

Extreme disturbances show greater influence on dolphin populations: A simulation approach

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Declaration

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All other research described in this report is my own original work.

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Abstract: In South Australia, discrete populations of bottlenose dolphins inhabit two large gulfs, Spencer Gulf and Gulf St Vincent. In each gulf, dolphin population abundance has been estimated and key threats; climate change, habitat disturbance (shipping and noise pollution), fishery interactions and epizootic events, identified. The Population Consequences of Disturbance (PCoD) framework was developed to understand how disturbances can influence population dynamics. We used population estimates combined with population specific bioenergetics models to undertake a PCoD assessment and compared how these two populations respond to the identified regional threats. Populations were modelled over a five year period looking at the influence of each disturbance separately. As expected, extreme disturbance scenarios, in terms of frequency and intensity, had the biggest influence on population trends. However, the magnitude of the effect differed by population, with Spencer Gulf showing a 43% and Gulf St Vincent a 23% decline under high frequency and high impact epizootic scenarios. Epizootic events had the largest influence on population trends and reproductive parameters for both populations, followed by climate change. Modelling provides insight into how disturbances may affect different population, and so informs management on how best to mitigate their potential effects while there is still time to act.

Key Words: Bioenergetics, marine mammals, disturbances, Bayesian modeling, fecundity, population trends.

1. Introduction

Anthropogenic activities have been shown to affect all marine ecosystems, with temperate and tropical coasts seeing the biggest increase in these activities (Halpern et al., 2007; Halpern et al., 2008; Halpern et al., 2015). In these coastal regions there are a multitude of disturbances to populations that arise from for example climate change, shipping and boat traffic, fishing, and coastal development. Such disturbances have been shown to impact marine populations and ecosystems globally (Stock et al., 2018), including Australia (Robbins et al., 2017). For example, climate change, and the production of greenhouse gases that causes it, can affect ecosystems leading to rises in sea temperatures, increases in ocean acidity and changes in primary productivity (Barnett et al., 2001; Hegerl and Bindoff, 2005; Behrenfeld et al., 2006; Hoegh-Guldberg and Bruno, 2010). Furthermore, the destruction of marine habitats, over exploitation, and bycatch of non-target species resulting from fishing activities can be deleterious to populations (Kraus and Diekmann, 2018; Tulloch et al., 2019). Shipping may result in direct physical disturbances such as ship strikes, or indirect disturbances such as chemical and noise pollution, with the latter manifest in behavioral changes or induction of chronic stress to marine mammals (Rolland et al., 2012; Pirotta et al., 2019). Anthropogenic activities that lead to disturbances of organisms living in coastal environments are likely to increase in the future (Halpern et al., 2015).

Southern Australia is an area rich in biodiversity providing key habitat, breeding and/or foraging grounds for many marine species including key mesopredators such as common (*Delphinus delphis*) and bottlenose dolphins (*Tursiops* spp.) (Bilgmann et al., 2014; Pratt et al., 2018). Embayment's, including large gulfs, provide a relatively stable environment that may be used by dolphins either seasonally or year round (Stockin et al., 2008; Best et al., 2012; Filby et al., 2013; Mason et al., 2016). South Australia's coastline features two large gulfs, Spencer Gulf and Gulf St Vincent which coincide with human conurbations and so are where most human activities occur (Wolanski and Ducrotoy, 2014). Recently, systematic aerial line-transect surveys conducted in South Australia including Spencer Gulf and Gulf St Vincent, provided abundance estimates for bottlenose dolphins in each of these gulfs (Bilgmann et al., 2019). The gulf waters provide habitat for two geographically separated and genetically distinct populations of coastal bottlenose dolphins (*Tursiops* cf. *australis*), one in each gulf (Bilgmann et al., 2007b; Pratt et al., 2018). Coastal dolphins, including these two gulf populations, are exposed to a number of anthropogenic threats, which has raised concerns that these may lead

to population declines (Filby et al., 2017). An expert elicitation conducted for 38 threatened, protected and iconic marine-associated species in Spencer Gulf suggested that the key disturbances that affect bottlenose dolphins in Spencer Gulf were climate change, boat traffic, coastal modification and activities, and fishing (Robbins et al., 2017). Epizootic events, such as cetacean morbillivirus (CeMV) have also occurred in the area, and epizootics are an issue facing marine mammals globally and have been linked to extreme temperature events (Van Bresse et al., 2014; Kemper et al., 2016). Combining these estimates of abundance, population structure, and anthropogenic disturbance makes it possible to use simulations to predict whether these disturbances may be of sufficient severity to affect bottlenose dolphin populations in South Australia in the near future.

Bottlenose dolphins (*Tursiops* spp.) are one of the most common species of marine mammals globally (Leatherwood and Reeves, 1990; Connor et al., 2000). They occur in temperate to tropical waters and are ubiquitous in coastal and pelagic environments (Connor et al., 2000). To date there are two species of bottlenose dolphin recognized worldwide, the common bottlenose dolphin (*Tursiops truncatus*), which occurs across the distribution range and are of medium size (2.5-3.8m) (Montagu, 1821; Wells and Scott, 2009); and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), which occurs in coastal waters in the Indian and western Pacific Oceans and is smaller (2.7m) than *T. truncatus* (Ehrenberg, 1833; Wang, 2018). Recent genetic work from Australia has suggested there may be a third species occurring in coastal waters in southern Australia, colloquially known as the Burrunan dolphin (*Tursiops cf. australis*) however this classification remains contentious (Charlton-Robb et al., 2011; Moura et al., 2013; Perrin et al., 2013; Charlton-Robb et al., 2015; Pratt et al., 2018). Crucially for the efficacy of this study, there are no obvious demographic or morphological features distinguishing Burrunan dolphins from Indo-Pacific bottlenose dolphins.

Bottlenose dolphins are highly social, with coastal populations occurring in groups of 2-50 individuals, and offshore populations seen in large aggregations of hundreds of individuals. These groups inhabit fission-fusion societies in which individuals join and leave groups regularly over the course of their lives (Möller, 2012). Individuals produce a single calf after a 12-month gestation period which is dependent on its mother for approximately three years (Table 1) (Perrin and Reilly, 1984; Wells and Scott, 1999; Mann et al., 2000; Kogi et al., 2004; Wang and Yang, 2009). According to the International Union for Conservation of Nature (IUCN) Red List, *T. truncatus* is listed as a species of least concern due to its large range, while

T. aduncus is listed as data deficient (Hammond et al., 2012a; Hammond et al., 2012b). Though bottlenose dolphins are globally abundant, the pressures on populations vary, with some occurring in areas of high human activity. Interactions between humans and dolphins range from hunting for meat and oils, capture for aquaria as a popular entertainment attraction, to ecotourism activities such as dolphin watching and swim with dolphin programs (Frohoff and Packard, 1995; Bejder et al., 2006; Wells and Scott, 2009; Steckenreuter et al., 2011; Steckenreuter et al., 2012; Wang, 2018). Besides these directed interactions with humans, bottlenose dolphins are also indirectly influenced by other human activities including increased competition for prey resources, bycatch, spread of epizootic events, as well as noise pollution all of which have been shown to affect population structure and size and induce behavioral changes (Chilvers and Corkeron, 2001; Kemper and Gibbs, 2001; Bejder et al., 2006; Kemper et al., 2016; Zanardo et al., 2017). With populations under increasing pressure from anthropogenic disturbances, informed management decisions may aid in the development of marine protected areas, species management, and the identification of key threats to populations to help mitigate negative impacts of disturbance. In Spencer Gulf, for example, industrial development has been forecasted to increase, thus it is important to assess the ongoing effects of anthropogenic threats to resident species (Robbins et al., 2017).

Bottlenose dolphins have been shown to be generalist, opportunistic predators allowing them to be flexible with prey availability and they may employ a number of foraging tactics based on ecological conditions (Giménez et al., 2017). The availability of food in a region has been shown to be important for the continued presence of dolphins, especially when experiencing high levels of disturbance (Bearzi et al., 2008). Stomach content and stable isotope analysis have shown that the diet of bottlenose dolphins largely consists of bony fishes and cephalopods (Amir et al., 2005; Giménez et al., 2017), including the two populations of the South Australian gulfs (Gibbs et al., 2011). Studies from captive *T. truncatus* have reported that an average adult bottlenose dolphin eats roughly 1900 kg of food per year, with food requirements for calves increasing rapidly until the age of three where it plateaus (Kastelein and Wiepkema, 1997; Kastelein et al., 2002; Kastelein et al., 2003). In studies from captive animals, there was no observed rise in food intake during pregnancy of individual dolphins, but during lactation there was an increase, especially during the first six months (Kastelein and Wiepkema, 1997; Kastelein et al., 2002; Kastelein et al., 2003). Estimating the food intake of an animal and the energy content of its prey items can provide us with an estimate of the energy requirements for this animal, and this can be extended to an entire population (Barros and

Wells, 1998; Gibbs et al., 2011; Bejarano et al., 2017; Giménez et al., 2017). Information on the rate of food intake of bottlenose dolphins in the wild is limited, but can help estimate their carrying capacity in the environment they inhabit, individual and population energy requirements and interaction with anthropogenic activities such as fisheries (Kastelein and Wiepkema, 1997). With increasing fishing pressures in many coastal environments, declines in megafauna populations, including dolphins, have been seen and attributed to increased competition for food, entanglement, and boat strikes (Bearzi et al., 2006; Bearzi et al., 2009). Understanding information on demographic traits, energy requirements, food availability, and energy expenditure can help provide information on the bioenergetics requirements of a population which can be used to apply the Population Consequences of Disturbance (PCoD) framework (New et al., 2014; Pirota et al., 2018a) to build a model to assess the impacts of disturbance on a population.

The PCoD framework was designed specifically for marine mammals, and with its applications covers a range of disturbances and species (Pirota et al., 2018a). The PCoD framework originated as a way to assess the impacts of noise on marine mammals, known as the Population Consequences of Acoustic Disturbance (National Research Council, 2005). The original model was used to assess noise pollution such as that produced by shipping and naval seismic tests, and how these might impact a population in terms of the reduced fitness of individuals (Costa, 2012). The framework was modified to include other types of disturbance, individual's physiology, acute and chronic effects of disturbance, and individual health, resulting in the development of the PCoD framework (Schick et al., 2013a; Schick et al., 2013b; New et al., 2014). Early PCoD studies included a report of how changes in lipid mass of southern elephant seals (*Mirounga leonina*) could be used as a measure of the effects of environmental change on individuals and subsequent population dynamics. The model suggested that with increased disturbance came a reduced maternal lipid mass, leading to decreased weaning mass of pups, and a subsequent change in pup survival that would have the potential to impact the population dynamics (New et al., 2014). Conversely, bottlenose dolphins from Moray Firth in Scotland were not shown to suffer adverse effects from up to a six-fold increase in boat activity, with no change to spatial distribution, time budget or social structures (New et al., 2013). More recently PCoD has been used to show that a 30% reduction in energy acquisition in foraging grounds for gray whales (*Eschrichtius robustus*) could lead to a reduction in calf survival and fitness resulting in declines in population growth for an already critically endangered population (Villegas-Amtmann et al., 2017). It is clear that the

PCoD framework can provide valuable insights into the level of impact a disturbance could have on a population, as well as show when populations are robust to withstand impacts from disturbances.

