Annex 2: An evaluation of the evidence of the impact of fishing closures around breeding colonies of African Penguins

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1. Introduction

Based on the precarious conservation status of the African Penguin after a decrease of 60% of the global population in 6 years (2001-2007), an island closure feasibility study was approved in 2008, by the former Department of Marine and Coastal Management (now Department of Agriculture, Forestry and Fisheries (DAFF) and the Department of Environmental Affairs (DEA)) in cooperation with the South African Pelagic Fisheries Association. The aim of this study was to evaluate the power of a long-term experiment to detect the effects of island closures around penguin colonies on penguin life-history parameters and foraging behaviour, and potential benefits to improve the conservation status of African Penguins.

However, to find out whether island closures affect penguins, one should ideally be able to choose identical islands at random from a large pool and randomly assign interventions (open or closed) to them. In reality, we only have a small number of diverse islands available for experimentation. The area (extending 20 km seaward from the low-water mark) around the largest breeding colony in the Western Cape, Dassen Island, was closed to purse-seine fishing over a period of 2 years (1 January 2008 - 31 December 2009) while nearby Robben Island, where fisheries continued, served as a reference point for the prevailing environmental conditions. A year later, in the Eastern Cape, St. Croix was closed to fishing (1 January 2009 – 31 December 2011) while nearby Bird Island was kept open.

Concurrent with the start of the closure project, a number of related datasets have been collected on a number of traits that pertain to different aspects of the penguins' biology. Some of the studied traits, such as foraging behaviour, are flexible and reflect immediate reactions of the birds to changes in the environment (Hamer et al. 2006). Other traits are more buffered against environmental variation but are more closely linked to fitness and population growth, such as adult survival (Davis et al. 2005). Between these extremes, there are data on a suite of intermediate traits, such as chick condition, chick growth, chick survival and reproductive success.

Although a two-year period was initially intended for that feasibility study, data demonstrated early on that this period was insufficient to allow experimental power to be estimated for all the traits monitored. This was mainly because of the short time series of data available for some of the penguin traits being monitored, specifically penguin foraging behaviour for which monitoring only started in 2008. For this reason it was decided to prolong the feasibility study until such time as the data allow sufficiently precise estimates of the effects of interest.

Following deliberations of the Pelagic Scientific Working Group, its subsidiary body the Island Closure Task Team and the International Stock Assessment Panel, at the end of 2010, agreement was reached that the study be extended for four years. It was further agreed on that alternation between open and closed islands be implemented (Table 1) to optimise the outcome of the study taking account of the sometimes conflicting objectives of (a) rapid alternation to maximise contrast for more precise estimation, (b) a slower alternation to take account of possible autocorrelation in the penguin indices being monitored, and (c) the desirability to integrate the feasibility study and experiment to lead to earlier answers.

This experimental island closure study provided the unique opportunity to examine how fishing around the islands affects seabird populations and to disentangle this effect from other variables. To take full advantage of the data, the statistical analysis would ideally account for the connection between the different traits through the biology of the species (Figure 1). Research is underway that will allow us to understand the links shown in Figure 1. For now, we examine the statistical effects of closure on individual fitness components using univariate analyses.

2. Selection of response variables and the time frame of interest

The following data sets were originally identified by the ICTT as being potentially useful to assess the power of an experiment to determine analyses the impact of island closures: (1) chick condition; (2) chick growth; the foraging related responses (3) trip duration (h), (4) foraging path length (km), (5) maximum foraging distance away from the colony (km); (6) the proportion active to potential nests, and (7) breeding success.

As the study progressed, it became clear that certain traits originally identified as being "potentially useful" might not be as useful as they first appeared; this was the case for the proportion of active nests to potential nests as well as breeding success (chicks fledged/pair/year or breeding attempt). The proportion of active to potential nests has been called into question as the penguin population has decreased. As African Penguin adult survival has declined (Sherley et al. 2014), it is likely that a greater proportion of birds surviving from year to year would be unable to reunite with their partner from the previous season. It would therefore become harder to distinguish between potential nest sites that represent failed breeding attempts and those that represent sites guarded by a bird unable to reunite with their former mate. These birds may later move and guard additional sites, adding a greater degree of subjectivity to the assessment of potential nests and raising questions over the comparability of this measure over time. Breeding success has not been used in this report as this integrates various components of reproduction (hatching success, chick survival and condition) through the whole season and each of these components may respond to different pressures.

In addition, both of these traits suffer from the caveat of being presented as a single annual estimate, recorded without error. Because the associated variance is not recorded, the estimates may be influenced by small methodological changes and the presence of outliers and it would be difficult to detect this or account for it in statistical analyses. A concern of this nature has been raised about the breeding success time-series in the past and this is why Robinson (2013) used two disparate time-series for this trait at Robben Island. A more appropriate way to analyse breeding success would be to estimate (with known precision) the survival of the eggs and chicks (Pichegru 2013, Sherley et al. 2013). Nest content survival has been analysed for Robben Island (Sherley et al. submitted, summarised in Annex 4), but the data still need to be processed into the correct format to allow a similar analysis for the Dassen Island time-series.

An appropriate way to analyse the active nest proportions would be as a series of binomial trials within each year (i.e. is each nest surveyed active [1] or not [0]). However, even this would be problematic as penguin nests are not fixed in time or space and differ in their detectability. For example, a pair may begin to make a nest site under thick vegetation, fail in their first attempt and then move a few metres and make a new nest in the same year. The old nest may be (a) counted as abandoned, (b) counted as a potential nest, (c) missed altogether and by the following season may be unobservable. In contrast, natural burrows and artificial nests represent nest sites that can remain fixed and directly observable over many years. A more appropriate time-series of occupied nest counts of a number of marked burrows exists for Dassen Island (Durant et al. 2010) and these could be analysed to investigate whether closure has influenced breeding participation using binomial regression. However, a directly comparable time-series does not exist for Robben Island. As such, these traits were not included in our analysis framework and will form the focus of future analyses.

For all traits, the full data set (information from each bird or nest monitored) was used, rather than just using the annual means. Similarity between observations on penguins measured in the same month, and in the same year (because of similar weather and other environmental conditions etc.), and the correlation between them, was specifically modelled by including month, nested in year as a random effect in all models. Where traits were recorded more than once on the same penguin, or on chicks from the same nest, Bird ID or nest ID were also used, nested in month, nested in year to account for their correlation.

