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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.

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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; Żydelis 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.

2. Methods

2.1. Potential biological removal

The Potential Biological Removal (PBR) algorithm was developed by Wade (1998) to estimate the number of additional mortalities that a population can sustain each year. It is estimated by:

$$PBR = \frac{1}{2}R_{max}N_{min}f \quad (1)$$

where R_{max} is the maximum intrinsic growth rate of a population, N_{min} is a conservative estimate of population size and f is a recovery factor between 0.1 and 1 (Wade, 1998). However, given the difficulty of estimating R_{max} , Niel & Lebreton (2005) suggested supplementing it with an estimate of the maximum annual population growth rate, λ_{max} , using:

$$R_{max} = \lambda_{max} - 1 \quad (2)$$

Niel and Lebreton (2005) used the principles of life history theory (Charnov, 1993) and the predictable relationship between maximum population growth rate, age at first reproduction and adult annual survival probability across species to estimate the maximum annual population growth rate:

$$\lambda_{max} \approx \frac{(s\alpha - s + \alpha + 1) + \sqrt{(s - s\alpha - \alpha - 1)^2 - 4s\alpha^2}}{2\alpha} \quad (3)$$

where, s is annual adult survival probability and α is the age at first reproduction (Niel and Lebreton, 2005). Using the three equations above, it is possible to estimate a value for PBR using only an estimate of population size (N_{min}), adult annual survival probability (s) and age at first breeding (α).

Black-legged kittiwake (*Rissa tridactyla*) was selected for testing PBR as it is a species thought to be negatively impacted by offshore wind farms (Dierschke et al., 2016; Furness et al., 2013; Garthe and Hüppop, 2004), it is a species for which demographic rates are relatively well known (e.g. Coulson and White, 1959; Frederiksen et al., 2005, 2007; Horswill and Robinson, 2015; Oro and Furness, 2002) and breeding colonies around the UK exhibit differing trends including stable and declining (JNCC, 2016). PBR was used to estimate a sustainable harvest for a theoretical population of kittiwakes, with age at first breeding of four and maximum annual adult survival probability of 0.911 (Frederiksen et al., 2004). As recommended by Dillingham and Fletcher (2008), this highest published value for adult survival was used, rather than a mean value (Horswill and Robinson, 2015) as was used in the Leslie matrix model below. Dillingham and Fletcher (2008) recommend using the maximum annual adult survival probability as, in their adaptation of PBR, adult survival is negatively correlated with maximum population growth rate. Life history theory predicts that species with high adult survival will have low productivity and low maximum population growth rate (Charnov, 1993). Consequently, Dillingham & Fletcher (2008) make the precautionary recommendation of using the highest plausible estimate of adult survival probability to ensure that the PBR estimate is derived from the lowest plausible maximum population growth rate. The theoretical colony was arbitrarily assumed to comprise 12 000 individuals. The PBR algorithm uses a value for population size, N_{min} , which is defined as the 20th centile of the estimated population size (Dillingham and Fletcher, 2008; Wade, 1998). For this study, N_{min} was estimated at 10000 individuals. This was informed by the variance estimated around kittiwake population sizes in the UK (JNCC, 2016). The recovery factor, f , was allowed to vary between

0 and 1 in increments of 0.1. The PBR value was used to set a fixed annual harvest. This number of individuals was harvested each year from the theoretical kittiwake population.

2.2. Matrix model

A deterministic age-structured Leslie matrix model was used to quantify the change in population size through time, with an annual PBR-derived harvest. Parameters used in the population models were drawn from the literature and are presented in Table 1. The model was structured as a post-breeding census, with the first age class comprising the number of birds that fledged per breeding individual that calendar year. Starting with a stable age distribution, the model was projected over 25 years. This time period was selected as this is the standard anticipated duration of operation for offshore wind farms in the UK and the typical period over which offshore wind farm impacts are assessed for marine bird populations (e.g. WWT Consulting, 2012). Models were run assuming stable, increasing and declining population trends (Table 1).