The majority of PCoD models have used an individual energy store as a measure of health, either adopting a bioenergetics approach (Christiansen and Lusseau, 2015; Beltran et al., 2017; McHuron et al., 2017; Farmer et al., 2018) or through the use of arbitrary scaled metrics (Nabe-Nielsen et al., 2014; Pirotta et al., 2014; Pirotta et al., 2015; Pirotta et al., 2018a). Bioenergetics provide a conceptually simple tool to assess the energy requirements of both individuals and populations, and how changes in food availability or loss of foraging can influence an individual's energy store and thus their ability to support essential life functions (McHuron et al., 2017; Villegas-Amtmann et al., 2017; Pirotta et al., 2018a; Pirotta et al., 2018b). Energy is required by all organisms, and all have evolved different strategies and trade-offs in order to acquire energy for maintenance, activity, growth, and reproduction (Iverson et al., 2010).

Marine mammals are a particularly difficult group in which to study energetics due to the inaccessible nature of their habitat, even when nearshore, and for some species also because of their large body size. The high proportion of blubber, which provides insulation as well as energy stores, makes it difficult to effectively calculate metabolic rates due to its changes in thickness and composition at different life stages and ages (Struntz et al., 2004; Iverson et al., 2010). Basal metabolic rate (BMR) is defined as the amount of energy required for maintenance by a post-absorptive, thermally neutral individual at rest, with studies on both terrestrial and marine organisms showing a linear relationship between the lean mass of the organism and the amount of energy required (Kleiber, 1947; 1975). BMR is a less useful measure for totally aquatic marine mammals due to their high blubber content and their aquatic existence. However, with the addition of a species and population specific multiplier, BMR can provide an accurate estimate of an individual's field metabolic rate (FMR), or the energy required by a free living, active individual (Boyd and Hoelzel, 2002; Iverson et al., 2010; Costa and Maresh, 2018). Metabolic efficiency is the amount of energy that remains and can be used by an individual after accounting for fecal and urinary loss and indigestibility, in endotherms this energy is acquired through the ingestion of food (Boyd and Hoelzel, 2002; Iverson et al., 2010). Individuals also have additional energy requirements during reproduction, in particular females during lactation who must provide a lipid-rich milk to their offspring to aid the calf's increased

energy acquisition and promote growth (Costa and Maresh, 2018). For bottlenose dolphins, there is no direct measure for the increase in energy requirements due to lactation. However, estimates have been made of higher food intake for lactating females compared to non-lactating females, with values of a 48-86% increases in energy expenditure during lactation (Cockcroft and Ross, 1990a; Cheal and Gales, 1991; Kastelein et al., 2002; Kastelein et al., 2003; Bejarano et al., 2017). Due to the different bioenergetics requirements between age classes, reproductive stages and size, realistic demographic information is required for the population to provide an accurate representation of the energy requirements.

To assess the impacts of disturbances on populations and species, information about their demography is required, specifically information on the sex ratios, birth rate, survival, and population structure, to ensure the model is representative of the system of interest. Anthropogenic disturbances, such as climate change, have also been linked to shifts in the demography of dolphin populations, with extreme events such as a recent heatwave event in Western Australia resulting in a roughly 10% decline in calf survivorship compared to other years (Wild et al., 2019). Most population models are developed with a sole focus on females in the population, due to females' relatively greater investment in offspring production and survival (King et al., 2015). Therefore, an understanding of a population's sex ratio is important so as to not under or overestimate the amount of female reproductive output in the population within the model. In bottlenose dolphins, the identification of sex in the wild is logistically difficult, though biopsy sampling has provided some insight into population sex ratios (Möller and Beheregaray, 2001; Bilgmann et al., 2007a; Möller et al., 2008; Quéroutil et al., 2010). Fortunately, demographic traits in bottlenose dolphins are relatively uniform within species, with only slight variation between populations for both reproduction and mortality rates (Table 1).

Table 1- Demographic information for bottlenose dolphins used to estimate model parameters that were unknown for the two populations. Asterisk indicates values obtained within the South Australia study sites for the coastal bottlenose dolphin form.

Parameter	<i>T. truncatus</i>	<i>T. aduncus</i>
Age at first reproduction: female (years)	5-13 ^[1]	12-15 ^[4]
	5-12 ^[2]	6-14* ^[5]
	5-14 ^[3]	>12 ^[6]
Maximum age of reproduction: female (years)	48 ^[1, 7]	32 ^[5]

Maximum lifespan (years)	57 ^[7, 8] 58 ^[9]	40-50 ^[4] 43-50 ^[2] 35 ^[5]
Gestation (years)	1 ^[1, 3, 10]	1 ^[4] 1 ^[6]
Yearly Birth Rate	0.055 ^[11] 0.082 ^[12] 0.072 ^[13] 0.075 ^[14] 0.060 ^[15] 0.12 ^[16] 0.049 ^[17] 0.090 ^[18] 0.0625 ^[19] 0.040 ^[20]	0.071 ^[4] 0.064 ^[21] 0.071 ^[22]
Sex ratio (M:F)	2.2:1 ^[23] 1:0.67 ^[24] 1:1 ^[26]	1:1 ^{* [4, 22, 25]}
Offspring dependence (mean years)	5.4 ^[7]	3.4 ^[22] 4.6 ^[27] 4.1 ^[4]
Interbirth Intervals (mean years)	2 ^[3] 3 ^[17, 18, 28, 29] 2.7-3.5 ^[13] 3.3 ^[14] 4.5 ^[30] 3.8 ^[16] 5.4 ^[7] 4.3 ^[19] 5.3 ^[20]	3.4 ^[22] 3-6 ^[6] 3.8 ^[21] 4.6 ^[27]
Age at first solids (months)	4-11 ^[10] 8-18 ^[32] 6-19 ^[33] 11 ^[34]	
Age at weaning (months)	18-20 ^[10] 14-35 ^[32] 26-34 ^[33] 20 ^[34]	36-47 ^[27]
Mortality age 0-1	0.19 ^[11] 0.20 ^[29] 0.11 ^[13] 0.15 ^[14] 0.38 ^[15] 0.45 ^[16] 0.18 ^[32] 0.16 ^[18] 0.42 ^[19]	0.13-0.29 ^[4] 0.30 ^[35] 0.13 ^[22] 0.29 ^[27]

1. (Wells and Scott, 2009), 2. (Odell, 1975), 3. (Kemper et al., 2014), 4. (John and Yang, 2009), 5. (Kemper et al., 2019), 6. (Möller, 2012), 7. (Wells and Scott, 1999), 8. (Wells and Scott, 2009), 9. (Wells et al., 2008), 10. (Perrin and Reilly, 1984), 11. (Wells and Scott, 1990), 12. (Blair et al., 1981), 13. (Baker et al., 2017), 14. (Norrman et al., 2015), 15. (Sanders-Reed et al., 1999), 16. (Robinson et al., 2017), 17. (Bearzi et al., 1997), 18. (Fruet et al., 2015), 19. (Tezanos-Pinto et al., 2015), 20. (Henderson et al., 2014), 21. (Steiner and Bossley, 2008a), 22. (Kogi et al., 2004), 23. (Fernandez and Hohn, 1998), 24. (Mattson et al., 2006), 25. (Bilgmann et al., 2007a), 26. (Currey et al., 2008), 27. (Mann et al., 2000), 28. (Cockcroft and Ross, 1990b), 29. (Haase and Schneider, 2001), 30. (Arso Civil et al., 2017), 31. (Fortuna, 2007), 32. (Kastelein et al., 2002), 33. (Kastelein et al., 2003), 34. (Peddemors et al., 1992), 35. (Steiner and Bossley, 2008b)

The PCoD framework, when implemented from start to finish, is data hungry, requiring a great deal of information on the species and specific population of interest (King et al., 2015). As a result, it is often necessary to use surrogate data from another species, proxy relationships or inferences from some broad assumptions (Pirodda et al., 2018a). Because of these limitations, the application of the PCoD framework is not appropriate in all cases, but there is available a clear step-by-step decision tree to aid researchers in choosing the most appropriate approach (Pirodda et al., 2018a). As with any models, a level of uncertainty exists with the PCoD framework, whether from the selection of parameters, environmental stochasticity, or the variation arising from individuals, and it is necessary to quantify this uncertainty throughout the modelling process (Harwood and Stokes, 2003; Milner-Gulland and Shea, 2017; Pirodda et al., 2018a). For the consequences of disturbance on the population, uncertainty can be incorporated as the distribution of potential outcomes, allowing for precautionary interpretation of results that are used to inform management decisions (Pirodda et al., 2018a).

In this study I apply the PCoD framework to assess the potential effects of disturbances on two distinct populations of bottlenose dolphins in the South Australian gulfs over time. I develop a species-specific bioenergetics model, which is used together with ecological and demographic information to implement the framework. The two South Australian gulf populations differ in their size and in their habitat, implying that their responses to disturbance may also be different. I assess the potential consequences of a range of different disturbance scenarios that are specific to what is biologically realistic for each population (Robbins et al. 2017). The model provides information on how these two populations may respond to such disturbance events, and how these responses may differ. The modelling has the potential to inform conservation management by enabling threat prioritization and determining which disturbances likely have the largest effect on the respective populations. The output of these

models can help inform management decisions through the prioritization of threat mitigation within South Australia's gulfs.

2. Methods

A bioenergetics model was built for bottlenose dolphins in southern Australian gulf waters using available data and information from the literature. This bioenergetics model was then used within the PCoD framework to investigate the potential impacts of four different disturbances on two genetically distinct populations of bottlenose dolphins in South Australia. The PCoD framework looks at how the exposure to stressors (stimuli occurring in the internal or external environment of an animal that changes its homeostasis) or disturbance events (an external stimulus that invokes a physiological or behavioral response in an individual, similar to that evoked by a predator or threat) may lead to a physiological and/or behavioral change. These physiological and behavioral changes can have both chronic effects on the health of the individual, which can also lead to further changes in the individual's behavior and physiology, or acute effects on their vitality rates. Looking at how the disturbance or stressor affects individuals can provide insights into the population dynamics and improve understanding of the potential consequences (Fig 1).

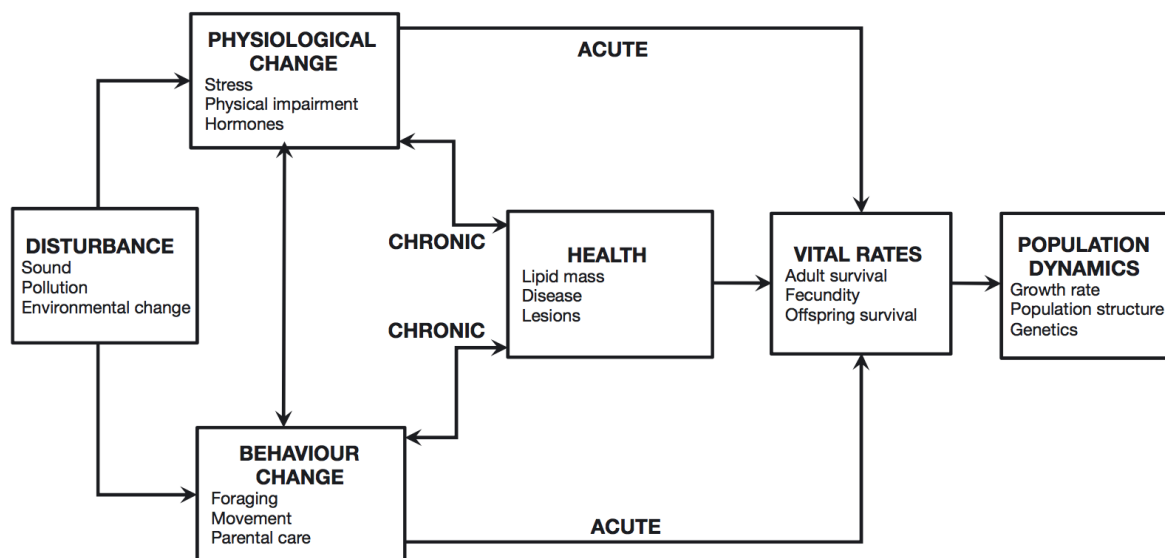


Figure 1. General framework for modeling the population consequences of disturbance (PCoD) from New et al. (2014). Each box in the framework represents a variable for an individual that changes over time. The arrows connecting the boxes show the causal flow for changes in these variables. Causality of these changes can be either acute and happen suddenly

such as predation or mortality, or they can be chronic and have a gradual effect such as reduced energy acquisition or illness.

