



# How the movement characteristics of large marine predators influence estimates of their abundance



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## ABSTRACT

Understanding animal movement provides information that helps design effective conservation initiatives. We intuitively understand that the way animals move at large scales determines the extent of their home range and their migratory patterns – and we know that these features are relevant to decisions about the location, size and distribution of protected areas. It is less intuitively obvious that knowledge of movement characteristics at finer scales can also have conservation implications. By modelling the small to intermediate scale movement (1–10<sup>3</sup> m) of a large marine predator in a shallow coastal environment, we show how different assumptions about movement patterns influence estimates of species abundance derived from field observations. Foraging behaviour, statistical properties of the swimming path and average speed exert the greatest impact, suggesting that these should be the focus of further experimental work. Better data would inform our understanding and considerably reduce the uncertainty in abundance estimation, improving conservation-related decision making.

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## 1. Introduction

Estimates of the abundance of large predators help inform choices about which species and which areas need protection, and how to monitor the effectiveness of protection (Hughes et al., 2014; Pimm et al., 2014). The abundance of large predators cannot usually be observed directly, but can only be inferred indirectly from counts of individuals, which is usually obtained from very sparse spatial and temporal sampling. Estimating abundance from individual counts is further complicated, partly because of observation biases, but also because predators move and it can be difficult to discriminate between different individuals. It follows that the way predators move affects (i) the probability of detecting an individual at a given location during a certain time interval and (ii) the probability that two separate detections are due to two different individuals, rather than a single individual seen twice.

Detailed understanding about how marine predators move is still lacking so we need to make some assumptions. Often, this is done without making the assumptions explicit (Boschetti et al., 2011a). The aim of this paper is to show how these assumptions

affect estimates of abundance obtained from camera surveys, using remote underwater video surveys of sharks (e.g. Vanderklift et al., 2014) as a test system. Identifying which assumptions have the greatest influence on estimates of abundance provides information about which components of a predator's movement deserve more experimental attention, and the extent to which this will help conservation decisions.

Computer models of animal behaviour have been used to simulate field surveys in order to assess species abundance and distribution or to test survey design (Turnock and Quinn, 1991; Zollner and Lima, 1999; Horne et al., 2007; Ward-Paige et al., 2010; Rees et al., 2011; McCauley et al., 2012; Petrovskaya et al., 2012; Chandler and Royle, 2013; Vanderklift et al., 2014). Depending on model complexity, these approaches require the model developer to make explicit (in the computer code) a number of assumptions about movement patterns. Very simple models may approximate animal movement by Brownian motion leading to diffusion-like area cover (Rowcliffe et al., 2008). A model user may then need to provide the size and centres of home ranges. As an output, the model may provide, say, the probability of detecting an animal at different positions in space. This, obviously, depends on the assumed movement type (in this case Brownian motion). However, how detection probability depends on the assumed movement type might not be clear to the model user. At the other extreme, more complex models may allow the user to control a larger number of

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movement parameters, including the animal's speed, the type of movement (e.g. Brownian vs Correlated Random Walk), preferential directionality, time dependence, space dependence, and so on. The requirement to provide many parameters entails more a priori biological knowledge, which is often lacking. Some users may feel that in these circumstances, uncertainty in model outcomes increases with model complexity. However, these requirements highlight that if movement assumptions are not made explicitly by the model user, they are made implicitly by the model design, often leaving the user unaware of both these choices and their implications. Only once these assumptions are made explicit will the user be able to appreciate the potential impact these choices can have on the model's behaviour.

In this work we provide an example of how uncertainty in some parameters controlling animal movement can affect estimates of abundance. We describe a model to simulate the movement of blacktip reef sharks (*Carcharhinus melanopterus*) in coastal reefs. We then use this model in an inverse mode (Tarantola, 1987; Symons and Boschetti, 2012) to estimate shark abundance. By showing which movement parameters most affect estimates of abundance and uncertainty, we also provide information on which of these parameters further experimental work should focus. We do so by working at the intersection of three approaches, which are well established in various disciplines, including ecological studies. First, we explicitly recognise that numerical modelling can vastly improve both processes understanding, data analysis and field work design, along the lines of the 'virtual ecology' approach (Zurell et al., 2010). Second, we place emphasis on understanding how processes at one scale can manifest as patterns at different scales, usually referred to as 'pattern-oriented modelling' (Grimm and Railsback, 2012) in ecology and more generically as the study of emergence in complexity science and applied mathematics (Shalizi and Crutchfield, 2001; Prokopenko et al., 2009). Third, we emphasise visual description of our results with the specific aim of developing an intuition for how movement patterns influence estimates of abundance. Intuition is a necessary component of any scientist's work, but can be faulty and lead to considerable systematic and recurrent judgement mistakes even in experts (see Boschetti et al., 2011b, and references within); computer modelling with explicit visualisation capabilities can be very helpful in developing and checking our intuition.