Density-dependence was incorporated into some model scenarios, such that productivity varied with population size following the Weibull function, which was found to be a realistic function for a range of seabird species (Cury et al., 2011):

$$D = \max D \cdot \exp(-a \cdot N^b) \quad (4)$$

where, D is productivity, $\max D$ is the biologically plausible maximum value for this parameter, N is the population size, a is a scale parameter and b is a shape parameter. To test how the PBR-derived harvest affected population size in relation to compensatory or depensatory density dependence the shape parameter (b) was initially set as 1 or -1, respectively. A total of nine population models were run, for combinations of increasing, stable and declining populations with compensatory density dependence, depensatory density dependence and no density dependence.

The strength of the density dependent relationship may also influence how the PBR-informed harvest affected population size through time. To investigate this, assuming a population subject to compensatory density dependence, we considered values of b ranging from 0.5 to 1.5 in increments of 0.25, a plausible range for seabird populations (Cury et al., 2011).

2.3. Harvest model

The PBR-informed harvest was applied only to the adult age class, following breeding each year. For each value of f (0–1 in 0.1 increments), a PBR-informed harvest was derived. For each of the nine population models described above, PBR-informed harvests based on each of the 11 values of f were considered, giving a total of 99 model scenarios.

Whilst PBR can be used in an adaptive management context to vary annual harvests informed by previous population sizes, in an offshore wind farm EIA context it is generally used to identify a single harvest, based on recent population size. The harvest is presumed to be mortality from bird collisions with wind turbines causing individuals to be 'removed' from the population. Therefore, to be representative of the way in which PBR is used in an EIA context, we removed a PBR-informed constant number of individuals from the modelled population each year, irrespective of population size.

3. Results

From a population of 12 000 kittiwakes, the PBR algorithm

Table 1
Demographic parameters used for each model scenario prior to PBR-informed harvests being removed from the modelled population. Models assume a starting size of 12 000 individuals, age at first breeding of 4 and a sex ratio of 0.5. Adult survival was taken from mean values presented in Horswill and Robinson (2015). Immature survival was assumed to be equal to adult survival. Juvenile survival was taken from Coulson and White (1959). Productivity was based on a range of values presented in Mavor et al. (2008). Growth rate was derived from a deterministic population model using presented demographic parameters and run over 25 years.

		Adult Survival	Immature Survival	Juvenile Survival	Productivity	a	b	Growth Rate
Density Independent	Increasing	0.86	0.86	0.79	0.70	—	—	1.02
	Stable	0.86	0.86	0.79	0.56	—	—	1.00
	Declining	0.86	0.86	0.79	0.44	—	—	0.98
Density Dependent (compensatory)	Increasing	0.86	0.86	0.79	0.85	5.6×10^{-5}	1	1.02
	Stable	0.86	0.86	0.79	0.56	9.8×10^{-5}	1	1.00
	Declining	0.86	0.86	0.79	0.30	1.6×10^{-4}	1	0.99
Density Dependent (depensatory)	Increasing	0.86	0.86	0.79	0.62	8835	−1	1.02
	Stable	0.86	0.86	0.79	0.56	9852	−1	1.00
	Declining	0.86	0.86	0.79	0.44	12264	−1	0.94

yielded values for a potential sustainable harvest of between 59 ($f = 0.1$) and 597 ($f = 1.0$) individuals (Table 2).

The presence and form of density dependence acting on a population makes a substantial difference to the way in which the population will respond to additional mortality, as does population status (Fig. 1). Annual removal of a PBR-derived harvest from a population is frequently not sustainable over a 25 year projection (i.e. populations were continuing to decline after 25 years of harvesting), particularly when populations are already declining (Fig. 1).