2.1. Study Region

Two sites were used in this study: Spencer Gulf and Gulf St Vincent. Both of which are large embayments on the southern coast of Australia (Fig 2) and share a number of characteristics, such as a relatively shallow depth, extremely limited inflow of fresh water (inverse estuaries) and relatively stable environmental conditions (Nunes and Lennon, 1986; Tanner, 2003). Many species can be found in these gulfs including fish, birds, sharks, and mammals, and they also provide breeding and foraging grounds for resident coastal bottlenose dolphins (Robbins et al., 2017). The dolphins in each gulf are genetically distinct populations with negligible gene flow for both males and females between the two populations and among those of neighboring coastal waters (Pratt et al., 2018). Dolphins within these two gulfs show high site fidelity, making these areas key habitat for the two populations (Pratt et al., 2018). Systematic aerial line-transect surveys covering both gulfs provided recent abundance estimates of bottlenose dolphins in Spencer Gulf (N=2431, 95% CI=1530-3862; N=1952, 95% CI=1169-3260, for summer/autumn and winter/spring respectively) and Gulf St Vincent (N=708, 95% CI=318-1576; N=1202, 95% CI=657-2201, for summer/autumn and winter/spring respectively) (Bilgmann et al., 2019). The mean number of individuals across both seasons was used as the total population size for each gulf respectively (2,192 for Spencer Gulf; and 955 for Gulf St Vincent) as a conservative estimate for total yearly abundance. In the simulation, half the total population size (1096 for Spencer Gulf; and 478 for Gulf St Vincent) was used with only females being modelled and an expected population sex ratio of 1:1.

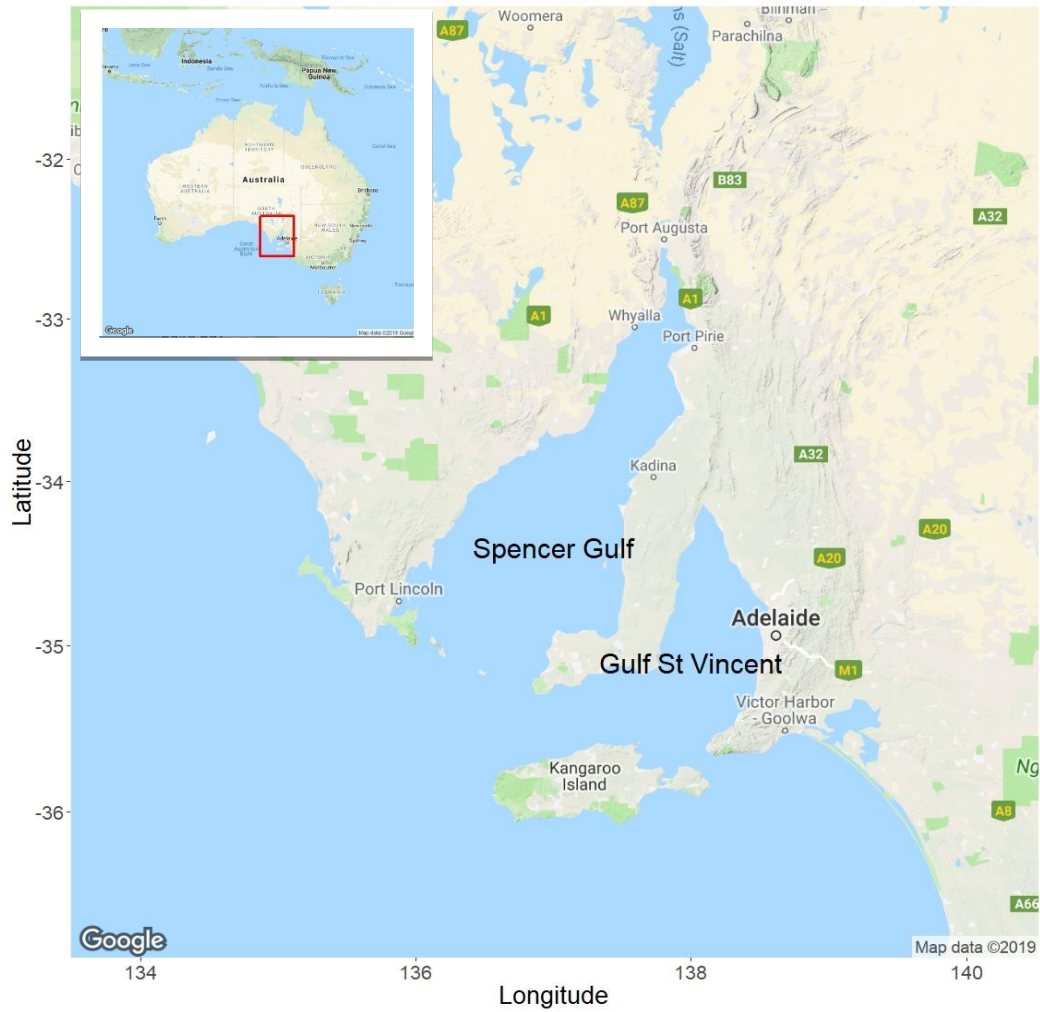


Figure 2. Map of the study regions of Spencer Gulf and Gulf St Vincent located in southern Australia.

2.2. Bioenergetics model

Demographic information was compiled for bottlenose dolphins to provide the best estimates for parameters that are unknown for these two study populations (Table 1), the mean averages were used to provide the best estimate of these values. The majority of parameters obtained from surrogates came from coastal populations, providing comparable estimates for the study populations used here. Information on energetics was derived directly from the gulf populations, and surrogate data from other populations or bottlenose dolphin species were used when population specific information was unknown.

2.2.1. Growth curve

Bioenergetics models require a field metabolic rate (FMR), which can be calculated from a linear relationship with body mass (Kleiber, 1947; Costa and Maresh, 2018). Body mass of individuals is derived from the length of individuals (Equation 2). Data on female dolphins within the study region in South Australia were obtained from strandings data, which were used in the development of a growth curve for females in these populations (Kemper et al., 2019). The curves were calculated using the formula:

$$L = a \times \exp(-b \times \exp(-c \times X)) \quad (1)$$

where L is an individual's total length in cm, a is the asymptote where growth begins to plateau, b is the lower asymptote where the slope begins, c is the intrinsic growth rate, and X is the age of the individual in years (for a full list of model parameters see Table 2). Length of individuals was assumed to be distributed normally around the mean, μ_L , with a standard deviation of 10 cm to account for the natural variation in size among individuals of the same age within the population based upon the growth curve (Kemper et al., 2019). The length of the individuals was then converted to body mass using a *Tursiops* derived model between length and mass (Hart et al., 2013):

$$M_F = 10^{-4.29} \times L^{2.73} \quad (2)$$

where M_F is an individual female's body mass (kg) and L is her total length (cm).

Table 2- List of model parameters, their definition, and the distribution they were sampled from.

Parameter	Definition	Distribution
X	Age of individual (years)	-
L	Total length of the individual (cm)	-
M_F	Female body mass (kg)	-
BMR	Basal metabolic rate (MJ/ day ⁻¹)	-
E_a	Maximum energy intake (MJ/ day ⁻¹)	-
Se	Seasonal variation of prey availability	-
P	Mean energy content of prey (MJ/kg ⁻¹)	-
A	Metabolic efficiency	$U(0.78,0.92)$
E_D	Actual daily energy intake (MJ/ day ⁻¹)	-
E_B	Mean energy store in lipids (MJ)	-
E_M	Max energy store in lipids (MJ)	-
E_l	Additional energy requirements of lactation (MJ/ day ⁻¹)	-
E_S	Individuals energy store (MJ)	-

2.2.2. Energetics

Female body mass from equation 2 was used for the calculation of individual basal metabolic rate (BMR, $M \text{ day}^{-1}$) using Kleiber's Law (Kleiber, 1947):

$$BMR = 0.293 \times M_F^\alpha \quad (3)$$

where α is the slope ($\alpha = 0.75$ for individuals six years and older, $\alpha = 0.82$ for individuals younger than six to account for the increased costs associated with growth) (Riek, 2008).

To obtain field metabolic rate (FMR), a multiplier of 3-6 has been suggested for bottlenose dolphins, though work on the mitochondrial density and lipid content of muscle tissue suggests that bottlenose dolphins actually have a moderate metabolic cost of living compared to other cetacean species (Spitz et al., 2012). Sympatric Australian sea lions (*Neophoca cinerea*) showed higher BMR during stages of fat accumulation (Ladds et al., 2017a) and the dolphin populations in Sarasota Bay, USA, the population from which the suggested multiplier was derived tend to live in waters with greater yearly variation in temperature than those in southern Australia. This results in greater fluctuations in blubber thickness and composition ($11^\circ\text{-}33^\circ\text{C}$ in Sarasota Bay, USA vs $14^\circ\text{-}26^\circ\text{C}$ in Spencer Gulf, South Australia) (Lackenby et al., 2007; Iverson, 2009; Barbieri et al., 2010). Therefore, a multiplier of 2-5 times BMR was used to account for the reduced variability in temperature in southern Australian waters. Given that the exact multiplier is not known, the uncertainty in this value was incorporated by selecting the multiplier from a uniform distribution, $U(2, 5)$, for each female in the population. The addition of this multiplier provides an estimate for the FMR of bottlenose dolphin in southern Australia, consistent with those used for other species (Bejarano et al., 2017; Ladds et al., 2017b; Ladds et al., 2017a; Costa and Maresh, 2018).

2.2.3. Metabolic efficiency

Accounting for the efficiency of energy uptake from food is also required, as not all food that is ingested by individuals is assimilated as energy. Some energy in prey cannot be accessed (e.g. squid beaks), and some is lost as waste through urine and feces. Metabolic efficiency is therefore the percentage of the total potential energy that is actually assimilated by an individual. For bottlenose dolphins the metabolic efficiency of a fish diet, when accounting for fecal waste ranged between 89%-96% (Reddy et al., 1994). Energy from urinary

loss is still unknown for bottlenose dolphins, but in pinnipeds it ranges between 7% - 10% (Keiver et al., 1984; Ronald et al., 1984; Fisher et al., 1992). As a result, these values were used as a proxy in the two dolphin populations, given a uniform 0.78-0.92 ($U(0.78, 0.92)$) for metabolic efficiency in the model (Bejarano et al., 2017).