The time frame of the data is also important. In the analyses that follow, only data from 2008 to 2013 are considered. This covers the time when the manipulation of fishing was in place. Analysing data prior to 2008 is an exploratory analysis rather than one that confirms predictions from an experiment or manipulation, and may result in spurious effects (Anderson et al. 2001). In addition, when analysing long time series relating to penguins and food availability, one needs to be mindful of two ecosystem regime shifts that have taken place in the southern Benguela, the first in the mid-1960s after the first collapse of sardine at the west coast, and the second in the early 2000s, which went along with the change in spatial distribution of small pelagics (Howard et al. 2007, Blamey et al. 2012). Therefore data from pre-2003 may not be directly comparable to data post-2003.

3. Methods

The principle underlying the design of the experimental closure to fishing is that the closures of the paired islands (Robben and Dassen and St Croix and Bird islands) alternate over time in order to potentially detect a closure effect in the case the closed island performs differently to the expectation for the year. Linear-mixed-effect models were used to analyse the effect of alternating closures around Dassen, Robben, Bird and St. Croix islands, on the response variables (traits): (1) chick condition, (2) chick growth, and the foraging related responses (3) trip duration (h), (4) foraging path length (km) and (5) maximum foraging distance from the colony (km).

Linear-mixed-effects models were used for all modelling, because there were several sources of correlation in the data, which would lead to violation of independence in the data and over-estimated precision of the closure effect, unless they were explicitly modelled as random effects. For example chick condition index appears to be sensitive to food availability on both monthly and annual time-scales (Waller 2011). The random effects were nested in the order: Year/Month and where appropriate an additional level, such as penguin ID or nest ID, was included. Modelling was done using the 'lme' function in the R package 'nlme' (Pinheiro & Bates 2000) and fitted using REML. Both the random terms and the residual error were assumed to be normally distributed, with variance terms estimated from the data. Residual plots were examined to ensure that the underlying assumptions of normality and homogeneity of variance were not violated and where necessary the data were log-transformed for analysis.

The main aim was to determine the island-specific closure-effect, so the interaction term 'Island' × 'Closure' was included as fixed effect for all response variables. Closure was a categorical variable, as per the design in Table 1. The estimates of coefficients and associated significance levels (*p*-values) for closure effect on the two islands were obtained using REML estimation. Different covariates were adjusted for by including them in the models as fixed effects. These covariates are described in the sections dealing with each specific trait. Where effect sizes are presented, these are the effect sizes with any continuous covariates in the model held at their individual mean.

Chick condition

Chicks were measured for their head length (tip of bill to back of skull) and weighed for mass on Dassen and Robben islands from 2008 to 2013. Condition was estimated following the methods in Lubbe et al. (2014), which assigns a body condition index to each chick based on a reference data set for Robben Island in 2004. Chicks with head lengths < 75 mm were excluded from the analysis as the method has not yet been developed for small chicks (ca. 20 days of age or less). In total, measurements of 3743 chicks were included for Dassen Island and 4325 chicks for Robben Island.

For both the East and West Coast models, the nested random effect structure considered the month in which each chick was measured, nested in the year of monitoring (Random effects: Year/Month). For the West Coast, the fixed effects were the Island-Closure interaction, the sardine biomass west of Cape Agulhas in the November of the year prior to penguin breeding ($SSB\text{-}W_{y-1}$) and the anchovy recruitment biomass estimated in May of the same year (ARB) to account for changing environmental conditions between years (Fixed effects: Island x Closure+ $SSB\text{-}W_{y-1}$+ ARB). For the East Coast, the fixed effects were the Island-Closure interaction, the sardine biomass east of Cape Agulhas in the November of the year prior to penguin breeding ($SSB\text{-}E_{y-1}$) and the anchovy biomass

Cape Agulhas in the November of the year prior to penguin breeding (SSB-E_{y-1}) (Fixed effects: Island x Closure+ SSB-E_{y-1}+ ASB-E $_{y-1}$). The response variable was not transformed in either case.

Chick growth

Measurements were collected from chicks of known identities in the penguin colonies at Robben Island (n = 347, 2008-2009, 2011-2013), Dassen Island (n = 344, 2008-2013), Bird Island (n = 479, 2008-2013) and St. Croix Island (n = 350, 2008-2013). Nests and chicks were individually marked so that their identity could be confirmed on subsequent visits. Chicks that were measured at least twice over a period of 10 to 79 days were retained for analysis. To avoid disturbance at nests with small chicks, chicks were not measured before they had a head length of c. 70 mm. As a result age of the chicks was not known exactly and we used the method in Bonato et al. (2013) to estimate growth where age is unknown. This method uses the principle underpinning robust regression to generate one growth coefficient per chick from all $n(n - 1)/2$ pairs of measurements for each chick (see Tjørve & Underhill 2009, Sherley 2010, Bonato et al. 2013 for details). Here we calculated a Gompertz growth rate coefficient (k_G) for each chick. The details are in Sherley (2010).

For both the East and West Coast models, the nested random effect structure considered the unique nest ID in which each chick was measured, nested in month, nested within each year of monitoring (Random effects: Year/Month/Nest ID). Both zeros and negative values are biologically plausible as chicks can lose weight under poor conditions. For the West Coast, the fixed effects were the Island-Closure interaction, the sardine biomass west of Cape Agulhas in the November of the year prior to penguin breeding (SSB-W_{y-1}) and the anchovy recruitment biomass estimated in May of the same year (ARB), and a variable denoting the sampling period (in days) over which each chick was measured (SP). The latter was of importance as there is a significant, though biologically uninteresting (chicks growing slowly take longer to fledge so are found more often by researchers), linear relationship between growth rate and the sampling period (Sherley, 2010).

For the East Coast, the fixed effects were the Island-Closure interaction, SSB-E_{y-1}, SSB-E_{y-1} and the sampling period (Fixed effects – West Coast: Island x Closure+ SSB-W_{y-1} + ARB + SP; East Coast: Island x Closure + SSB-E_{y-1} + ASB-E $_{y-1}$ + SP). The response variable was not transformed in either case.