We describe all equations used in the model and provide the information needed to reproduce our results. We start by reviewing some approaches commonly used to model animal movement. We then treat the estimation of predator abundance as an inverse problem and show how a model of animal movement can be used to fit observations from underwater video cameras. We proceed by describing the model used in this work and show how parameters controlling the modelled predator movement impact visitation patterns and, in turn, estimates of abundance. In doing so, we model realistic settings in a shallow reef environment from Western Australia and apply our results to a real data set. We conclude by discussing the implications of our results in terms of future experimental work and its potential impact on decision-making in marine conservation.

## 2. Analysis of animal movement

Animal movement can be analysed at a number of levels, each characterised by its own implicit temporal and spatial scale (Crist et al., 1992; Barraquand and Benhamou, 2008; Getz and Saltz, 2008; Nathan et al., 2008; Fronhofer et al., 2012; Benhamou, 2014). Here we consider four levels of analysis. At the finest level, we have what (Getz and Saltz, 2008) define as 'fundamental movement elements',

which animals perform in their daily activities (e.g. stepping, speeding, lounging, stopping, standing) and which are mostly determined by the physical and physiological characteristics of the species. At the next level, fundamental movement elements are combined to carry out specific activities (e.g. habitat choice, foraging, avoiding predation, mating, resting). These represent 'decisions' and reactions carried out at scales of fractions of seconds to minutes and can be seen as incorporating the 'causal' mechanics responsible for animal movement. At the third level, longer time series of unit movements result in geometric patterns at the scale of minutes to days and metres to kilometres, depending on the species. These geometric patterns are usually analysed in terms of shape, spatial extent covered and search and foraging efficiency, which can be interpreted as global properties emerging from actions at finer scales. While the first level describes the mechanics and the second level supposedly includes the immediate 'causes' of movement, the third level can be seen as providing an additional evolutionary feedback resulting from its adaptive efficiency (Kareiva and Shigesada, 1983; Viswanathan et al., 1999; Bartumeus et al., 2002; Reynolds et al., 2007b; Bartumeus et al., 2008; James et al., 2011b; Humphries et al., 2012; Kawai and Petrovskii, 2012; Reynolds, 2012a; Sims et al., 2012; Palyulin et al., 2014). In the literature the first and second levels of analysis are usually referred to as 'mechanistic', while the third level is often referred to as 'statistical' (Bartumeus, 2009; Gautestad, 2012).<sup>1</sup>

The fourth level is represented by the actual field observations. Data collection is usually carried out at a scale intermediate between the mechanistic and statistical levels, but at a resolution considerably sparser than both. This is where much of the debate on whether the statistical movement patterns of large predators are best described by Lévy flights, Brownian Motion or Correlated Random Walks arises (Bartumeus et al., 2005; Jansen et al., 2012; Reynolds, 2012c; Sakiyama and Gunji, 2013). In most circumstances, including the datasets we have collected, discriminating between these statistical distributions is difficult (Edwards et al., 2007; Sims et al., 2007; Gautestad, 2012; Humphries et al., 2012) because they are affected by how the animal movement depends on the local environment and the distribution of prey, as well as by distortions imposed by the resolution or rate of measurements (Zollner and Lima, 1999; Codling and Hill, 2005; Benhamou, 2012; Ferreira et al., 2012; Patrick et al., 2014). As a result, it is important to think of field observations as a product of the complex interactions between an animal's actions and the features, which constrain (e.g. physical obstacles) or alter (e.g. prey–predator distribution, habitat distribution, currents, winds) these actions (Getz and Saltz, 2008).

Information about movement patterns of large marine predators is mostly derived from studies of oceanic species, undertaken in the open ocean, which can be considered essentially unbounded (Humphries et al., 2010). In coastal reef ecosystems this is rarely, if ever, the case. When information does come from coastal ecosystems, the constraints imposed on animal movement by physical obstacles are rarely explicitly discussed. Even if we had high resolution observations and their impact was discussed, unravelling the unconstrained movement patterns from the effect of the constraints would be very difficult. As a result care should be used in adopting statistical movement characteristics observed in one environment (open ocean, say) to a very different one (coastal ecosystems).

<sup>1</sup> This terminology may lead to the misleading conclusion that the 'mechanistic' processes are deterministic and algorithmic and that stochasticity belongs only to the statistical framework. Nevertheless, here we decided to adopt this terminology out of consistency with current literature.

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