2.2.4. Food intake

Changes in the diet and energy content of prey in dolphins have been seen with warmer months showing a higher density of prey, but reduced quality and size (McCluskey et al., 2016). Habitat modelling from the two gulfs has revealed differences in the seasonal distribution of bottlenose dolphins, with a preference for upper gulf waters during winter/spring (cool season) and coastal waters during summer/autumn (warm season) (Bilgmann et al., 2019). Bottlenose dolphins in Spencer Gulf reportedly exploit the annual mass aggregation of breeding giant cuttlefish (*Sepia apama*), which occurs during the cooler months (Finn et al., 2009), though evidence of other seasonal differences in diet in southern Australia are not well known. Values for the average energy content of prey (P) were taken from studies looking at prey of bottlenose dolphins, giving a mean energy content of 4 MJ/ kg used for the warm season, and a value of 6 MJ/ kg in the cool season (Spitz et al., 2012; McCluskey et al., 2016). Mean values of prey energy content were consistent with energy densities for prey previously identified in the diet of these dolphin populations (Gibbs et al., 2011). In captive animals, individuals consume on average 2-10% of their body mass in prey daily, though for wild individuals this value is expected to be higher, averaging between 16-20% (Kastelein et al., 2000; Kastelein et al., 2002; Rechsteiner et al., 2013; Srinivasan et al., 2017). Values for seasonal variation of prey availability (S_e) were taken from the variation in daily prey consumption with 20% used for warm season and 16% used for the cool season (Rechsteiner et al., 2013; McCluskey et al., 2016). With the limited information on feeding in wild bottlenose dolphins, a conservative approach was used to estimate the maximum possible energy intake based upon the relationship between proportion of body mass and amount of food required:

$$E_a = M_F S_e P A \quad (4)$$

where E_a is the maximum possible energy acquisition (MJ/day), and A is the individual metabolic efficiency.

2.2.5. Energy stores

Bottlenose dolphins, like most marine mammals, have a layer of blubber below their skin which aids in insulation, buoyancy, and locomotion, while also providing a lipid-rich energy store to cope with changes in food availability and reproductive events (Iverson, 2009). In common bottlenose dolphins, blubber stores have been shown to change over development, with sexually mature individuals and juveniles having the highest concentration of stores (Struntz et al., 2004). Information on the proportion of mass composed of blubber was used to estimate the average proportion of body mass that is blubber (Struntz et al., 2004). The average proportion of the blubber that is lipids (β_1) for different age groups was then used to calculate the average energy store for individuals (β_1 : for juvenile = 0.1702; for adult and sub-adult = 0.1496).

$$E_B = \frac{\beta_1 M_F \times 39.42}{2} \quad (5)$$

where E_B is the individual's mean energy store (MJ). A lipid energy density of 39.42 MJ/kg was used as per Blaxter (1989), which is consistent with other estimates used in marine mammal energetics models (Rechsteiner et al., 2013; Christiansen and Lusseau, 2015; Beltran et al., 2017; Farmer et al., 2018). Not all blubber is accessible as an energy store, so the total potential energy in an individual's lipids was halved to give the lipid stores, E_S . This decision was based upon studies showing a 50% reduction in lipid content of blubber for emaciated individuals compared to robust individuals, with remaining blubber believed to be structural or serve another purpose such as insulation or streamlining (Koopman et al., 2002; Struntz et al., 2004). A maximum energy store (E_M) was also calculated by means of equation 5, using the maximum proportion of mass that was blubber, and the maximum proportion of blubber that was lipids (β_2) instead of β_1 (β_2 for juvenile = 0.2106; and for adults and sub-adults = 0.216) (Struntz et al., 2004).

2.2.6. Reproductive requirements

Physical maturity in bottlenose dolphins is often associated with the total length of the individual rather than age. For dolphins in the two study populations, physical maturation was set to $L = 210$ cm based upon the average length of maturity from these populations (Kemper et al., 2019). The model accounts for the changes in energy requirements for lactating females

and calves. For lactation, an energy multiplier of 48-86% was applied to FMR for the increased energy requirements of the mother (E_l) (Kastelein et al., 2002; Kastelein et al., 2003). The energy multiplier was also added to the E_A of lactating individuals over the lactation period to account for the additional food requirements to meet their increased metabolic costs.

2.3. Simulations

To account for heterogeneity of individuals within the population, ages for individuals were drawn at random between age after weaning (four years) and expected maximum age (32 years) based upon known information on bottlenose dolphin population structure (Stolen and Barlow, 2003; Mattson et al., 2006). A four year average interbirth interval was assumed for the population (Kemper et al., 2019) (Table 1), with the reproductive status of females at the beginning of the simulation distributed evenly between pregnant, reproductively active and the stages of lactation (first, second or third year).

To account for natural variation in prey availability, energy intake was incorporated by drawing an individual's daily food intake (E_D) taken from a normal distribution centred on a mean of E_a . For lactating individuals the additional energy costs of lactation (E_l) were applied from the date of their calf's birth until 11 months after birth, when the calf begins to forage independently (Table 1) (Peddemors et al., 1992; Kastelein et al., 2002; Kastelein et al., 2003). From month 11 the additional energy cost to lactating mothers was decreased linearly until the start of month 28 when the mother ceased lactation and the calf was presumed weaned (Table 1). For the calves that weaned, half were assumed to be female, with the remainder male. Female calves were added to the population after weaning as a juvenile individual, independent from their mother. For each day in the simulation, E_D was calculated for each individual and values greater than energy requirements of FMR were considered to result in an energy surplus, which could be used for the E_L for lactating individuals, or added to the energy store, E_S . On days when E_D was below the energy requirements, the required energy could be metabolized from E_S , with values for E_S below zero resulting in the death of the individual. The daily flow of energy can be summarised as a flow diagram (Fig 3).

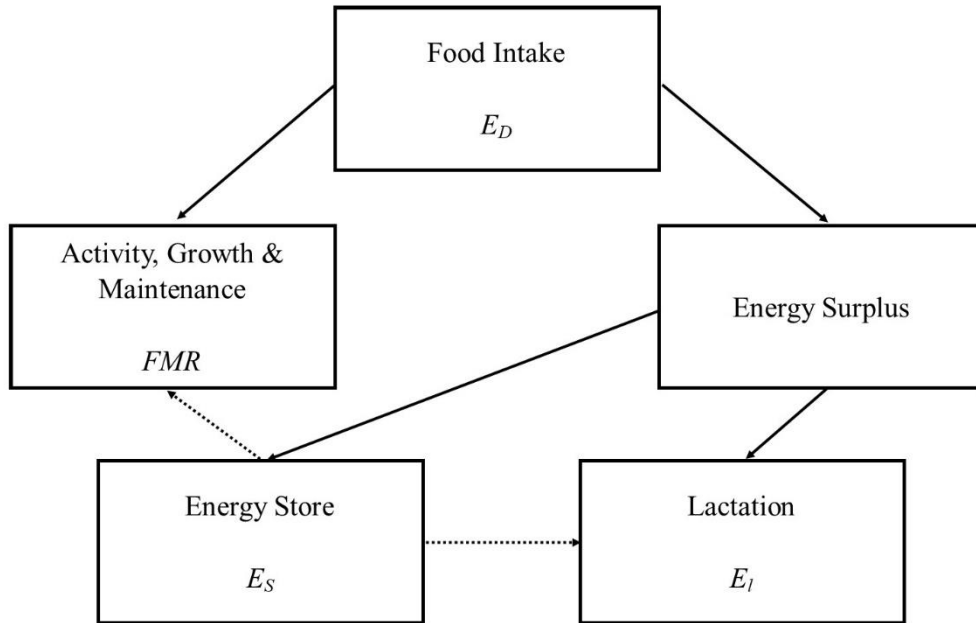


Figure 3. Schematic showing the movement of energy of an individual within the population. The solid lines indicate the direct flow of energy from food intake. Dotted lines indicate the flow of energy from the energy store required when food intake is not sufficient.

Females are assumed to have a lower energy store threshold (E_T) which was drawn from an uniform distribution with a lower limit equal to three-quarters of the FMR and the upper limit equal to twice the FMR , $U(0.75FMR, 2FMR)$, for each individual. For lactating and pregnant females, if the threshold value was reached, individuals were assumed to prioritize their own survival and abandon the calf or abort the fetus. Lactating females used surplus energy to provision the calf, with any remaining added to E_s . As females are assumed to prioritize their own survival, if a lactating female was forced to metabolize energy from her E_s to meet her own needs, she would only fully provision to the calf if her stores were greater than her FMR and the cost of lactation E_L , otherwise the calf would be under provisioned. Calves that were under provisioned incurred a higher chance of mortality based upon the proportion of their energy intake over the year that they did not acquire from their mothers and could not otherwise mitigate for. A visual representation of the model structure for one day in the simulation is summarised in a decision tree (Fig 3).

Each simulation was run over a period of five years, with births and conceptions taking place on the first day of each year (January 1), representing the peak birthing period for bottlenose dolphins in these populations, given the average 12 month gestation period. Seasonal differences in prey quality were incorporated with the inclusion of two seasons, changing from a warm season to a cool season halfway through each year. Individuals E_S was set to the mean energy store in lipids (E_B) at the start of the simulation. Yearly growth was determined by the proportional difference in the yearly average between E_S and E_B , with individuals acquiring more energy growing proportionally more, and individuals acquiring less energy growing proportionally less than average for their age. Lactating individuals who died during the simulation also lost their calf, due to the calf's high maternal dependency. Natural mortality rates ($\mu_m=0.024$, $\sigma_m=0.0198$) were applied to the populations to account for predation and illness, as well as an increased mortality rate (0.35) for individuals over the age of 35 years to account for uncertainty in the maximum age of bottlenose dolphins in the populations.

Using the model structure described in Figure 3, both dolphin populations were simulated using the statistical programming language R version 3.5.3 (R Core Team, 2017). The simulations were performed to assess the population dynamics under no disturbance scenario and with the inclusion of disturbances (described below) to compare potential impacts, with 1000 iterations of the five year period performed for each scenario.

2.3.1. Disturbance Scenarios

The disturbances explored were those considered the most likely to impact bottlenose dolphins in South Australian populations, based upon Robbins et al. (2017). The fourth, a morbillivirus outbreak, was included due to its history in southern Australia and prevalence in marine mammals (Van Bressem et al., 2014; Kemper et al., 2016). The scenarios consisted of a baseline with no disturbances, four climate change, fisheries related mortality, habitat disturbance, and four epizootic scenarios. Each scenario was applied to both populations with the estimate of the intensity of disturbance estimates specific for each gulf.

2.3.1.1. Climate change

Climate change was considered the disturbance most likely to impact the bottlenose dolphins within the gulfs, and was assumed to include issues such as changes to temperature,

frequency of storm activity, ocean acidification and warming, as well as increases in salinity. These shifts in climate can lead to changes in dolphin dispersal based upon thermal tolerances and fluctuations in survival and reproduction in extreme heatwave events, as well as variation in prey distribution and availability (Schumann et al., 2013b; Wild et al., 2019). Four climate change scenarios were considered for each population and were based upon historic sea surface temperature (SST) anomalies for the region from 1998-2018, SST data was sourced from the Integrated Marine Observing System (IMOS, 2019), which is a national collaborative research infrastructure, supported by the Australian Government. The four scenarios consisted of low (a warming event one anomaly higher than expected), moderate (a warming event two anomalies higher than expected), high (a warming event three anomalies higher than expected) and extreme (a severe heatwave). Frequency of occurrence for each event was based upon the SST anomalies and physical characteristics of each gulf. Each monthly anomaly from the historic data was recorded and the probability of occurrence calculated from their frequency over the past 20 years for each gulf. The chances of an event occurring in a given year for Spencer Gulf were 100% for low, 90% for moderate and 25% for high; while for Gulf St Vincent 100% for low, 85% for moderate and 15% for high. The chance of extreme events was set at 50% for both populations to simulate the potential effect of increased likelihood of heat events on the populations, with the potential high frequency of extreme events resulting from climate change. Changes in prey availability occurred with changes in ocean temperature, with extreme and high events resulting in a 25-35% reduction in food, moderate a 15-25% reduction, and low a 0-15% reduction. The reductions in food were applied to all individuals within the population, with the value for the reduction being drawn from a uniform distribution for each individual on each day of the simulated year.