If a population is already declining (Fig. 1c, f and i), then no matter what form of population regulation operates on that population, the additional mortality will be too much for the population and will cause a further decline. If the population exhibits a depensatory density dependent response, then that decline is accelerated and may lead to extinction within 25 years for larger harvests (i.e. larger values of f) (Fig. 1i). Compensatory density dependence does allow population growth rate to increase and this enables the population size to stabilise, albeit at a smaller population size of around approximately 40–60% of starting population size (Fig. 1f).

Stable populations also exhibit a decline below starting population size (Fig. 1a, d and g) but the decline is smaller than for populations that were declining prior to additional mortality. Unsurprisingly, both the density independent (Fig. 1a) and depensatory density dependent (Fig. 1g) scenarios show population trajectories that were still declining after 25 years and so could not be described as ‘sustainable’. Only the scenario with compensatory density dependence (Fig. 1d) appears to be sustainable, with the population stabilising at population sizes around approximately 70–95% of starting population size.

Populations that were increasing prior to additional mortality (Fig. 1b, e and 1h) generally continue to increase, except for the largest PBR-derived harvests with values for f close to 1. Note that

an increasing population is very unlikely to exhibit a depensatory density dependent response (Fig. 1h) unless a large additional mortality is imposed on the population causing the population to start to decline (e.g. largest values of f in Fig. 1b), at which point depensatory density dependence could accelerate that decline.

The strength of the compensatory density dependent response a population can exhibit is implicitly determined within PBR as a function of the point of maximum population growth rate in relation to population size. However, Fig. 2 illustrates that this also strongly influences population size after 25 years and hence sustainability of a PBR-derived harvest.

When the value for f is fixed, e.g. at $f = 0.5$ and strength of density dependence, b , is varied (Fig. 2c), the range in population size at 25 years is 1806 adults (from 5878 to 7684 adults). However, when the value for b is fixed, e.g. at $b = 1$ and f is varied (Fig. 2a, b, and c), then the range of population sizes at 25 years is nearly halved at 1006 adults (from 6883 to 7889 adults). In the case of the modelled kittiwake population, population size after 25 years was more strongly influenced by the strength of density dependence than the value selected for the recovery factor, f . The value for f selected interacts with the strength of density dependence, b , with higher values of f causing the strength of density dependence to result in a wider spread of final population sizes than for smaller values of f . Importantly, for smaller values of b , population trajectories show no indication of stabilising after 25 years and so could not be deemed sustainable, irrespective of the value of f selected. The density dependent response moderated or stopped population declines around 10–15 years for most values of b , once the increase in productivity caused by the density dependent response was recruited into the breeding population.

4. Discussion

Contrary to what has been previously presumed in many environmental impact assessments for offshore wind developments, removing a PBR-informed number of individuals from a population each year can cause population decline. The likelihood of a PBR-derived harvest causing a decline is strongly dependent upon the type of population regulation, the strength of any compensatory density dependence, population status and, to a lesser extent, the recovery factor value selected. When using PBR in an EIA context, a planned development is often presumed to have an acceptably small impact on a bird population so long as predicted additional mortality caused by the development was less than the PBR-derived harvest, irrespective of population status and processes regulating population size. Here we have demonstrated that this presumption is rarely true.

Our analyses demonstrated that the suitability of PBR as a tool in the EIA process for assessing impacts on marine bird populations is

Table 2
PBR values (number of individuals that can be removed from a population each year) derived from $N_{\min} = 10\,000$; $s = 0.911$; $\alpha = 4$, for a range of f values.