Foraging traits

African Penguins brooding chicks were equipped with GPS-TD (Temperature-Depth) loggers in the Western Cape at Robben Island (n = 103, 2008, 2010 -2013) and Dassen Island (n = 171, 2008-2013) and in the Eastern Cape at Bird Island (n = 293, 2008-2013) and St. Croix Island (n = 171, 2008-2013). Geographical position (using the World Geodetic System, WGS, standard) was nominally recorded once per minute and gave highly accurate information about the bird's positions at sea. Times for data collection were chosen in accordance with the penguin's breeding season at each locality. The devices weighed <2.5% of adult body mass and were attached midline on the lower back, following Bannasch et al. (1994) using overlapping layers of black waterproof tape (10 mm wide strip Tesa-Tape Nr. 4651, Beiersdorf) which matched the birds' plumage in colour and did not compromise feather structure (Wilson & Wilson 1989, Wilson et al. 1990). The time of the complete procedure, from capture to release back into the nest, was recorded and on average was less than 15 min. Loggers were deployed on breeding adult African Penguins in the evening and set to begin recording the next morning. After deployment, nest sites were monitored until the instrumented birds returned, allowing them to be recaptured and the logger removed. Previous studies showed no significant difference in the trip duration of instrumented versus non-instrumented African Penguins (Petersen et al. 2006, Pichegru et al. 2010). Both the logger deployment and bird handling is based on the guidelines recommended in Bannasch et al. (1994) and Wilson et al. (1997) to minimize stress and device-induced effects. All methods were approved by University of Cape Town's animal ethics committee. To account for birds performing multiple trips the unique bird ID was nested in month within each year of monitoring and was used as the random effects for both coasts (Random effects: Year/Month/Bird ID). The fixed effects were the island-closure interaction (Island × Closure), the SSB-W_{y-1} , SSB-E_{y-1}, the ARB (West Coast models only), ASB-E_{y-1} (for East Coast models only), season (for West Coast models only) and brood mass (kg) (Fixed effects structure - West Coast: Island × Closure + SSB-W_{y-1} + ARB + season + brood mass; East Coast: Island × Closure + SSB-E_{y-1} + ASB-E_{y-1} + brood mass). The response was log-transformed for all models for both coasts.

The biomass of sardine and anchovy is estimated twice a year, once in May (recruit biomass survey) and once in November (spawner biomass survey). The penguins feed their chicks mainly on young anchovy (surveyed in May, ARB in our models), but the adult sardine biomass has shown to be important for adult penguins (Crawford et al. 2008, Sherley et al. 2013, 2014).

For the most part, spawner and recruit biomasses are correlated for each fish species, so we limited the models to only ARB and SSB-W_{y-1} for the West Coast and ASB-E_{y-1} and SSB-E_{y-1} for the East Coast (considering that 80% of the penguin's diet in the Eastern Cape consists of anchovy (Crawford et al. 2011)).

While studies on the African Penguin have shown that the two sexes do not exhibit significant differences in "horizontal" foraging effort (i.e. those components that do not include diving behaviour; Pichegru et al. 2013) foraging effort does increase with brood mass (Pichegru et al. 2013). This is generally expected when parents adjust the amount of food delivered to meet the needs of their offspring (Drent & Daan 1980).

Unlike penguins at other breeding locations, on Dassen Island, penguins show two well-defined breeding seasons, in winter (May to August) and summer (November to February) (Wolfaardt et al. 2009). Considering different oceanographic conditions on this temporal scale, we added season as a fixed effect into our model for the West Coast colonies.

4. Results

Chick condition

West Coast

The models produced reasonable residual plots (Figure 2). Chick condition was higher in 'Closed' years at Robben Island than during 'Open' years (0.14 ± 0.03; t8003 = 4.91; $p < 0.001$; Figure 3). Condition did not differ significantly between 'Closed' and 'Open' years at Dassen Island ($p = >0.05$). The effect size at Robben Island was 59% of the mean for 'Open' years and the effect of the closure was sufficient to produce condition indices for 2012 and 2013 that approached the reference level from Robben Island in 2004 (Figure 4). The effect was also significant despite 2011 having the poorest condition so far measured for a west coast colony. This was likely driven by the fact that birds breeding at Robben Island fed on < 38% sardine and anchovy that year (Crawford et al. 2012).

This is the lowest percentage on record since diet sampling began in 1989 (Crawford et al. 2011). Thus, the closure benefited chick condition at Robben Island despite one year having unusually poor prey availability (Table 2).

East Coast

The residual plots indicated that the normality and homogeneity assumptions were met (Figure 5). Chick condition was better in 'Closed' years at Bird Island than during 'Open' years (0.11 ± 0.04; $t_{2421} = 2.50$; $p = 0.013$; Figure 6). However, condition was better during 'Open' years than 'Closed' years at St. Croix Island (-0.08 ± 0.04; $t_{2421} = -2.00$; $p = 0.047$; Figure 6). The latter was marginally significant. Thus, the closure benefitted chick survival at Bird Island, but not at St. Croix Island (Table 2).

Chick growth

West Coast

The models produced reasonable residual plots (Figure 7). Growth rates did not differ significantly between 'Closed' and 'Open' years at either Dassen Island (0.002 ± 0.004; $t_{381} = 0.51$; $p = 0.609$; Figure 8) or Robben Island (0.007 ± 0.004; $t_{381} = 1.60$; $p = 0.111$; Figure 8). In both cases, however, the trend was for faster growth during 'Closed' years than 'Open' years (Table 2, Figure 8).

East Coast

Again, the models produced reasonable residual plots (Figure 9). Growth rates did not differ significantly between 'Closed' and 'Open' years at either Bird Island (0.011 ± 0.007; $t_{550} = 1.56$; $p = 0.119$; Figure 10) or St. Croix Island (-0.005 ± 0.007; $t_{550} = -0.68$; $p = 0.496$; Figure 10). For Bird Island, the trend was for faster growth during 'Closed' years than 'Open' years, while the opposite was true for St. Croix Island (Table 2, Figure 10).

Foraging traits

For both the West Coast and East Coast models, the foraging behaviour response variables were log-transformed to achieve normally-distributed residuals and homogeneity of variance (Figure 11, Figure 12, Figure 13, Figure 14, Figure 15, Figure 16).

West Coast

Foraging effort for penguins did not differ significantly between 'Closed' and 'Open' years at either Robben Island or Dassen Island. For Robben Island, however, the closure status had a consistent positive effect, meaning that foraging effort was lower in 'Closed' years than during 'Open' years (Table 2) with a discernible decrease in all three traits (foraging trip duration (h), foraging path length (km), and max. distance to colony (km)) (Figure 17, Figure 18, Figure 19).

On Dassen Island, although birds stayed closer to the island during 'Closed' years (Table 2, Figure 19) trip duration (Figure 17) and foraging path length (Figure 18) increased with birds foraging for longer time periods and travelling slightly further overall distances (Table 2).