2.3.1.2. Habitat disturbance

For bottlenose dolphin populations in southern Australia, disturbances from noise, habitat modification, and coastal activities have been identified as potential threats (Robbins et al., 2017). This scenario focused on the impacts of shipping with the associated impacts of noise pollution on the populations. Information on the likelihood of individual dolphins being affected were derived from population density maps (Bilgmann et al., 2019), as well as yearly ship traffic densities for each of the gulfs. The proportions of each population likely to be affected differed. A total of 10-30% of individuals in Gulf St Vincent, and 10-20% of individuals in Spencer Gulf were assumed to be affected on each day of the simulation, with

the proportion drawn randomly each day. We assumed individuals affected by this disturbance would experience reduced foraging ability, resulting in a 5-30% reduction in food intake for each individual, drawn randomly from a uniform distribution.

2.3.1.3. Fishing interaction

Interactions between bottlenose dolphins and fisheries within the South Australian gulfs and adjacent state and federal waters have long been reported (Kemper et al., 2005). Though the incidence of reported interactions in the two gulfs are low, there are still likely to be mortalities resulting from fisheries bycatch, particularly within the haul and gillnet fisheries (Robbins et al., 2017). Based upon population density maps and information on reported dolphin bycatch mortalities with dolphins within the gulfs, we estimated 5% of the Gulf St Vincent population came into contact with fisheries during the warm season, and 20% during the cool season; for Spencer Gulf, 15% during the warm season and 5% during the cool season (Mackay et al., 2017; Bilgmann et al., 2019). For those individuals that came into contact with fisheries, 0-2% of the Gulf St Vincent population and 0-5% of the Spencer Gulf population would have a fatal interaction based upon the different fishing intensities within each gulf (Mackay et al., 2017; Bilgmann et al., 2019). This was a conservative approach based on current fishing methods and distribution of fisheries, and no scenarios investigated the potential for increased bottlenose dolphin – fishery interactions resulting from possible changes in any of the fisheries management or implementation.

2.3.1.4. Epizootic

Epizootic events have been recorded in southern Australia, with an outbreak of cetacean morbillivirus having occurred in Gulf St Vincent in 2013 (Kemper et al., 2016). Information on the patterns of morbillivirus outbreaks are largely unknown, and there is variability in the geographical extent, mortality rate and duration (Van Bresse et al., 2014). In the Mediterranean there have been three morbillivirus events separated by an average period of 11 years (Raga et al., 2008). Four scenarios for each gulf were simulated, looking at two levels of intensity and frequency. Low intensity events resulted in 15% mortality in the population, and high intensity events resulted in 50% mortality in the population. Changes in the frequency of the events were gulf specific, with Gulf St Vincent experiencing a low frequency with a probability of once every 11 years, and a high intensity event once every five years. Frequency

of occurrence for Gulf St Vincent was doubled for Spencer Gulf (22 years) due to no known records of cetacean morbillivirus outbreaks within this gulf.

3. Results

3.1. Population Trends

3.1.1. Climate change

Four different climate change scenarios were explored and then compared to a base scenario for each population that experienced no disturbance. For both the Spencer Gulf (Fig 4A) and Gulf St Vincent (Fig 4B) populations there was a 6% decline in the mean population over the five year simulation period in the extreme scenario. Uncertainty in the extreme scenarios for both populations were high, particularly the lower bound, showing the potential range of impacts for these populations (Fig 4A-B). High, moderate and low scenarios saw less than a 5% change in population for both populations over the five year simulation.

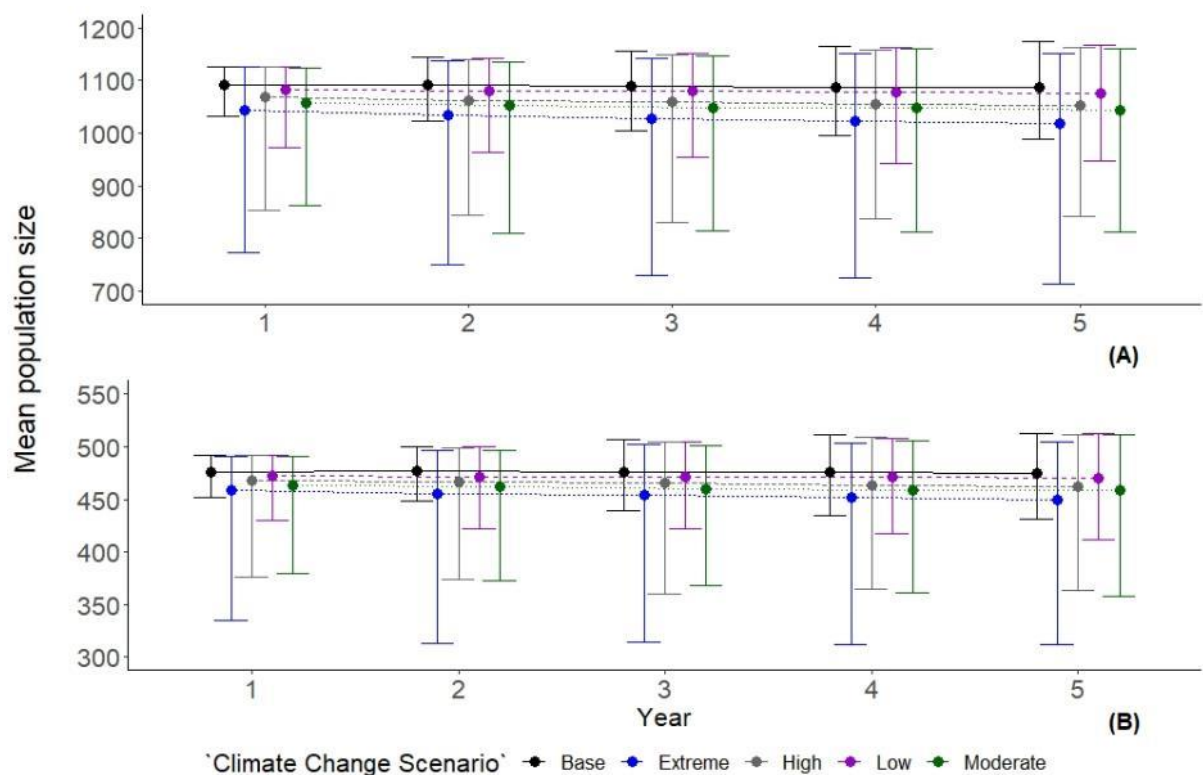


Figure 4. Population trends for Spencer Gulf (A) and Gulf St Vincent (B) under climate change scenarios, predicted over a five year period. Five scenarios were examined for each population: base with no disturbances (black); extreme climate scenario (blue); high climate scenario (grey); moderate climate scenario (green); and a low climate scenario (purple). Scenarios had varying probabilities of occurrence based upon historic climate events and resulted in a proportional reduction in food increasing with severity. Points indicate the mean and error bars indicate standard deviation of the simulations.

3.1.2. Habitat disturbance

Populations trends for both populations affected by habitat disturbance (noise pollution, boat traffic) showed similar trends to the base simulation, remaining stable over the five year simulation period (Fig 5).

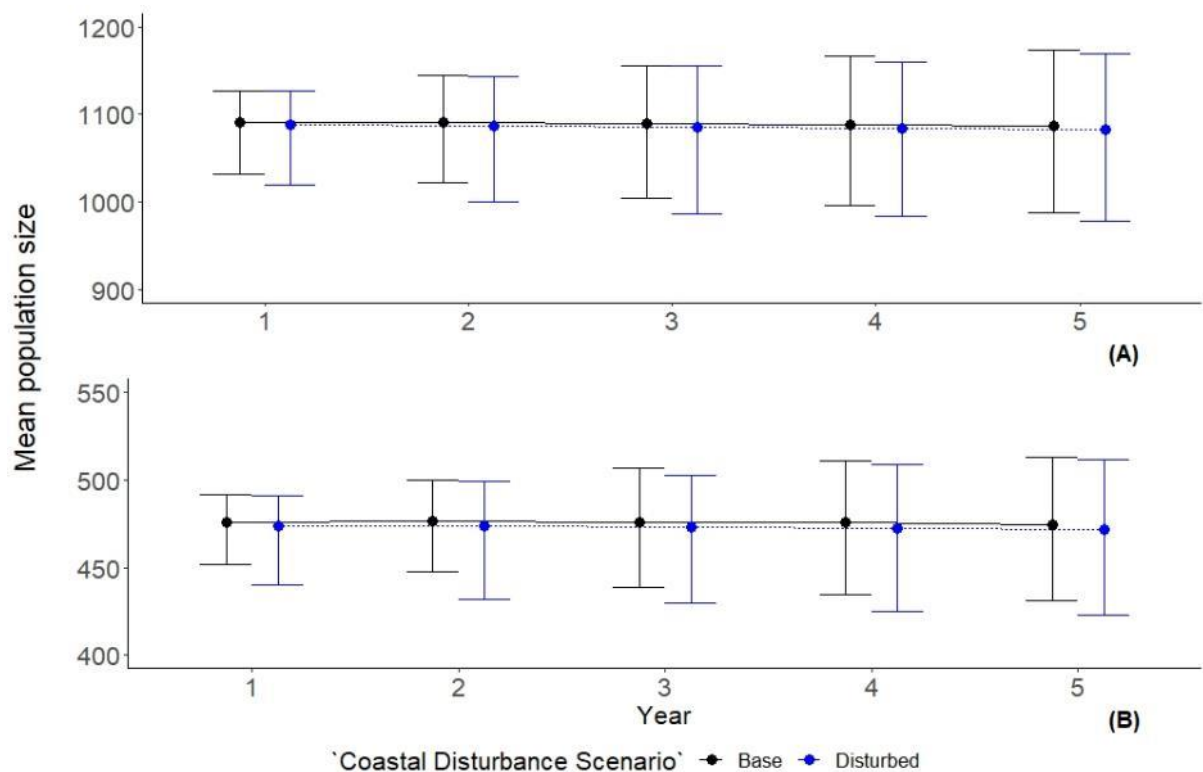


Figure 5. Population trends for Spencer Gulf (A) and Gulf St Vincent (B) with habitat disturbance scenarios, predicted over a five year period. Two scenarios are examined for each population: base with no disturbances (black); and disturbed scenario (blue). Scenarios resulted in a proportion of the population being affected, limiting their ability to forage while affected. Points indicate the mean and error bars indicate standard deviation of the simulations.

3.1.3. Fishing interactions

Populations trends for both populations experiencing fishery bycatch mortalities at the low rates we simulated showed similar trends to the base simulation, remaining stable over the five year simulation period (Fig 6).

