Title: ‘Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean’.

Running head: Tropical cyclone impacts on seabird survival.

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Keywords: *Pterodroma*, petrel, mortality, adult survival, juvenile survival, migration, hurricane, typhoon, climate change.

Primary research article

Abstract

Tropical cyclones are renowned for their destructive nature and are an important feature of marine and coastal tropical ecosystems. Over the last 40 years their intensity, frequency and tracks have changed, partly in response to ocean warming, and future predictions indicate that these trends are likely to continue with potential consequences for human populations and coastal ecosystems. However, our understanding of how tropical cyclones currently affect marine biodiversity, and pelagic species in particular, is limited. For seabirds the impacts of cyclones are known to be detrimental at breeding colonies, but impacts on the annual survival of pelagic adults and juveniles remain largely unexplored and no study has simultaneously explored the direct impacts of cyclones on different life history stages across the annual life cycle. We used a 20 year data set on tropical cyclones in the Indian Ocean, tracking data from 122 Round Island petrels and long-term capture-mark-recapture data to explore the impacts of tropical cyclones on the survival of adult and juvenile (first year) petrels during both the breeding and migration periods. The tracking data showed that juvenile and adult Round Island petrels utilise the three cyclone regions of the Indian Ocean and were potentially exposed to cyclones for a substantial part of their annual cycle. However, only juvenile petrel survival was affected by cyclone activity; negatively by a strong cyclone in the vicinity of the breeding colony and positively by increasing cyclone activity in the northern Indian Ocean where they spend the majority of their first year at sea. These contrasting effects raise the intriguing prospect that the projected changes in cyclones under current climate change scenarios may have positive as well as the more commonly perceived negative impacts on marine biodiversity.

Introduction

Extreme climatic events such as tropical cyclones (also known as hurricanes and typhoons, but hereafter referred to as cyclones) are an important feature of tropical marine, coastal and island ecosystems. Cyclones are typically considered destructive by nature, negatively impacting on human populations (Mendelsohn *et al.*, 2012, Peduzzi *et al.*, 2012), marine (Dewald & Pike, 2014, Perry *et al.*, 2014, Raynor *et al.*, 2013) and terrestrial biodiversity (Dunham *et al.*, 2011, McConkey *et al.*, 2004, Oli *et al.*, 2001, Rittenhouse *et al.*, 2010, Schoener *et al.*, 2004), but can have both short and long-term positive ecological impacts on marine and terrestrial ecosystems (Burslem *et al.*, 2000, Carrigan & Puotinen, 2014, Lugo, 2008).