East Coast

Foraging effort for penguins breeding at Bird and St. Croix islands in the Eastern Cape was consistently lower in 'Closed' years than during 'Open' years (Table 2, Figure 20, Figure, 21, Figure

22) with a discernible decrease in all three traits. The effect of closure had a significant effect on foraging trip duration for penguins breeding on Bird Island (-0.44 ± 0.17; t_{415}= -2.56; p = 0.011, Figure 20) and for foraging path length for penguins breeding on St Croix Island (-0.31 ± 0.14; t_{411}= -2.28; p = 0.023, Figure 21) with birds spending less time at sea (on Bird Island) and performing shorter trips (on St. Croix Island) during the closed years (Table 2).

5. Discussion

Prey supply has an important impact on bird biology, affecting activity, distribution, energetics, competitive abilities, breeding success and survival (e.g. Furness and Monaghan 1987, Montevecchi et al. 1988, Garthe et al. 1999). Foraging strategies of seabirds are determined by the spatial and temporal availability of different prey resources, the energetic costs of foraging and the rate at which food must be delivered to the nest during breeding (Lack 1968, Weimerskirch et al. 1994). Any alterations in the marine environment caused by either natural phenomena or human-induced activities require flexible behavioural responses by seabirds (Crawford 1998, Pichegru et al. 2010, 2012, Baylis et al. 2012). Whereas volant seabirds (for example, albatrosses and petrels) may exploit food sources distant from their breeding sites (Weimerskirch et al. 1993, Péron et al. 2010), penguins are constrained by both their fidelity to sites once breeding and their mode of locomotion (Wilson 1985, Hockey et al. 2005). Since swimming is slower and more energetically expensive than flying (Pinshaw et al. 1977, Schmidt-Nielsen 1999), penguins require predictable food resources close to their colonies during breeding (Boersma & Rebstock 2009, Ballard et al. 2010, Sherley et al. 2013).

Suggesting that shortage of food contributed to the ongoing decline in the African Penguin population, we wanted to test whether penguins breeding on islands that are open to fisheries work harder to provision their brood than do those breeding at islands around which the fisheries are closed. Therefore we hypothesise that the foraging behaviour of breeding African Penguins at ‘Closed’ islands will respond to the increase in available prey in the surrounding waters and that this in turn will be reflected in a decrease of foraging trip duration, foraging trip range and total distance travelled.

The savings in energy expenditure gained by the bird’s reduced foraging effort will be translated by the breeding adults into increases in their own body condition and, in terms of increased delivery of prey to their chicks, into an inevitable increase in chick condition, chick growth and thus fledging success (e.g. Ballard et al. 2010) (Figure 1).

The positive effect of closures on the foraging behaviour of African Penguins has been shown in this study (Table 2) and supports previous evidence of benefits from fishing closures to penguins (Sherley et al. submitted, summarised in Annex 4, Pichegru et al. 2010, 2012,). Pichegru et al. (2012) demonstrated the benefits of fishing exclusion on the foraging effort of African Penguins breeding in Algoa Bay, while showing that the size of the fishery catches around the colony negatively impacted penguins, even during times of closure. The study suggested that a larger exclusion zone is likely to benefit African Penguins more rapidly and buffer a potential increased fishing pressure at the border of the closure. The fact that foraging traits for Dassen Island showed contrasting effects to closure (Table 2) is likely due to a very low sample size in 2008 and 2009, when Dassen Island was closed to fisheries, due to logistical difficulties and financial constraints. The study period for ‘Closure’ has been too short to allow experimental power to be estimated for all the traits proposed and thus to produce clear-cut results.

Furthermore it should be noted that it has not yet been possible to measure the impact of closures on juvenile and adult survival, age at breeding and breeding participation due to the absence of individual marking of African Penguins since 2009. Flipper bands used to mark penguins in the past were deemed inappropriate, generally reducing penguin survival (Saraux et al. 2011). Juvenile and adult survivals, however, are traits with the most influence on the population dynamics of seabirds (Sæther & Bakke 2000, Votier et al. 2008). Parallel analyses from this study showed that closures benefit chick survival at Robben Island (Sherley et al. submitted, summarised in Annex 4), even though additional closed years are necessary for stronger evidence. With improved chick condition and reduced foraging effort during closure as demonstrated here in most cases, it is likely that closures will also improve juvenile and adult survival over a longer term. Carry-over effects from the breeding period can influence adult survival in seabirds, with the nutritional stress and energetic costs associated with breeding when food is limited causing higher mortality during the subsequent non-breeding period (e.g. Ratcliffe et al. 2002, Davis et al. 2005). In turn, chick body condition at fledging (e.g. Saraux et al. 2011), the size of key body structures (related to chick growth rates; e.g. Morrison et al. 2009) and pre-fledging mass (e.g. Braasch et al. 2009) can influence first-year survival in seabirds. However, robust estimates of changes in these traits would require a long-term datasets.

In addition, recruitment of first breeders to colonies and attempts to establish new colonies closer to present food availability are also likely to be benefitted by longer-term closures. This is because before breeding for the first time, African Penguins probably take their decision on where to breed based on several years of experience, including extensive travel throughout much of the breeding range (e.g. Whittington et al. 2005a). Age at first breeding usually varies between about three and six years (Whittington et al. 2005b) and consistently “good” conditions over equivalent periods may influence decisions on where to breed. Once breeding, African Penguins show strong fidelity to mates and breeding localities, to which they must return to find mates (Crawford et al. 2013). Research is currently underway that will help us to fill in these gaps and estimate all the links shown in Figure 1.

In conclusion, this study confirms that fishing closures can benefit African Penguins, thereby contributing to securing the objectives of the Biodiversity Management Plan for the African Penguin (BMP-AP). Combining fishing closures around islands with a suite of other management actions described in the BMP-AP currently implemented will achieve the objectives of halting penguin decline and subsequently increasing their numbers.

6. References

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7. Tables and Figures

Table 1: Schedule of fishing closures around the four penguin breeding islands.

Island	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
Dassen Island	**x**	**x**					**x**
Robben Island				**x**	**x**	**x**	
St Croix Island		**x**	**x**	**x**			
Bird Island					**x**	**x**	**x**
x = closed							

Table 2: The table shows the summary of the results obtained. In the final column a negative symbol means no benefit to penguins while a positive symbol means a positive benefit to the penguins of the closure. Where log transformed data were used to achieve normally distributed residuals and homogeneity of variance, effect sizes are presented as percentage changes. Significant effects are highlighted.