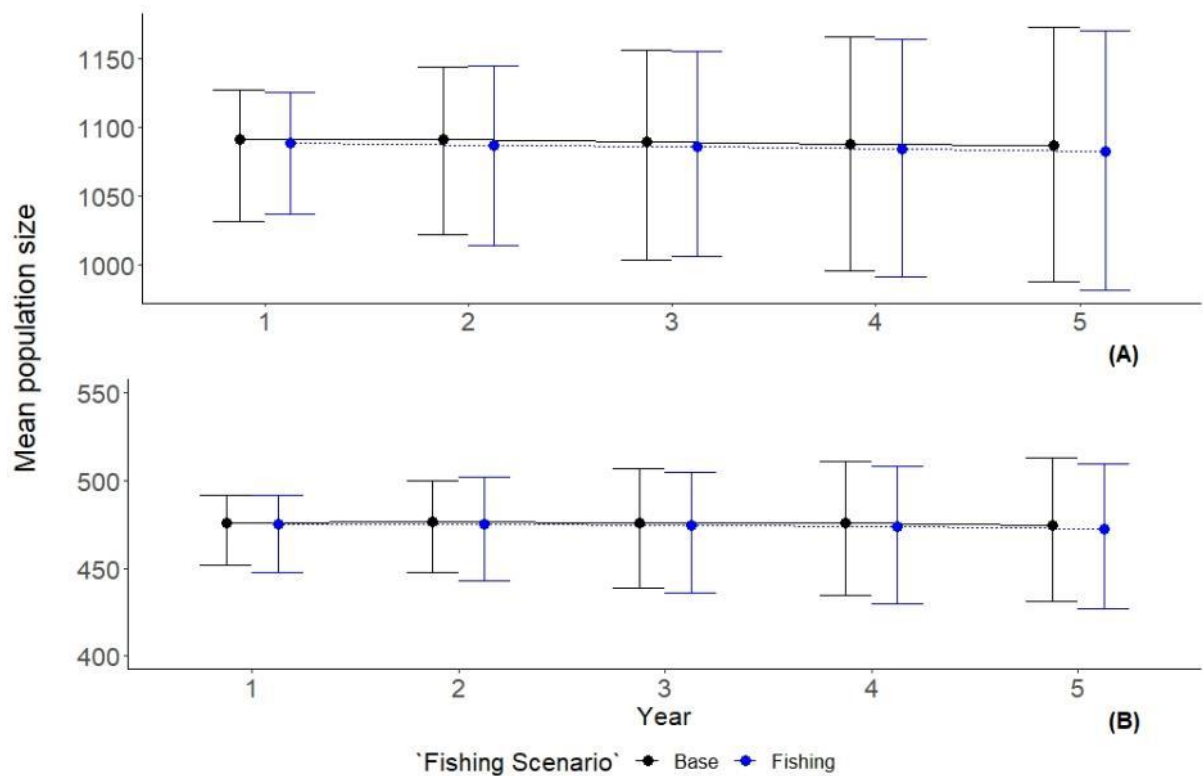


Figure 6. Population trends for Spencer Gulf (A) and Gulf St Vincent (B) with a fishing scenario based on low bottlenose dolphin – fishery interactions representative for the two gulfs with current fishing methods, predicted over a five year period. Two scenarios are examined for each population: base with no disturbance (black); and fisheries related mortality scenario (blue). Scenarios resulted in 5% and 20% of Gulf St Vincent and 15% and 5% of Spencer Gulf being affected during the warm and cool season respectively, with affected individuals having a 0-2% chance of mortality for Gulf St Vincent and 0-5% chance of mortality in Spencer Gulf, as a result of fishing interactions. Points indicate the mean and error bars indicate standard deviation of the simulations.

3.1.4. Epizootic

Epizootic events were modeled at two different frequencies coupled with two different impacts to the populations. The Spencer Gulf population showed a 43% decline in population

size with a high frequency and high impact scenario, and a 21% decline with a low frequency and high impact scenario (Fig 7A). Gulf St Vincent showed a similar trend to Spencer Gulf, though less severe, with a 23% decline with a high frequency and high impact scenario, and a 12% decline with a low frequency and high impact scenario (Fig 7B). For both populations, scenarios consisting of a low impact resulted in a less than 5% change in mean population size over the five year period (Fig 7).

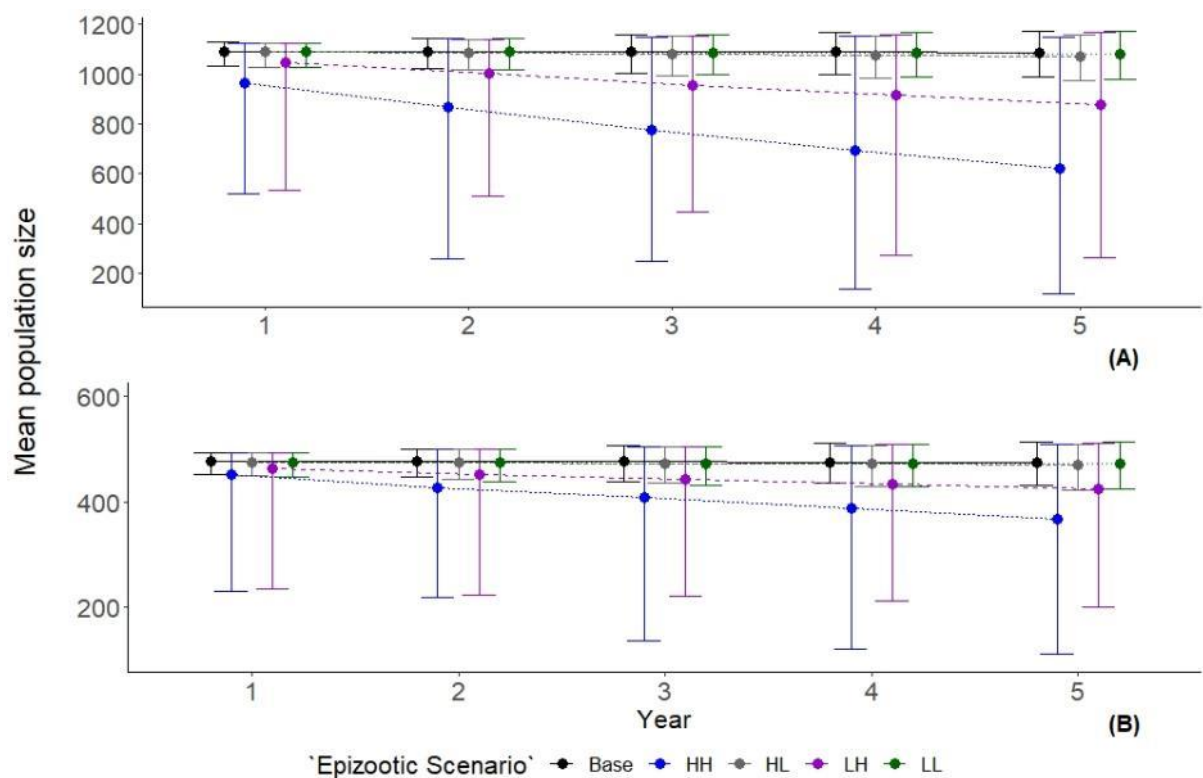


Figure 7. Population trends for Spencer Gulf (A) and Gulf St Vincent (B) with epizootic scenarios, predicted over a five year period. Five scenarios are examined for each population: base with no disturbances (black); high frequency and high impact [HH] (blue); high frequency and low impact [HL] (grey); low frequency and high impact [LH] (purple); and a low frequency and low impact [LL] (green). Scenarios had resulted in mortalities for individuals affected, with the level of impact determining the proportion of the population affected. Points indicate the mean and error bars indicate standard deviation of the simulations.

3.2. Reproductive Parameters

For both populations, changes in fecundity were estimated for each scenario. Changes in the number of failed pregnancies, number of calves born, the number of calves abandoned during the weaning period and the number of calves weaned were all simulated.

3.2.1. Climate change

Extreme climate change scenarios showed the greatest influence on reproductive parameters in both populations, with over a 70% increase in the number of failed pregnancies in Gulf St Vincent (Fig 8E), and an increase of over 80% for Spencer Gulf compared to base scenario (Fig 8A). Changes in the number of failed pregnancies were also seen in other climate change simulations with Spencer Gulf seeing a 39%, 62% and 16% increase for high, moderate and low scenarios respectively (Fig 8A), while Gulf St Vincent saw a 30%, 58% and 18% increase (Fig 8E). Changes were also seen in birth rates during the extreme scenario for both Spencer Gulf and Gulf St Vincent with a 10% and 9% reduction respectively (Fig 8B and F). Changes in birth rates for Spencer Gulf showed a 5%, 8% and 2% decrease, while Gulf St Vincent saw a 6%, 9% and 4% decrease in the high, moderate and low scenarios respectively. The rate of calf abandonment was also highest in the extreme scenario for both populations with a 128% increase in Spencer Gulf (Fig 8C) and a 123% increase in Gulf St Vincent (Fig 8G). The moderate scenario also showed an increased level of calf abandonment with a 100% increase for both populations compared to the base scenario. High and low scenarios had a 53% and 26% increase for Gulf St Vincent and a 65% and 29% increase for Spencer Gulf respectively (Fig 8C & G). The number of calves weaned showed a decrease in Spencer Gulf of 7%, 4% and 3% in the extreme, high and moderate scenarios respectively, compared to the base scenario (Fig 8D), while in Gulf St Vincent showed a decrease of 6% and 2% in the extreme and high scenarios (Fig 8H).

