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Research article

# Implicit assumptions underlying simple harvest models of marine bird populations can mislead environmental management decisions

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ABSTRACT

Assessing the potential impact of additional mortality from anthropogenic causes on animal populations requires detailed demographic information. However, these data are frequently lacking, making simple algorithms, which require little data, appealing. Because of their simplicity, these algorithms often rely on implicit assumptions, some of which may be quite restrictive. Potential Biological Removal (PBR) is a simple harvest model that estimates the number of additional mortalities that a population can theoretically sustain without causing population extinction. However, PBR relies on a number of implicit assumptions, particularly around density dependence and population trajectory that limit its applicability in many situations. Among several uses, it has been widely employed in Europe in Environmental Impact Assessments (EIA), to examine the acceptability of potential effects of offshore wind farms on marine bird populations. As a case study, we use PBR to estimate the number of additional mortalities that a population with characteristics typical of a seabird population can theoretically sustain. We incorporated this level of additional mortality within Leslie matrix models to test assumptions within the PBR algorithm about density dependence and current population trajectory. Our analyses suggest that the PBR algorithm identifies levels of mortality which cause population declines for most population trajectories and forms of population regulation. Consequently, we recommend that practitioners do not use PBR in an EIA context for offshore wind energy developments. Rather than using simple algorithms that rely on potentially invalid implicit assumptions, we recommend use of Leslie matrix models for assessing the impact of additional mortality on a population, enabling the user to explicitly define assumptions and test their importance.



## 1. Introduction

Globally, overexploitation is one of the main drivers of species extinction (Butchart et al., 2010; Hoffmann et al., 2010; Pimm et al., 2014). Conservation managers need to be able to assess whether too many individuals are being removed from a population, implementing appropriate remedial action if required. Frequently, this assessment is undertaken using population modelling approaches, such as Population Viability Analysis (PVA) (Beissinger and McCullagh, 2002) but these approaches require detailed knowledge of demographic rates, such as survival and productivity (Akçakaya and Sjögren-Gulve, 2000; Patterson and Murray, 2008; Reed et al., 2002). Obtaining accurate empirical demographic rates is not possible for many populations, especially those in need of conservation attention (Hernández-Camacho et al., 2015; Niel and Lebreton, 2005). Consequently, simple algorithms that require estimation of only a few demographic parameters have been developed for assessing sustainability of harvests (Milner-Gulland and Akçakaya, 2001). For example, Wade (1998) developed the Potential Biological Removal (PBR) algorithm for estimating the number of additional mortalities marine mammal populations can sustain. PBR is an approach designed to ensure that populations are maintained at, or restored to, an optimum sustainable population size, to meet legal requirements under the US Marine Mammal Protection Act (MMPA) (Cooke et al., 2012). This model requires knowledge of only two parameters, maximum population growth rate and population size. Recognising that estimation of a population's maximum growth rate can be challenging, PBR was adapted to use estimates of adult survival and age

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at first breeding to infer maximum population growth rate (Dillingham and Fletcher, 2008; Niel and Lebreton, 2005). The simplicity of this model and requirement to estimate only three demographic parameters (adult annual survival rate, population size and age at first breeding) has led to its increasingly widespread use in other situations.

Seabirds are a taxon for which some key demographic rates, particularly in relation to survival of juvenile and immature age classes, are poorly understood (Croxall et al., 2012; Lewison et al., 2012). Consequently, PBR is an appealing algorithm to use when assessing whether additional anthropogenic mortality is sustainable for marine bird populations. Marine birds are susceptible to bycatch from the fishing industry and PBR has been used to assess whether bycatch mortality was sufficiently large to be driving observed population declines (Dillingham and Fletcher, 2011; Genovart et al., 2016; Tuck, 2011; Žydelis et al., 2009). Recently, PBR has also been widely deployed during Environmental Impact Assessments (EIA) across Europe, in an attempt to assess whether the impacts of offshore wind farm developments on protected marine bird populations are compliant with environmental legislation. PBR was developed such that when levels of anthropogenic mortality exceed the PBR value, depletion of the population is likely (Wade, 1998). It was never designed to evaluate whether a particular level of mortality from a single source, such as offshore wind developments, would ensure a population remained at a desirable size (Green et al., 2016). Despite this, PBR has been used in an EIA context for offshore wind development. Offshore wind developments in Europe have the potential to affect marine bird populations for which demographic information is frequently sparse or absent (Horswill and Robinson, 2015; Lewison et al., 2012). Consequently, PBR appears to offer an appealing and quick method for assessing whether potential offshore wind farm impacts are acceptable or not for these data-poor populations. It has been used in Germany (e.g. Busch and Garthe, 2016), Netherlands (e.g. Leopold et al., 2014; Poot et al., 2011), Denmark (e.g. NIRAS, 2016) and the UK (e.g. SMart Wind Ltd, 2013).