Region	**Outcome**	**Colony**	**Effect**	**95% CI**		**p-value**	**Effect of closure on penguins**
WEST COAST	Max Distance	Dassen	-26%	-58%	30%	0.290	+
		Robben	-2%	-43%	66%	0.930	+
	Trip Duration	Dassen	44%	-14%	142%	0.166	-
		Robben	-7%	-44%	56%	0.790	+
	Path Length	Dassen	9%	-33%	78%	0.719	-
		Robben	-15%	-46%	35%	0.499	+
	Condition	Dassen	-0.022	-0.077	0.033	0.433	-
		Robben	0.140	0.084	0.195	< 0.001	+
	Growth	Dassen	0.002	-0.006	0.011	0.609	+
		Robben	0.007	-0.001	0.016	0.111	+
EAST COAST	Max Distance	Bird	-13%	-32%	11%	0.253	+
		St Croix	-21%	-39%	2%	0.069	+
	Trip Duration	Bird	-29%	-51%	3%	0.011	+
		St Croix	-3%	-34%	42%	0.433	+
	Path Length	Bird	-10%	-30%	16%	0.412	+
		St Croix	-26%	-44%	-4%	0.023	+
	Condition	Bird	0.111	0.024	0.198	0.013	+
		St Croix	-0.085	-0.168	-0.001	0.047	-
	Growth	Bird	0.011	-0.003	0.025	0.119	+
		St Croix	-0.005	-0.018	0.009	0.496	-

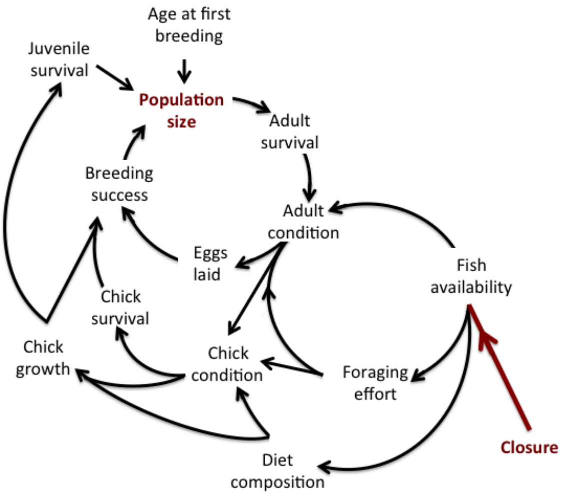

Figure 1: A conceptual model of the connections between penguin traits and food availability that relate to closures around penguin breeding islands

Chick condition

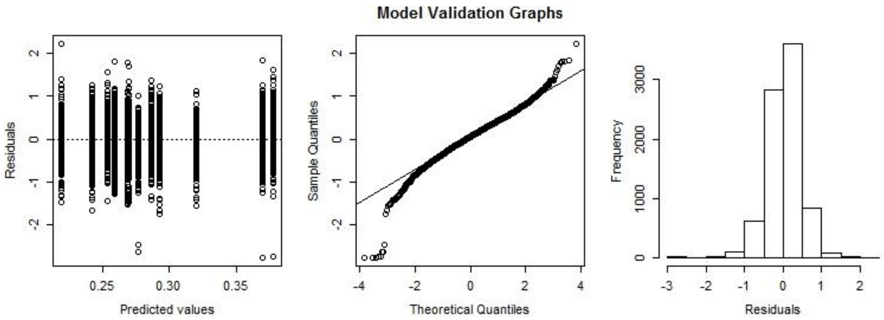

Figure 2: Model diagnostics for models of chick condition at Dassen Island and Robben Island.

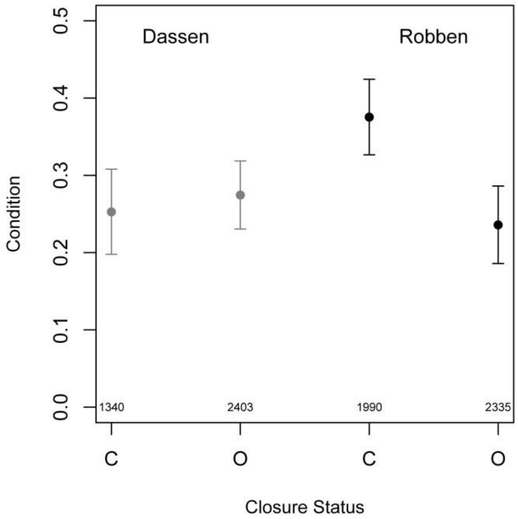

Figure 3: Modelled mean (± 95% confidence intervals) chick condition at Dassen Island and Robben Island during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.

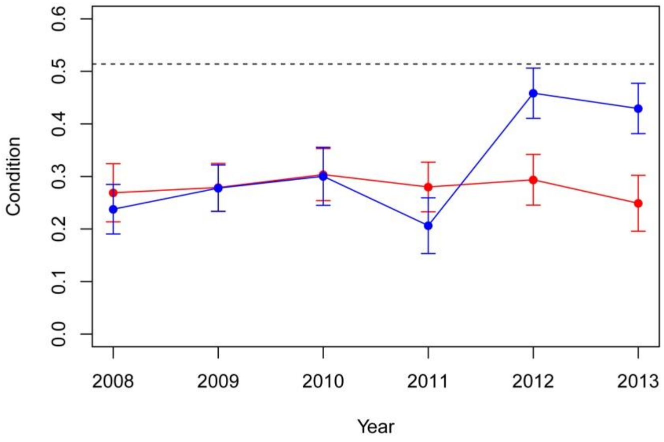

Figure 4: Annual mean (± 95% confidence intervals) chick condition at Dassen Island (red) and Robben Island (blue) from 2008 to 2013. The dashed line indicates the chick condition at Robben Island in 2004 (the reference year). Robben Island was closed to fishing in 2008 and 2009.

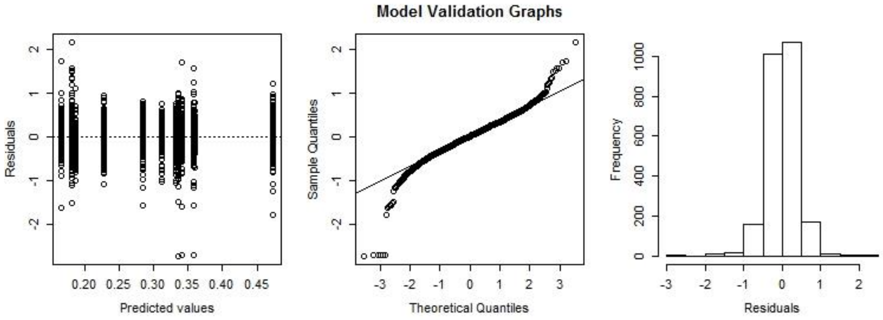

Figure 5: Model diagnostics for models of chick condition at Bird Island and St. Croix Island.