Recovery Factor (f)	PBR value (number of individuals)
0	0
0.1	59
0.2	119
0.3	179
0.4	238
0.5	298
0.6	358
0.7	418
0.8	477
0.9	537
1.0	597

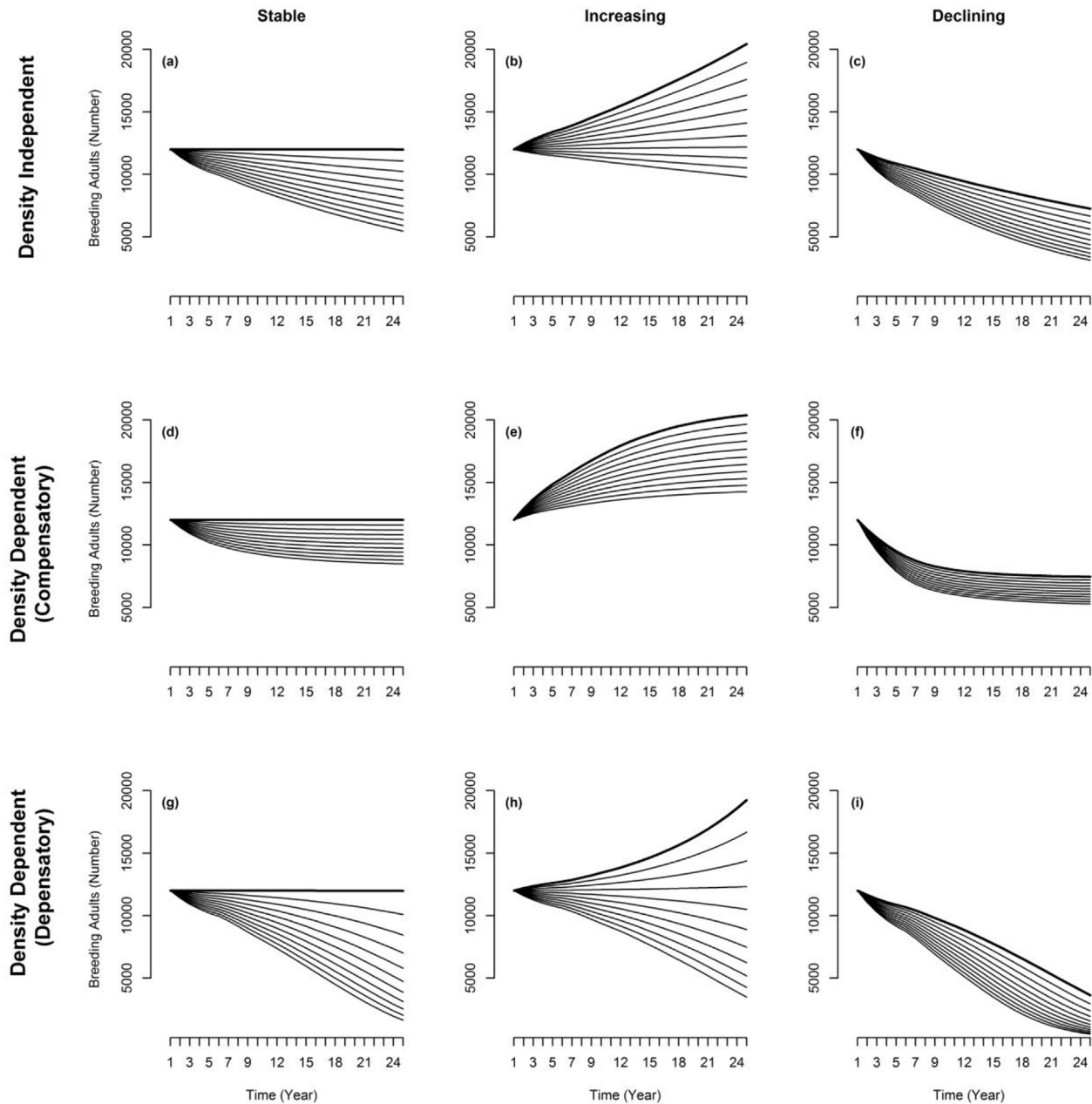


Fig. 1. Population size (number of adults) of the theoretical kittiwake population through time (year) in the presence of a PBR-derived annual harvest (see Table 1), with f varying from 0–1 in 0.1 increments. Each trajectory in the plots corresponds to a different value for f , the highest trajectory (dark line) for $f = 0$, the lowest trajectory for $f = 1$. Population status was stable, increasing or declining and population regulation was through compensatory or depensatory density dependence or was density independent.