Over the last 40 years the changes in cyclone frequency, rate of genesis and intensity in different hemispheres and ocean basins, primarily in response to a warming environment, have been well documented (Elsner *et al.*, 2008, Evan *et al.*, 2011, Kishtawal *et al.*, 2012, Kuleshov *et al.*, 2010, Webster *et al.*, 2005). In the Southern Indian Ocean cyclone region (hereafter referred to as SIO) there is weak evidence to show that cyclones are getting less frequent (Kuleshov *et al.*, 2010), but there is an increase in the frequency of strong cyclones (Kuleshov, 2014, Kuleshov *et al.*, 2010, Webster *et al.*, 2005), an increase in the lifetime maximum wind speed (Deo & Ganer, 2014, Elsner *et al.*, 2008) and an increase in the rate at which cyclones intensify (Kishtawal *et al.*, 2012). There is also a strong connection between the El Nino southern oscillation (ENSO) and cyclones in the SIO with ENSO affecting the frequency and spatial distribution of cyclones (Ho *et al.*, 2006). In El Niño years there were more cyclones in the western SIO (west of 75^0) than in La Niña years and in El Niño years cyclone tracks followed an earlier recurve to the east. In the Northern Indian Ocean cyclone region (hereafter referred to as NIO) there is no evidence for a change in the annual number of cyclones (Evan & Camargo, 2011, Webster *et al.*, 2005), but there are some regional variations within this trend. Cyclone genesis in the Arabian Sea has increased, yet declined in the Bay of Bengal (Deo & Ganer, 2014) and the duration of the pre-monsoon cyclone period in the Arabian Sea (May-June) is increasing with cyclones forming earlier (Deo & Ganer, 2014). There is also evidence for a recent increase in cyclone intensity in the NIO (Elsner *et al.*, 2008, Evan *et al.*, 2011, Webster *et al.*, 2005). Under a range of climate change scenarios these trends are predicted to continue (Gualdi *et al.*, 2008, Knutson *et al.*, 2010) and alongside other extreme weather events are predicted to have important consequences for biodiversity and human systems (Garcia *et al.*, 2014, Jentsch & Beierkuhnlein, 2008, Sainz de *et al.*, 2014). In order to understand the impacts of the projected changes in cyclone activity on biodiversity, we first need to understand how biodiversity is affected by current cyclone conditions both in the short and long-term. While a number of studies have explored this in terrestrial systems (see earlier examples and Ameca y Juárez *et al.* (2013), Moreno and Møller (2011)), documented impacts in marine systems are less commonplace despite this being the environment where cyclone genesis and their subsequent tracks primarily occur. In marine systems seabirds are a relatively well-studied taxa, in terms of their ecology and how they are influenced by environmental conditions (Barbraud *et al.*, 2012, Jenouvrier, 2013, Oro, 2014, Sydeman *et al.*, 2012) but studies in the tropics are still limited (Oro, 2014). Given the tropical nature of cyclones it is therefore unsurprising that only a small number of studies have examined their impacts on seabird ecology. To date studies have primarily concentrated on either coastal species at or near breeding grounds (Devney *et al.*, 2009, King *et al.*, 1992, Raynor *et al.*, 2013, Spendelow *et al.*, 2002) or the ‘inland-wrecks’ of pelagic species driven ashore by cyclones (Bugoni *et al.*, 2007, Hass *et al.*, 2012). Given that seabirds are typically long lived, with a relatively slow life history strategy on the slow-fast continuum (Saether & Bakke, 2000), their population growth rate is most likely to be sensitive to changes in survival and adult survival in particular, hence understanding how this might respond to cyclones is important, but clearly overlooked in tropical species. To the best of our knowledge the impact of cyclones on annual survival has only been examined in one (temperate) species, the Cory's shearwater (*Calonectris diomedea*), which breeds in the Mediterranean but migrates through the hurricane region in the Atlantic, where increasing storm frequency negatively impacts on adult survival (Boano *et al.*, 2010, Genovart *et al.*, 2013, Jenouvrier *et al.*, 2009b). No study has yet to explicitly examine this in the survival of a tropical seabird, which could be exposed to cyclones at both the breeding grounds and during migration.

Exploring the impacts of large-scale environmental factors, such as cyclones, on population demography is challenging because both location data are required to demonstrate where and when species of interest are exposed to environmental factors and long-term, detailed demographic data are required to then quantify any impact. In species with a migratory aspect to their life cycle, such as pelagic seabirds, these challenges are compounded and the need for year-round, extensive location data are particularly important to qualify the extent of exposure. In this study we interpret, for the first time, a long-term demographic data set on a tropical seabird in light of seasonal location data relative to the spatiotemporal distribution of an environmental factor (cyclones) likely to impact on survival. Our study is based in the Indian Ocean, which has three distinct cyclone regions, three cyclone seasons (Evan & Camargo, 2011) and exhibits long-term trends in cyclone metrics since the 1970s (Elsner *et al.*, 2008, Kishtawal *et al.*, 2012, Kuleshov *et al.*, 2010, Webster *et al.*, 2005). We first combined 20 years of cyclone tracks and three years of tracking data from adult and fledgling Round Island petrels (*Pterodroma arminjoniana*) to establish that these pelagic seabirds were exposed to cyclones at the breeding colony, during their annual migration and first year at sea, within the Indian Ocean. Secondly, we used a 20 year capture-mark-recapture (CMR) data set and the corresponding seasonal cyclone data to examine the impact of cyclones on adult and first year survival at different spatial scales.