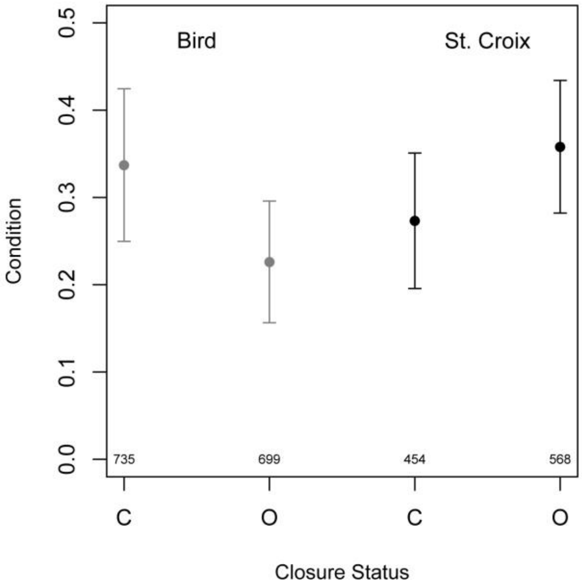

Figure 6: Modelled mean (± 95% confidence intervals) chick condition at Bird Island and St Croix Island during years where a 20 km radius around the island was closed to fishing 'C' or open to fishing 'O'. Numbers above the x-axis denote sample sizes.

Chick growth

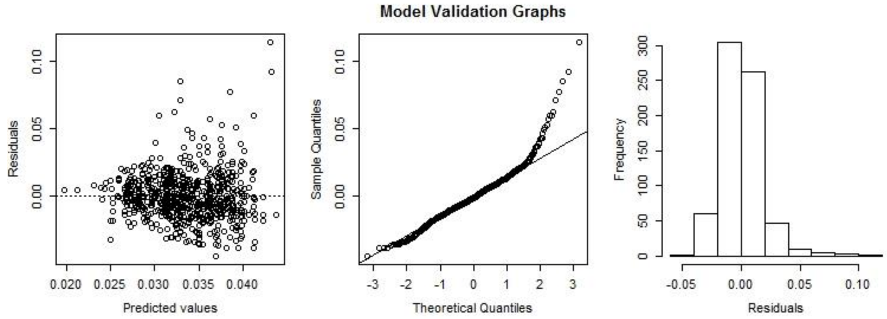

Figure 7: Model diagnostics for models of chick growth at Robben and Dassen islands.

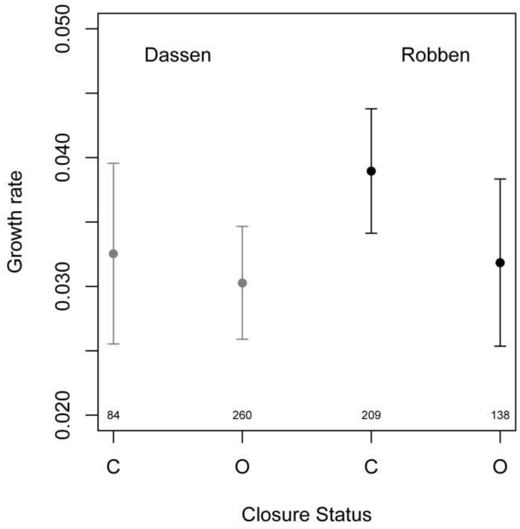

Figure 8: Modelled mean (± 95% confidence intervals) chick growth at Dassen Island (grey) and Robben Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.

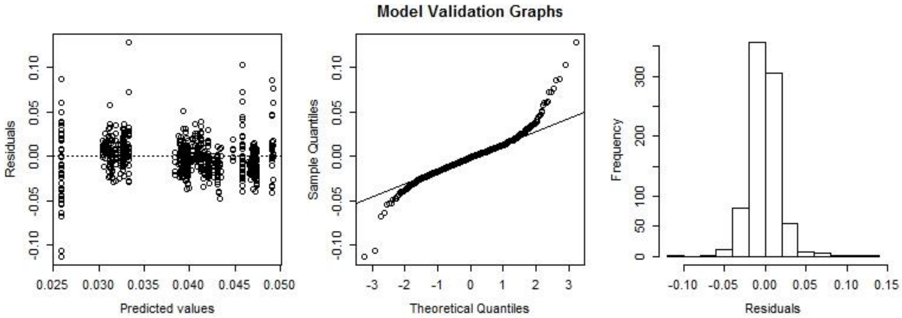

Figure 9: Model diagnostics for models of chick growth at Bird and St. Croix islands.

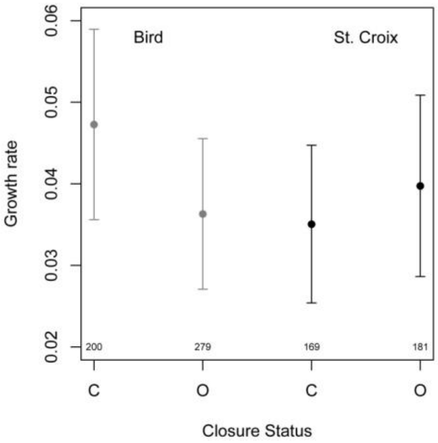

Figure 10: Modelled mean (± 95% confidence intervals) chick growth at Bird Island (grey) and St Croix Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.

Foraging traits

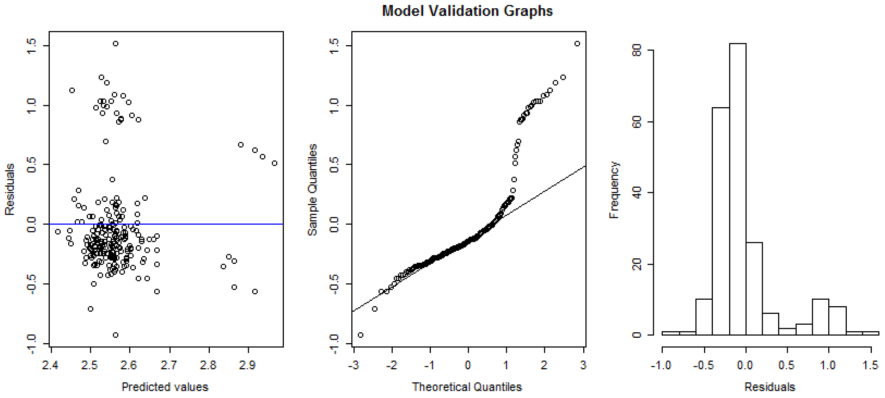

Figure 11: Model diagnostics for models of Foraging Trip Duration on the West Coast.