strongly linked to the trajectory of the population under consideration and the form of any regulation present. When applied to a declining population, a PBR-derived annual harvest will initially cause further decline, although this may be mitigated by the presence of compensatory density dependence. Consequently, where conservation management objectives are to maintain or restore a population there is little point using PBR, or any other population modelling approach, to conclude that additional mortality will only accelerate the rate of decline. Where populations are increasing, they may continue to increase in the presence of additional mortality, except in the case of PBR-informed harvests derived using large values for the recovery factor. In the case of stable populations, applying a PBR-derived annual harvest will generally cause population decline although the population may

stabilise at a smaller population size, depending on the form of population regulation operating.

We found that the strength of any density dependent processes operating on a population may influence future population size more strongly than the recovery factor, f . However, whilst clear guidance is given as to how to select values for f (e.g. Dillingham and Fletcher, 2008), the strength and form of any density dependent process operating on the population in question is rarely considered (Green et al., 2016). Consequently, an important determinant of whether or not a PBR-derived harvest will actually be sustainable is largely ignored. Our analyses demonstrate how the values selected for f interact with the strength of density dependence, such that when higher values of f are used, differing strengths of density dependence result in a wider spread of final

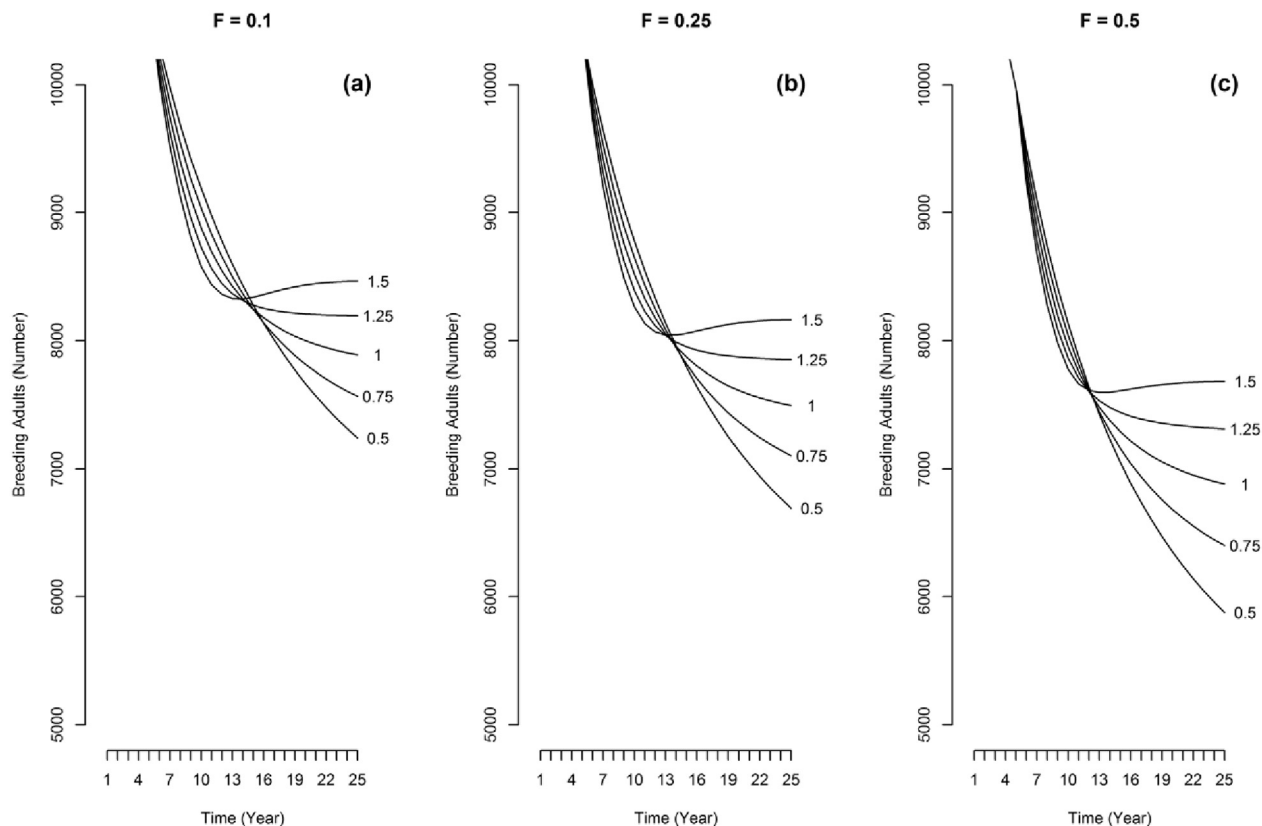


Fig. 2. Population size (Number of Breeding Adults) through time (Year) with varying strengths of density dependence in relation to f values of (a) 0.1, (b) 0.25 and (c) 0.5. Values for the shape parameter b associated with each population trajectory are given. Initial populations were assumed to be stable and subject to compensatory density dependence.

population sizes than for smaller values of f . As a result, where larger values of f are selected, for example in the case of strongly increasing populations, it is more important to understand the strength of the density dependent relationship operating on the population. Where weaker density dependent processes operate on the population, trajectories may not stabilise over the lifetime of a project and so could not be deemed sustainable, regardless of the value assumed for f .