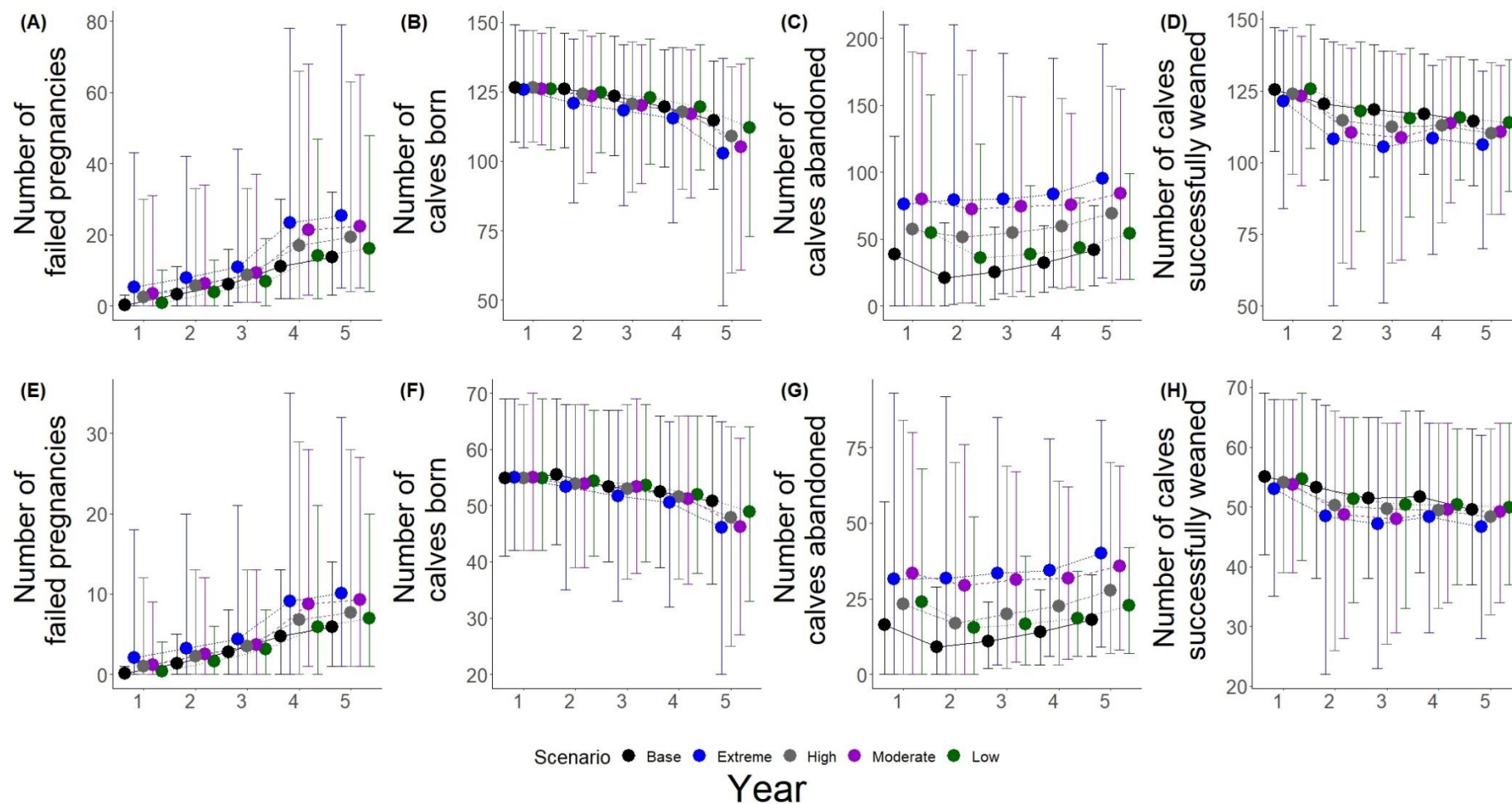


Figure 8. Reproductive parameters under climate simulations for both populations. Five scenarios presented with base (black), extreme (blue), high (grey), moderate (purple), and low (green). Figures (A-D) represent Spencer Gulf, figures (E-H) represent Gulf St Vincent. Figures (A) and (E) show the mean number of failed pregnancies for each scenario; figures (B) and (F) show mean number of calves born; figures (C) and (G) show the mean number of abandoned calves; and figures (D) and (H) show the mean number of calves that survived to weaning.

3.2.2. Fishing and Habitat disturbances

Fishing scenarios showed little change from the base scenario regarding reproductive parameters, with only a 1% decrease in birth rate and a 3% increase in calf abandonment for Gulf St Vincent (Fig 9E & G). Spencer Gulf also showed a 3% increase in calf abandonment (Fig 9C), but showed a 2% increase in the number of failed pregnancies (Fig 9A) and a 1% decrease in calves weaned (Fig 9D). Habitat disturbance resulted in an increase in the number of failed pregnancies from the base scenarios of 6% and 11% for Spencer Gulf and Gulf St Vincent respectively (Fig 9A & E). Changes in calf abandonment were also noted for both populations under habitat disturbance scenarios with a 13% and 8% increase respectively for Gulf St Vincent and Spencer Gulf. Changes in birth rate and calf weaning success showed a less than 2% change for both populations (Fig 9).

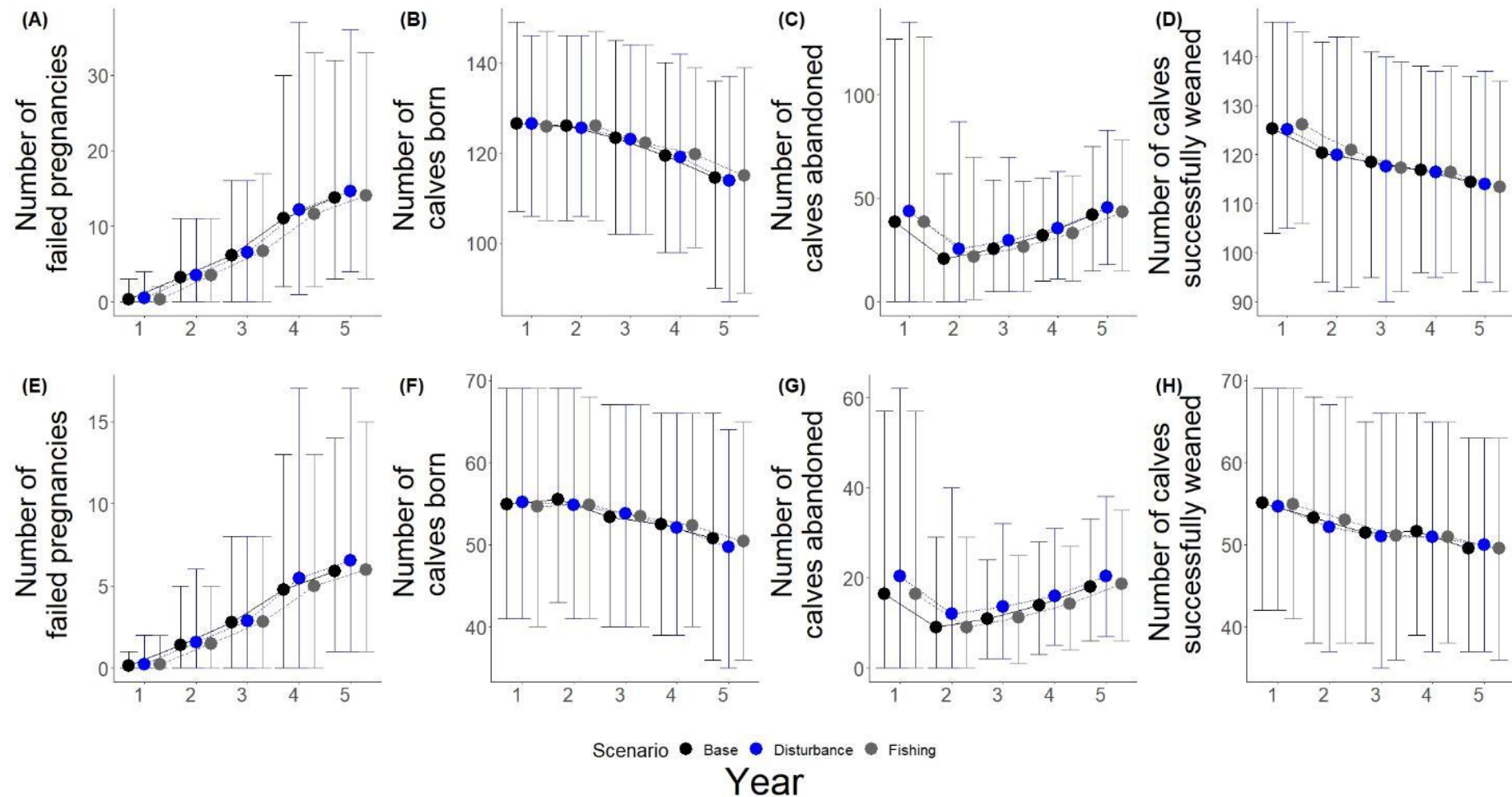


Figure 9. Reproductive parameters under fishing and habitat disturbance simulations for both populations. Three scenarios presented with base (black), habitat disturbance (blue), and fishing (grey). Figures (A-D) represent Spencer Gulf, figures (E-H) represent Gulf St Vincent. Figures (A) and (E) show the mean number of failed pregnancies for each scenario; figures (B) and (F) show mean number of calves born; figures (C) and (G) show the mean number of abandoned calves; and figures (D) and (H) show the mean number of calves that survived to weaning.

3.2.3. Epizootic

The combination of high frequency and high impact of disease outbreaks was seen to have the biggest influence on both populations, with low frequency and high impact having the second biggest influence on reproductive parameters (Fig 10). High impact scenarios showed an increase in the number of failed pregnancies for both populations, with Spencer Gulf having a 285% and 150% increase from base scenarios for high and low intensity (Fig 10A) while Gulf St Vincent showed a 150% and 90% increase for high and low intensity (Fig 10E). Low intensity scenarios resulted in a change of 10% or less on the number of failed pregnancies compared to base scenarios for both populations (Fig 10A & E). Changes in births, abandonment and successful weaning were seen for both populations during high intensity scenarios, with Gulf St Vincent showing a 16% reduction in births, 130% increase in calf abandonment, and a 23% reduction in weaning success during high frequency and high impact scenarios, and a 9% decrease in births, 88% increase in calf abandonment and a 10% reduction in weaning success during low frequency and high intensity scenarios (Fig 10F-H). Spencer Gulf saw a 35% and 16% reduction in births, a 247% and 157% increase in calf abandonment and 43% and a 20% decrease in weaning success during high impact scenarios for high and low frequencies respectively (Fig 10B-D). High frequency and low impact scenario saw a 14% increase in calf abandonment in the Spencer Gulf population (Fig 10C), while births, calf abandonment and weaning success for both populations showed a less than 5% change from base scenarios (Fig 10).