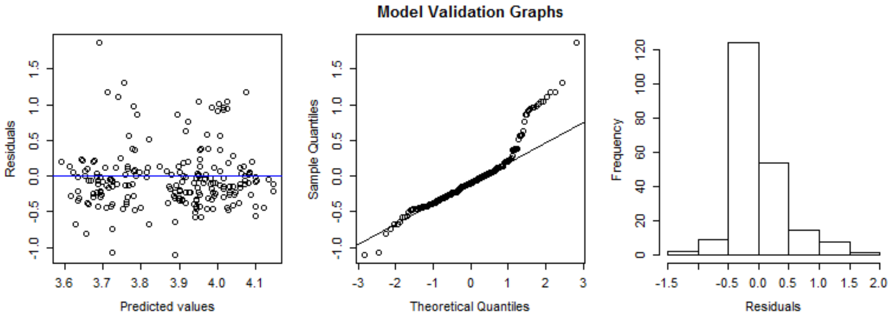

Figure 12: Model diagnostics for models of Foraging Trip Path Length on the West Coast.

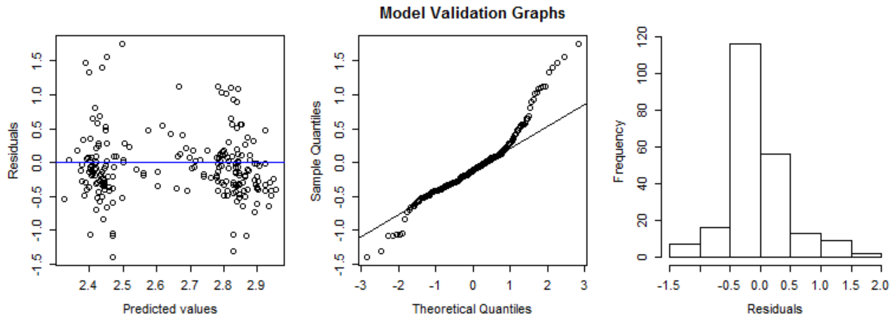

Figure 13: Model diagnostics for models of Maximum Foraging Distance on the West Coast.

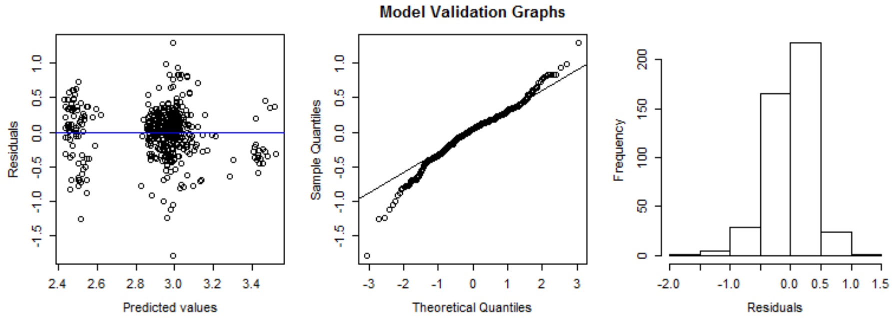

Figure 14: Model diagnostics for models of Foraging Trip Duration on the East Coast.

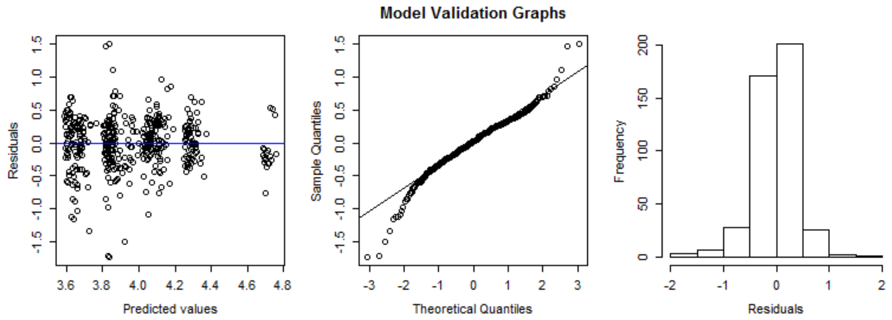

Figure 15: Model diagnostics for models of Foraging Pathlength on the East Coast.

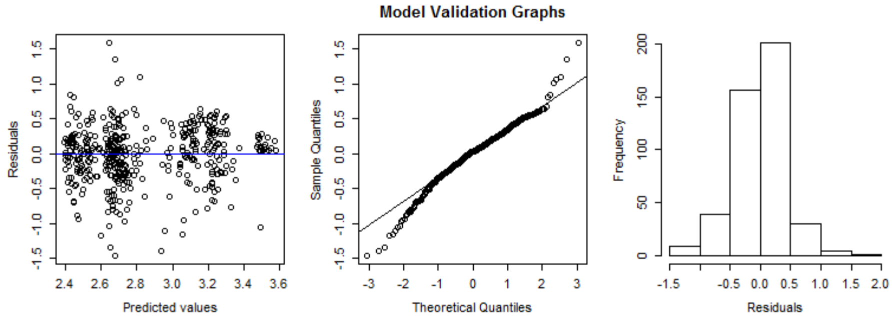

Figure 16: Model diagnostics for models of Maximum Foraging Distance on the East Coast.

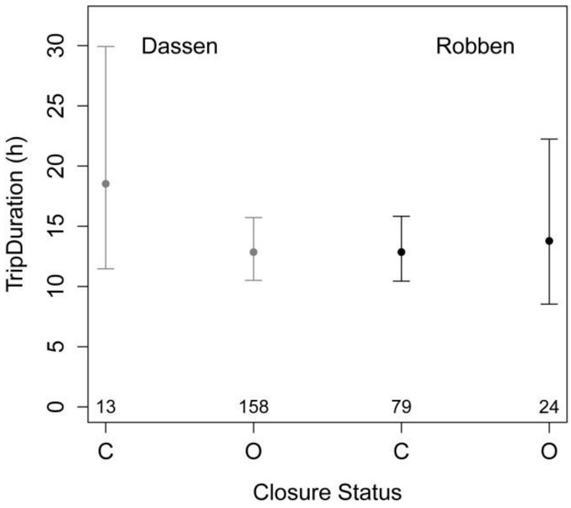

Figure 17: Modelled mean (± 95% confidence intervals) Trip Duration (h) at Dassen Island (grey) and Robben Island (black) during years where a 20 km radius around the island was closed to fishing 'C' or open to fishing 'O'. Numbers above the x-axis denote sample sizes.