Whilst both the trajectory of the population under consideration and the form of any density dependent processes operating can strongly influence the sustainability of PBR-informed harvests, both parameters may also be subject to significant uncertainty. A recent analysis of seabird population trends highlighted widespread gaps in the availability of census data for many species (Palczyński et al., 2015). This is true, even in countries like the UK which have well-established seabird monitoring programmes; the cost associated with carrying out regular, whole population censuses means that there is often limited data with which to assess colony-level population trends for many species (JNCC, 2016). Similarly, a recent review of density dependence in seabirds (Horswill et al., 2016) revealed a broad range of relationships, which may be situation-specific. As a result, it is difficult to determine the impact that any PBR-derived harvest may have at a population level, in an EIA context. Of course, data deficiencies are also an issue when using Leslie matrix models (Radchuk et al., 2016) but, unlike PBR, it is possible to explicitly consider the most appropriate assumptions to make about population trajectory and regulation. Additionally, matrix models provide estimates of future population size in the presence and absence of additional mortality, which PBR does not. Our analyses illustrate that it cannot be presumed that applying a harvest smaller than that identified by PBR to any population will

ensure that population size remains within management objectives.

4.1. Other considerations when using PBR in an EIA context

It is important to consider whether management objectives for the populations under consideration match those implicit in PBR. PBR originates in the US Marine Mammal Protection Act (MMPA) (16 U.S.C. 1361), which required that marine mammal populations should not be permitted to diminish beyond the point at which they cease to be a significant functioning element of the ecosystem, taken to be 50–85% of carrying capacity (Wade, 1998). In contrast, the EU Birds Directive (2009/147/EC) requires classification of Special Protection Areas (SPA) for certain bird populations and that the SPAs are managed to enable the protected populations to maintain themselves on a long-term basis as a viable component of their natural habitats (Epstein et al., 2015). In the UK, this is often presumed to mean restoring or maintaining a population at a size similar to that at the time of protected site classification. Management objectives that are implicit in PBR may differ markedly from those in other conservation management contexts; if these aren't given adequate consideration, application of a PBR-informed harvest may result in desired management objectives not being met.