Materials and methods

Study site, species and data collection

This study was conducted at Round Island Nature Reserve (19.85° South 57.78 ° East), a 219 ha island situated 23km off the North coast of Mauritius, Indian Ocean. The climate is strongly seasonal, dominated by two monsoon periods, the warm and wet North East monsoon (NEM) and the cooler, drier South West Monsoon (SWM) (Fig. 1). The former typically runs from October to April (i.e. austral summer) and includes the tropical cyclone season and the latter from May to September (i.e. austral winter) (Schott & McCreary Jr, 2001). Five species of seabird breed on Round Island including the Round Island petrel (*Pterodroma arminjoniana*), which is a long-lived, gadfly petrel (300-500g). The classification of the petrel on Round Island has proved confusing since its discovery in 1948, and recent genetic evidence suggests that there are at least three species of *Pterodroma* breeding and hybridising on the island (Brown *et al.*, 2011, Brown *et al.*, 2010). Unpublished ringing and tracking data suggest that immigration from both the Pacific and Atlantic Oceans continues, but to what extent remains unclear. Round Island petrels breed all year round, with chicks and eggs found in any month of the year, but there is a peak in egg-laying in August-October (Tatayah, 2010). Petrel activity (i.e. eggs, chicks and adults) is typically lowest on the island in May each year (Fig. 1) and hence a petrel year runs from June to May, thereby spanning two calendar years and is referred to by the first calendar year, i.e. season 2001 = 2001/2002. The petrels are surface nesters, nesting under rock ledges, in clusters of boulders and in the native tussock grass *Vetivera arguta*. Not all petrels that return to Round Island attempt to breed each year, but along with breeding petrels remain at Round Island for around six months. When not at Round Island these petrels are pelagic, typically performing a six month migration to other regions in the Indian Ocean including the Arabian Sea, Somali basin, Bay of Bengal and Western Australian basin. Adult petrels return to Round Island each year and therefore typically spend half the year at the island and half the year on migration and the timing of this process is consistent from one year to the next (unpublished analyses). Juvenile (first year) petrels fledge at around 90 days old (Tatayah, 2010), remain in the vicinity of Round Island for up to two weeks post-fledging and then stay away from the island for at least one year spending time in the Mascarene basin, Somali basin, Arabian Sea and Bay of Bengal, before returning aged ~18 months or older. In the 1970s and 1980s sporadic ringing of a small number of petrels (63) on Round Island occurred, and in 1993 a population monitoring programme was initiated involving regular surveys of breeding sites, monitoring of breeding success, ringing of chicks (aged >70 days) and adults (with South African Bird Ringing Unit numbered steel rings) and their subsequent recapture (Tatayah, 2010). As part of the surveys petrels are recaptured when breeding, i.e. found on an egg or chick, and also when resting on the island. Petrels are also known to compete for nest sites, and also rest in nest sites, and hence can be found in nest sites with chicks and eggs that are not their own (Tatayah, 2010), therefore we are unable to consistently distinguish between breeding and non-breeding individuals and hence immature or sub-adults and adult petrels. Prior to the establishment of a permanent field station on the island in 2001, this monitoring programme was conducted as part of the four, one week management trips conducted each year. Post 2001 the petrel population has been monitored on a monthly basis.