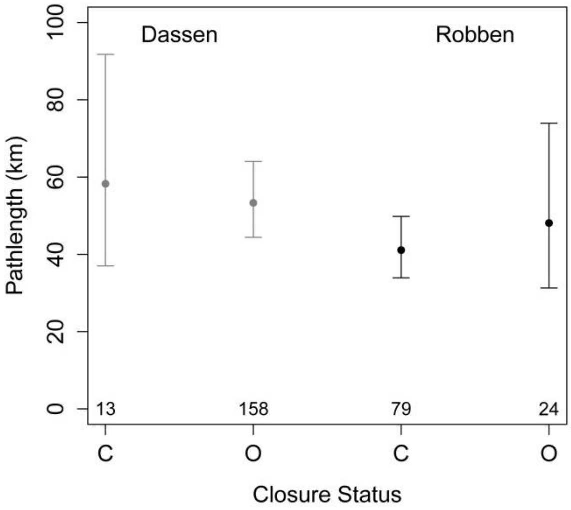

Figure 18: Modelled mean (± 95% confidence intervals) Pathlength (km) at Dassen Island (grey) and Robben Island (black) during years where a 20 km radius around the island was closed to fishing 'C' or open to fishing 'O'. Numbers above the x-axis denote sample sizes.

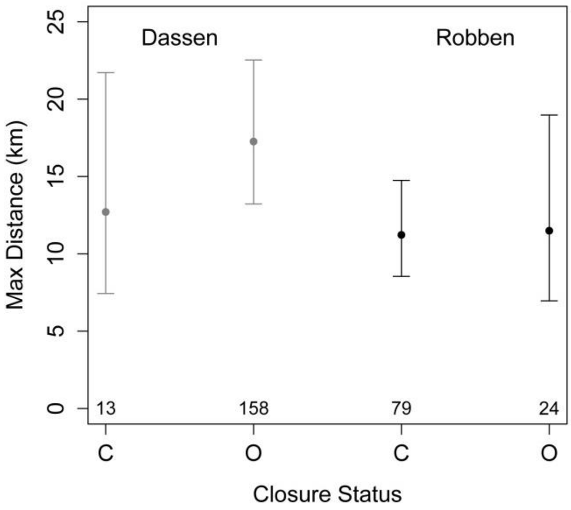

Figure 19: Modelled mean (± 95% confidence intervals) Max Distance (km) at Dassen Island (grey) and Robben Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample

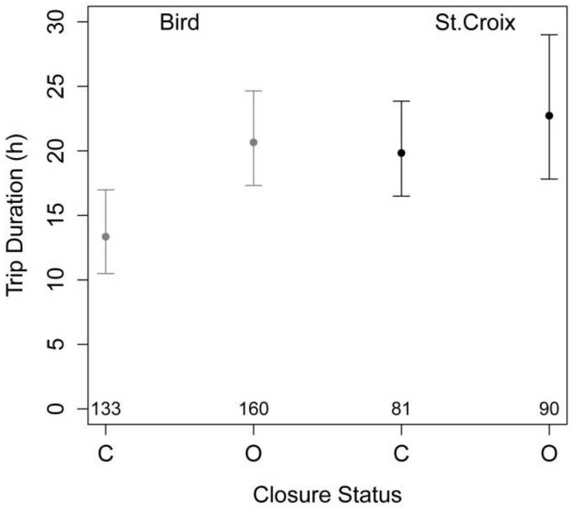

Figure 20: Modelled mean (± 95% confidence intervals) Trip Duration (h) at Bird Island (grey) and St. Croix Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.

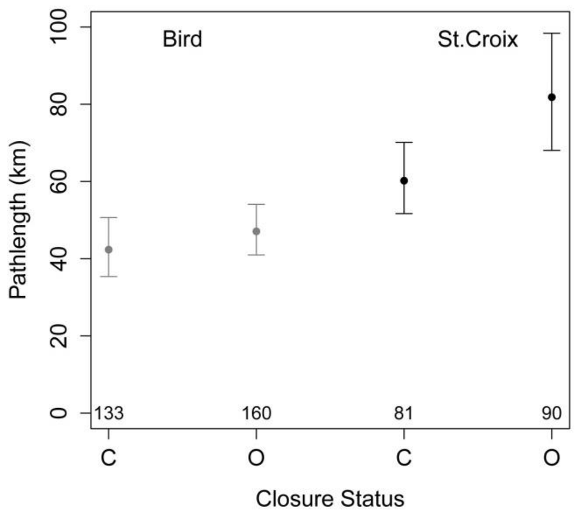

Figure 21: Modelled mean (± 95% confidence intervals) Pathlength (km) at Bird Island (grey) and St. Croix Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.

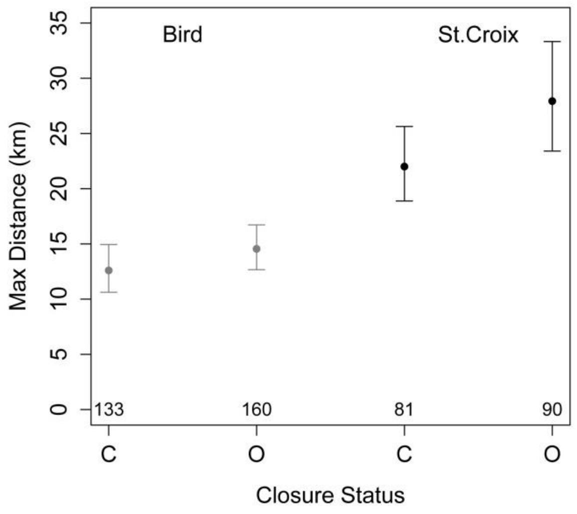

Figure 22: Modelled mean (± 95% confidence intervals) Max Distance (km) at Bird Island (grey) and St. Croix Island (black) during years where a 20 km radius around the island was closed to fishing ‘C’ or open to fishing ‘O’. Numbers above the x-axis denote sample sizes.