The PBR algorithm can indicate whether a particular level of mortality would enable a population to recover to a population size defined by a management objective (Wade, 1998) but only if all additional mortality is compared with the PBR-derived harvest. In the case of marine birds and offshore wind farms, this may include additional mortality arising from pressures including: other marine renewables developments, bycatch from commercial fisheries, hunting, and pollution (Merkel et al., 2016; Provencher et al., 2017;

Votier et al., 2005; Žydelis et al., 2009). However, when estimating the threshold for the PBR-derived harvest, the survival rate used should exclude these additional anthropogenic sources of mortality (Dillingham and Fletcher, 2008). Furthermore, mortality needs to be of a harvest type that does not affect resource availability. When marine birds are displaced from an area due to construction of an offshore wind farm, the consequent habitat loss is likely to reduce carrying capacity, thereby reducing per capita resource availability and so removing the ability of the population to exhibit a compensatory density-dependent increase in population growth rate. Thus, PBR cannot be used to assess the potential impacts of displacement on marine bird populations.

The adaptation to the initial PBR algorithm (Wade, 1998) by Niel and Lebreton (2005) means that lower estimates of survival yield higher estimates for the PBR-derived harvest (Dillingham and Fletcher, 2008). Consequently, by incorporating estimates of survival which already account for the additional mortality, sustainable harvesting levels are likely to have been over-estimated. In reality, acquiring an estimate of adult survival that is unaffected by anthropogenic mortality is unfeasible, although use of a small recovery factor accommodates uncertainty around adult survival rate (Dillingham and Fletcher, 2008; Wade, 1998).

The recovery factor, f , is a subjective parameter that the user must define, yet it can influence the PBR-defined harvest by a factor of 10. Wade (1998) recommend using a value of $f = 0.5$ to accommodate uncertainty in parameter estimates and Dillingham and Fletcher (2008) related values of f to the IUCN status of a population, using $f = 0.5$ for least concern, $f = 0.3$ for near threatened and $f = 0.1$ for threatened species (IUCN, 2001). Whilst the recovery factor is a subjective variable, it is at least an explicitly user-defined parameter, whereas other factors that strongly influence the size of a PBR-defined harvest, such as strength of density dependence, are not explicitly defined.

The consequences of applying inappropriate conservation management measures informed by misuse of PBR will be context-dependent. For example, using PBR in an adaptive management context as is done for deriving an annual cull for Scottish seal populations, where the PBR value is regularly updated, dependent on recent population counts and trends (Thompson et al., 2016) will carry minimal risk. If an incorrect value for PBR is used, the seal population will respond and a new higher or lower value for PBR can be selected in subsequent years. However, the risk of PBR misinforming appropriate management action causing undesirable outcomes increases in other applications, where it is not possible to directly alter mortality on an annual basis, such as for offshore wind farm developments.

4.2. Limitations of the approach we have used here

The highest published estimate for black-legged kittiwake adult survival (Frederiksen et al., 2004) was used to estimate the PBR-informed harvest whereas a mean value for adult survival (Horswill and Robinson, 2015) was used in the Leslie matrix model. As noted by Dillingham and Fletcher (2008), Niel and Lebreton's (2005) adaptation of PBR leads to an increased PBR-informed harvest when lower estimates of adult survival are used. Consequently, to avoid overestimating PBR, it is important to use the highest known estimate of adult survival. Leslie matrix models, however, have a positive relationship between adult survival and population growth rate and so use of a mean estimate is recommended. By using different values for adult survival, our results will tend to underestimate the negative consequences of using a PBR-informed harvest on future population size.

PBR was developed to indicate the maximum level of additional mortality a population can withstand while recovering to a desired

population size and management target (Wade, 1998). In our simulations, we harvested the theoretical kittiwake population at the PBR-derived harvest rather than a smaller harvest, less than the PBR value. Consequently, our findings may slightly exaggerate the declines that would occur in a population if a harvest smaller than the PBR value was taken annually. Additionally, density dependence was assumed to follow the Weibull function but other forms of density dependence might slightly alter the impact of a PBR-derived harvest on a population. These limitations do not alter the conclusions that PBR is not generally a suitable tool for use in EIA for offshore wind farm developments and potentially in other settings too.

