphins in Aberdeen harbour. Unpublished MSc thesis, University of Aberdeen, Aberdeen.
- Punt, A. E. & Donovan, G. P. (2007) Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission. *ICES Journal of Marine Science* **64**: 603–612.

- R Development Core Team (2010). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Richard Robinson Consulting (2009) Moray Firth Marine Traffic Study: Final Report for the Moray Firth Partnership. Unpublished.
- Richardson, W. J., Greene, C. R., Jr., Malme, C. I. and Thomson, D. H. (1995). Marine mammals and noise. San Diego, CA: Academic Press.
- Roszbach, K. A., and Herzing, D. L. (1997) Underwater observations of feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Marine Mammal Science*, **13**, 498-503.
- Rowe, L.E., Currey, R.J.C., Dawson, S.M. and Johnson, D. (2010) Assessment of epidermal condition and calf size of Fiordland bottlenose dolphin populations using dorsal fin photographs and photogrammetry. *Endangered Species Research*, **11**, 83–89.
- Royle, J. A., K. U. Karanth, A. M. Gopaldaswamy and N. S. Kumar. 2009. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology* 90(11), 3233-3244.
- Stanton, B. R. and Pickard, G. L. (1981) Physical oceanography of the New Zealand fjords. New Zealand Oceanographic Institute Memoirs.
- Stockin, K. A., Lusseau, D., Binedell, V. and Orams, M. B. (2008) Tourism affects the behavioural budget of common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Marine Ecology Progress Series*, **355**, 287-295.
- Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D. and Aureli, F. (2011), Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos* 120: 1608–1617.
- Thompson, P. M., McConnell, B., Tollit, D. J., Mackay, A., Hunter, C. and Racey, P. A. (1996) Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N.E. Scotland. *Journal of Applied Ecology*, **33**: 1572-1584.
- Thompson, P. M., Wilson, B., Grellier, K. and 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**: 1253-1263.
- Thompson, P.M., Brookes, K., Cheney, B., Cândido, A., Bates, H., Richardson, N. and Barton T. (2010) Assessing the potential impact of oil and gas explorations on cetaceans in the Moray Firth. First year Report for DECC, Scottish Government, COWRIE, and Oil & Gas UK.
- Thompson PM, Cheney B, Ingram S, Stevick P, Wilson B and Hammond, P.S. (Eds) (2011). *Distribution, abundance and population structure of bottlenose dolphins in Scottish waters*. Scottish Government and Scottish Natural Heritage funded report. Scottish Natural Heritage Commissioned Report No.354, Scottish Natural Heritage, Perth UK.
- Whitehead, H. and Payne, R. (1981). New techniques for assessing populations of right whales without killing them. In *Mammals in the Seas*, vol. III. FAO Series No. 5, 189-211.

- Williams, J. A., Dawson, S. M., and Slooten, E. (1993) The abundance and distribution of bottlenosed dolphins (*Tursiops truncates*) in Doubtful Sound, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 2080-2088.
- Williams, R., Lusseau, D. and Hammond, P.S. (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, **133**,301–311.
- Williams, R., Ashe, E., Sandilands, D. & Lusseau, D. 2011. Stimulus-dependent response to disturbance affecting the activity of killer whales. Report to the 63rd International Whaling Commission Scientific Committee meeting. SC/63/WW5
- Wilson, B., Thompson, P. M. and Hammond, P. S. (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, **34**: 1365-1374.
- Wilson, B., Hammond, P. S. and Thompson, P. M. (1999) Estimating size and assessing status of a coastal bottlenose dolphin population. *Ecological Applications* **9**: 288-300.
- Yazdi, P., Kilian, A., and Culik, B. M. (1999) Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). *Marine Biology*, **134**, 601-607.