European directives (e.g. EIA Directive (85/337/EEC); Birds Directive (2009/147/EC); Habitats Directive (92/43/EEC)) require assessment of the effects of proposed developments on the environment. Offshore wind farms potentially impact seabird populations by causing direct mortality from collision with turbines and by indirect mortality and/or reduced productivity from changes in energy budgets caused by displacement from preferred habitat or the perception of a wind farm as a barrier (e.g. Dierschke et al., 2016; Drewitt and Langston, 2006; Furness et al., 2013; Garthe and Hüppop, 2004; Masden et al., 2009). Consequently, PBR, along with other approaches, has been used in Europe to determine whether a level of potential mortality from planned offshore wind farm developments is consistent with legal requirements to maintain or restore marine bird populations. Assessments that used PBR assumed that the proposed development would not have an adverse impact on protected bird populations if the anticipated additional mortality from the development was less than the PBR value (Busch and Garthe, 2016; Leopold et al., 2014; NIRAS, 2016; Poot et al., 2011). However, the simplicity of PBR is only achieved through multiple assumptions about the parameters that do not require estimation, such as most demographic rates and processes regulating population size. For example, productivity and immature survival rates are implicitly determined by the value for adult survival rate selected, based on allometric relationships, and productivity and adult survival are assumed to remain constant with age (Niel and Lebreton, 2005). These assumptions are rarely considered when using PBR in an EIA context.

PBR is a simple model based on harvest theory. It assumes that a population can compensate for additional mortality through a compensatory density-dependent response, i.e. that as population size is reduced, survival, immigration and/or productivity increases, leading to augmented population growth rates that can maintain the population at a particular size despite the additional mortality. The model identifies the theoretical maximum number of individuals that can be removed annually from a population, which will occur when the population is at its maximum population growth rate. This is equivalent to Maximum Sustainable Yield from harvest theory (Murphy and Smith, 1991; Wade, 1998). The harvest can be reduced to a more precautionary level through use of a recovery factor, *f*, normally in the range 0.1–1.0, to account for uncertainty in parameter estimates such as population size and to reduce the risk of inadvertent overharvesting (Dillingham and Fletcher, 2008; Wade, 1998).

Marine bird populations often exhibit density dependent regulation (Horswill et al., 2016). For example, smaller Northern gannet *Morus bassanus* colonies had higher per capita population growth rates than larger colonies (Davies et al., 2013; Lewis et al., 2001) and great skuas *Stercorarius skua* started breeding at a younger age in smaller colonies (Furness, 2015). However, even though a population has the theoretical potential to undergo density dependent increases, there are circumstances where a particular population may not be currently capable of exhibiting a compensatory density-dependent response to a decrease in population size. For example, the study population may be part of a meta-population and may act as a sink, e.g. an individual seabird colony may be insufficiently productive to be self-sustaining and may be dependent on immigration to remain at the observed population size (Bicknell et al., 2014). Consequently, the meta-population may be capable of exhibiting a compensatory density-dependent response at a broader spatial scale that the individual colony cannot (Frederiksen et al., 2005). Also, a reduction in available resources, e.g. a decrease in prey availability, will result in a decline in population size to a new carrying capacity but with no density dependent response possible as per capita resource availability will not have increased. Alternatively, the density dependent response may not be compensatory. For example, seabird populations can exhibit depensatory density dependence, also known as the Allee effect (Allee and Bowen, 1932; Stephens and Sutherland, 1999) where populations show a decrease in adult survival and/or productivity as population size decreases, as well as an absence of any relationship between population size and growth rates. In a review of density dependence in seabird populations, Horswill et al. (2016) found depensatory density dependence most frequently reported for populations of small gulls and terns where it was consistently attributed to increased predation at lower population sizes.

PBR has been used in multiple contexts beyond its original application (Wade, 1998). Here we examine use of PBR in an EIA context for assessing impacts of planned offshore wind developments on marine bird populations. When using PBR in an EIA context, practitioners do not generally consider whether the population of interest is capable of exhibiting a compensatory density dependent response to additional mortality. Instead, it is assumed that removing a number of individuals from a population each year that is less than the PBR-derived harvest will be 'sustainable' (e.g. Busch and Garthe, 2016; Leopold et al., 2014; NIRAS, 2016; Poot et al., 2011; SMart Wind Ltd, 2013). We use a Leslie matrix model to illustrate the consequences of the type and strength of density dependence and population trajectory differing to that implicitly assumed when using PBR to assess the sustainability of additional mortality. We also review previously published evidence on the consequences of not meeting other assumptions of the PBR algorithm and make recommendations on use of simple algorithms versus Leslie matrix models for assessing sustainability of harvests.