5. Conclusions

PBR is a simple algorithm that is easy to apply and, when used correctly, offers a quick assessment tool to assist conservation managers. When the assumptions of PBR are met, it can be a useful tool to indicate whether a single source of mortality is likely to be the primary driver of population declines or whether other sources of mortality are also likely to be contributing, allowing targeted conservation action. For example, for marine birds, PBR can be used to assess whether an observed population decline can be entirely attributed to by-catch mortality or is likely to be due to multiple potential sources of mortality (Dillingham and Fletcher, 2011; Milner Gulland and Akçakaya, 2001; Žydelis et al., 2009). However, we have demonstrated that PBR should not be used in an EIA context, to avoid drawing false conclusions about the potential impact of planned offshore wind developments. PBR was never designed to identify a level of harvest that would enable populations to be maintained at their current size.

Whilst PBR cannot be used in an EIA context for assessing offshore wind development impacts, it can be used in other contexts. When using PBR, we recommend the following:

1. PBR should be used at a broad biological scale which encompasses meta-population processes, as the wider population is much more likely to be capable of exhibiting compensatory density dependence than individual colonies.
2. It is important to assess all sources of additional mortality against the PBR-derived harvest (Žydelis et al., 2009).
3. All additional mortality needs to be of the form of removal of individuals from a population without altering per capita resource availability (e.g. bycatch, hunting) rather than indirect mortality caused by reduced carrying capacity (e.g. reduction in prey availability, displacement from an offshore wind farm development site) (but see Moore (2013) for a suggested approach to incorporating indirect mortality into PBR).
4. The highest possible value for adult survival should be used, ideally an estimate obtained prior to major anthropogenic impacts (Dillingham and Fletcher, 2008).
5. Management objectives need to be compatible with those implicit within PBR, i.e. aiming to maintain a population at around 50–85% of carrying capacity, dependent on the value for the recovery factor that is selected and the strength of density dependent response (Cooke et al., 2012; Wade, 1998).

Ideally, PBR should only be used to undertake a retrospective qualitative assessment of whether current mortality that is driving an observed population decline is likely to be due to a single source or multiple sources (e.g. Dillingham and Fletcher, 2011; Genovart et al., 2016; Žydelis et al., 2009). PBR can also be used in an adaptive management context, where the risks of inappropriate management action from incorrect use of PBR are mitigated through the ability to reduce or increase mortality rates in the near future, e.g.

to control of an increasing population of a pest species (Runge et al., 2009). Generally, in agreement with Green et al. (2016), we do not recommend use of PBR in an EIA context (which includes Habitat Regulation Assessment in the UK) to define a level of future additional mortality a protected population can sustain.

Simple algorithms, such as PBR, are appealing to conservation managers as they require little data to parameterise them (Milner-Gulland and Akçakaya, 2001). However, these algorithms will depend on multiple assumptions about other population parameters that are not explicitly defined. So long as all these other assumptions are clearly defined and are met and these simple algorithms are applied in the correct way, these tools offer a quick and simple approach to informing conservation management. However, these implicit assumptions can easily be overlooked leading to erroneous conclusions and, potentially, inappropriate conservation management actions. Additionally, meeting these assumptions can be challenging, e.g. in the case of PBR, it is difficult to be confident of population status and processes regulating population size. Rather than using these algorithms with implicit and non-transparent assumptions, we recommend using simple Leslie matrix models to undertake Population Viability Analysis (e.g. Brook et al., 2003; Horswill and Robinson, 2015; Thompson et al., 2000). Whilst matrix models do require the user to specify demographic rates and population processes, where these are not known the user can make explicit assumptions about these rather than that being implicitly assumed within the algorithm framework (Cook and Robinson, 2016). Whilst making these explicit assumptions, the user can consider the validity of each assumption and ensure they are realistic for that particular context, unlike the implicit assumptions of the simple algorithms. Crucially, these assumptions can, and should, be presented in a way which is transparent and can be discussed with all stakeholders.

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