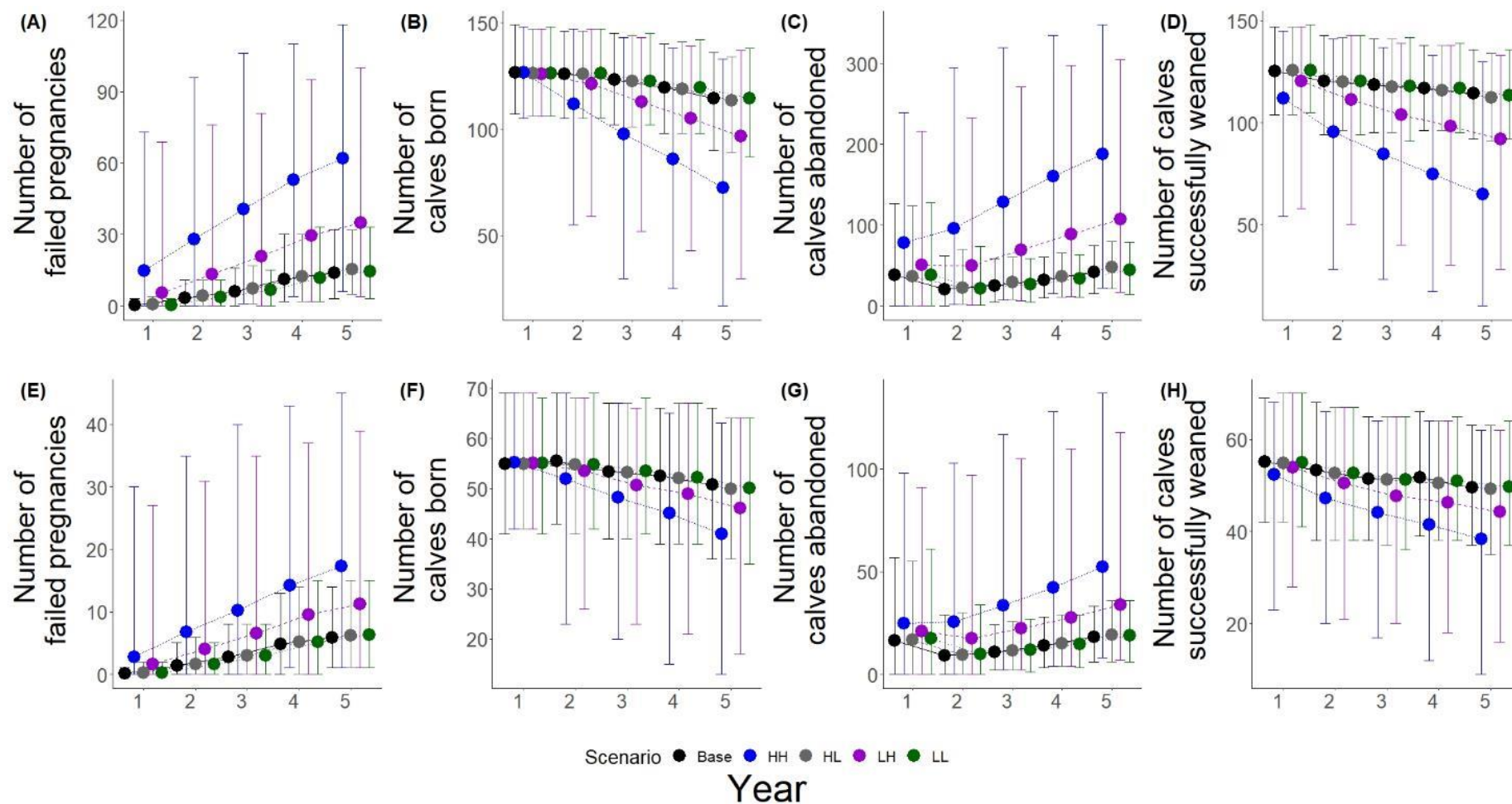


Figure 10. Reproductive parameters under epizootic simulations for both populations. Five scenarios presented with base (black), HH – High frequency/ high impact (blue), HL – high frequency/ low impact (grey), LH – low frequency/ high impact (purple), and LL – low frequency/ low impact (green). Figures (A-D) represent Spencer Gulf, figures (E-H) represent Gulf St Vincent. Figures (A) and (E) show the mean number of failed pregnancies for each scenario; figures (B) and (F) show mean number of calves born; figures (C) and (G) show the mean number of abandoned calves; and figures (D) and (H) show the mean number of calves that survived to weaning.

4. Discussion

Using the current knowledge of population size, life history traits and current threats expected to affect bottlenose dolphins in the South Australian gulfs, I was able to model the bioenergetics of these populations while exploring how different disturbances could influence population trends and reproduction. Modelling two similar but different sized populations provided insights into how a species may respond to disturbances of differing intensities, whilst simultaneously considering the influence population size may play in the mitigation of disturbances. Increased information on population specific parameters as well as predicted disturbances, could be included into the model in the future to further assess specific events and provide a clearer representation of these populations. The simulation outcomes were checked at each stage of the model to ensure representative output based upon the population parameters and expected influences of disturbances.

According to the results of the simulations, epizootic events, such as morbillivirus had the greatest influence on population trends (Fig 7) and reproduction (Fig 10) for both populations. The intensity of the disturbance was the most important factor, with both high and low frequencies coupled with high impacts resulting in population declines of 43% and 21% for Spencer Gulf and 23% and 12% for Gulf St Vincent for high and low frequencies respectively (Fig 7). High impact scenarios were shown to have wide variation in the output for both the high and low frequency scenarios. Pregnant or lactating females being affected by epizootic events are likely have a greater influence on population trajectories due to potential changes to birth rates and calf survival. Low impact scenarios, at either high or low frequencies showed little variation from the baseline scenarios for both populations. The impact of morbillivirus outbreaks has varied between populations with some events resulting in mortality of more than half the population, though further information is still needed on the frequency of events (Guardo et al., 2005). Environmental variables such as reduced prey availability, higher than average sea surface temperatures and toxic contamination as well as population densities are likely to play a role in the outbreak of infectious diseases such as morbillivirus (Van Bresse et al., 2014; Kemper et al., 2016). The incorporation of population density and individual interactions to model the spread of disease could further provide valuable insight into the potential impact of these events on the populations.

Climate change scenarios also showed a decreasing in population trends for both populations (Fig 4). Extreme scenarios were shown to have the greatest influence on both populations with a 6% decline over the modeled five year modelled period compared to the baseline population. These results are comparable to the reported changes in survival following an extreme heatwave event in Western Australia that resulted in a 5.9-12.2% decline in the abundance of bottlenose dolphins (Wild et al., 2019). Both extreme and moderate climate scenarios also showed an increase in the number of failed pregnancies, number of calves born and calves lost before weaning for both populations (Fig 10A-C & E-G). The reduction in food availability modelled as part of these scenarios is likely to be the driver behind these results, with the increased metabolic need, especially for lactating females, leading to reduced reproductive success; again, similar to that experienced post heatwave in Western Australia (Wild et al., 2019). Scenarios focusing on climate impacts showed wide variation in simulation output, due in part to our uncertainty in how these ecosystems will respond to climate change events, how severe these events may be, and what impact this will have on prey in southern Australian waters. Climate change is likely to affect bottlenose dolphins by changing the abundance and distribution of prey, an extreme events result in major loss of seagrass which provides habitat for many of their prey species (Thomson et al., 2015). While these extreme climatic events have been shown to impact some populations, others show stable population trends following these events, with factors such as habitat range and preference likely to play an important role (Sprogis et al., 2018). Physical characteristics of the two South Australian gulfs, including negligible freshwater inflow (inverse estuaries), shallow depths, and their limited outflow makes these environments vulnerable to the effects of climate change, and potentially leading to the amplification of their effects with rises in ocean temperatures, increased heatwaves, and increases in salinity (Nunes and Lennon, 1986; Petrusevics et al., 2009). Habitat modelling for bottlenose dolphins in South Australia's gulfs have reveal preferences for shallow, coastal waters, similar to other populations of coastal bottlenose dolphins globally, with these habitats most vulnerable to climate change in the future due to their physical characteristics (Simon and Emer, 2002; Torres et al., 2003; Bilgmann et al., 2019). Community dynamics of seagrass have also been shown to be affected by changes in extreme temperature events, with areas being dominated by early successional species post heatwave, leading to changes in ecosystem functions (Nowicki et al., 2017). Information on the habitat and abundance of prey species and their response to changing climatic conditions is important to further understand how climate change could influence bottlenose dolphins living in southern Australia.

Both fishing and coastal disturbance scenarios showed little variation from those of the baseline scenario with regards to population trends and reproductive parameters (Fig 5-6 & 8-9). Fishery related mortalities are less likely to occur for bottlenose dolphins within the two gulfs, with common dolphins (*Delphinus delphis*) most likely to be bycaught by fisheries in these regions (Bilgmann et al., 2008; Hamer et al., 2008; Bilgmann et al., 2014). Disturbances from noise, boat traffic and coastal activities have revealed a range of responses in bottlenose dolphin populations. Global studies have shown changes in the short term responses of dolphins to boat traffic, with increases in the mean dive intervals in the presence of boats, changes in breathing synchrony, and residency patterns (Hastie et al., 2003; Lusseau, 2003b; 2005), while in contrast, a simulation approach found no effect of exposure to disturbance on calf survival (Pirrotta et al., 2015). Swim with dolphin operations running in Gulf St Vincent saw a change in the energy budget of bottlenose dolphins, with an increase of milling behavior during interactions, and an increase in feeding post interaction compared to prior (Peters et al., 2012). The response of populations can range from habituation or sensitization to the effects of boat disturbance to the avoidance of areas, with the motivational state of the individual likely to play a role in their response. It is also possible that the energy benefits of an area may be outweighed by the impacts of disturbance, resulting in movement to suboptimal foraging areas (Gibeau et al., 2002; Lusseau, 2003a). Coastal disturbances are unlikely to affect the entire population uniformly, and the importance of individual variation in habitat use and behavior is key to understanding how individuals in a population may react when presented with a disturbance (Agrelo et al., 2019).

The variation seen in scenarios, especially the extremes, represents the uncertainty in how these populations may respond to a given disturbance. The level of variation in the extreme scenarios could be explained by the intensity of the disturbance paired with the frequency at which they occur. In addition, there is a substantial amount of individual variation, with reproductively active individuals having a greater influence on the population trajectory. When pregnant or lactating females were affected there were increased rates of failed pregnancies and lower calf survival, which had direct effect on the population dynamics. Reproductive output is of importance to population viability, comparable to survival, even in slow growing species (Manlik et al., 2016). Understanding reproduction and how it may be affected by disturbances can provide insight into long term population trends (Manlik et al., 2016). The variation in the simulations reflects the many uncertainties in our model, both reducible and

aleatory, and represents a distribution of potential outcomes for the two dolphin populations when faced with disturbances of different frequency and intensity, allowing for their precautionary interpretation for management (Pirotta et al., 2018a).

The PCoD model described in this study investigated the potential impact of different disturbances on the bottlenose dolphin populations in two of southern Australia's gulfs. Disturbance scenarios were assessed individually, though the likelihood of a single event occurring in isolation is unlikely, and each disturbance is likely to be amplified by other environmental and physical pressures on populations. Increases in ocean temperature have been linked to disease outbreaks such as morbillivirus, which affect the distribution of populations and can also change the abundance and seasonal distribution of prey (Schumann et al., 2013a; Van Bressem et al., 2014). The combination of these events could have synergistic effects on populations exposed to additional stressors, such as boat traffic, affecting time spent in certain foraging grounds, and interactions with fisheries could increase with the competition for a reduced prey source resulting from changing climate. Assessment of the interaction of multiple stressors on populations can provide insight into their cumulative effects, but also offer a greater range of uncertainty due to the complex nature of these interactions (National Academies of Sciences, 2017). A modified approach to the PCoD framework, the Population Consequences of Multiple Stressors (PCoMS) can be used to look at the impact of multiple disturbances by taking the temporal and spatial distribution of populations and stressors to investigate their impacts on populations (National Academies of Sciences, 2017).

Dolphins are highly social and live in groups of a fission-fusion nature, with larger groups offering greater protection, but can also providing a greater chance of detection by predators and increased competition for food (Lusseau et al., 2003). Furthermore, increased population density is also being linked to the spread of pathogens and viruses, including morbillivirus (Raga et al., 2008). A recent study of social cohesion of individual dolphins living in the Adelaide metropolitan area of Gulf St Vincent has identified two social communities occupying quite different habitats with little social overlap (Zanardo et al., 2018). Stable isotope analysis and dolphin stomach content analysis have also revealed niche differentiation in bottlenose dolphins within Spencer Gulf (Gibbs et al., 2011). Given the social structure of individuals within these populations it is likely that disturbances will have a greater impact on social groups occupying particular areas of high human activity compared to social groups in less urbanized areas. With further understanding of the social structure of dolphins within these

populations, the design of models can be improved to look at spatially explicit responses to disturbances incorporating information on group size, group composition, habitat type and site-specific disturbances to see how they vary within each population.

Species are under increasing pressure from anthropogenic disturbance from human activities, whether it is from climate change, habitat modification and loss, noise pollution or disease outbreaks. Research and management are important tools to understand and protect populations and species affected. In this model, the mean change in population trends and reproductive parameters were presented in order to provide insight into how these disturbances could affect these two bottlenose dolphin populations. Extreme events were seen to have the greatest influence on the population trends and reproduction of dolphins during simulations. The understanding that different species may respond differently to the same disturbance is widely accepted, but differences in response can also show large variation within a species (Harding et al., 2019; Radford et al., 2019). Population differences such as population size, habitat quality, genetic variation need to be considered to understand how and why different populations may vary in their responses to disturbances. Individual differences in behavior and physiology, such as thermal tolerance, habituation and immune response, are important to consider when interpreting simulation results applicable to population management. Informed management of marine species is required if wishing to mitigate the effects of disturbances on populations. Modeling provides a powerful tool to understand how potential disturbances may impact a population, either before they occur or while there is still time to act.

5. References

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