Tropical cyclones

The Indian Ocean has three cyclone regions; two in the NIO, the Arabian Sea (AS) and the Bay of Bengal (BoB) and one in the SIO North of 40^0 South (Fig. 2a). In the AS & BoB the cyclone season is bimodal (May-June & October-December), with 90% of cyclones occurring in May/June and November (Evan & Camargo, 2011). Cyclones are more frequent and more intense in the May/June period (Evan & Camargo, 2011). In the SIO the main cyclone season runs from December to April (Webster *et al.*, 2005) and in order to comply with our nomenclature for a petrel year, we chose to label cyclone seasons by the first of the two years that they span (i.e. 2001=2001/2002 season), ensuring consistency between both petrel and cyclone related data. We accessed data on storms from the International Best Track Archive for Climate Stewardship (IBTrACS) (Knapp *et al.*, 2010). We included data from 1993-2012 and only those storms that were classified as tropical cyclones, whereby they exceeded a maximum sustained wind speed of 63 km/h (or 33 knots) (Evan & Camargo, 2011). For each cyclone we calculated its accumulated cyclonic energy over its lifetime (ACE) (Bell, 2003) and summed these for each region to generate regional values of ACE. We generated kernel density estimations (plate carrée projection, cell size 10 km and search radius of 180km) for each of the three cyclone regions for both cyclone tracks and cyclone ACE.

Exposure of petrels to tropical cyclones

Adult petrel distribution

Between November 2009 and February 2010 and November 2010 and February 2011 we deployed 135 and 85 British Antarctic Survey MK15 geolocators respectively on adult petrels. Geolocators were attached to the tarsus via 1mm or 0.75mm thick salbex (an industrial grade PVC, Sallu Plastics, UK) rings, which including this attachment weighed 3.6 g (<1.0% of the mean adult mass: 374 g). Loggers were deployed predominantly on birds that were captured while resting (94.1%) on the island and not directly observed in a breeding attempt i.e. incubating an egg (2.7%) or brooding a chick (3.2%). Geolocators were recovered between October 2010 and November 2012, either during the standard monthly petrel breeding surveys or during occasional specific searches for geolocators. All loggers underwent a three-five day calibration period at a known location prior to deployment and post-deployment this process was repeated.

Data from recovered, viable geolocators were downloaded and decompressed into light, temperature and immersion data using ‘BAS Track’ software provided by the British Antarctic Survey. We used light and immersion data from the loggers to determine the start and end dates of the overwinter migration period for petrels from Round Island. The last day of the petrel at Round Island was taken as the start date of the migration period and the first day back at Round Island as the end date. Locations of the petrels during their overwinter migrations were estimated using the R package ‘TripEstimation’ (Sumner *et al.*, 2009, Thiebot & Pinaud, 2010) run in the software R (R Core Team, 2008) (see Supporting Information (SI) for details).

Juvenile petrel distribution

In November-December 2009 we deployed 24 British Antarctic Survey MK15 leg-mounted geolocators on Round Island petrel chicks that were within ~10 days of fledging. Tag deployment and recovery protocols followed that for adults. All chicks fledged and by November 2015 12 of these Geolocators had been recovered. However, only viable data were obtainable from six of these due to tag failure. Due to tag memory issues, and the resulting absence of light data and corresponding SST data, we were unable to derive locations using the method described for adults, so we adopted an alternative approach. To determine the location of these six individuals during their first year at-sea post fledging, light data were processed using a threshold method (Phillips *et al.*, 2004). Times of sunrise and sunset events were estimated from the light data and converted to locations using TransEdit and BirdTracker software (British Antarctic Survey). We used a threshold setting of 10, a sun elevation angle of -3.0 and the compensation for movement filter. All locations within 21 days either side of the equinox periods were excluded as were all locations that occurred over land and we removed any unrealistic locations based on flight speeds which exceeded 80 kmh. This resulted in 3441 locations encompassing the Somali basin, Arabian Sea, Bay of Bengal and Western Australian Basin. We divided these locations according to the three different cyclone seasons and generated kernel density estimations (plate carrée projection, cell size 10km and search radius of 180km) for each cyclone season.

Petrel and cyclone distribution

We mapped the kernel densities for both adult and juvenile petrels and the corresponding cyclone tracks and ACE to provide a visual representation of the exposure of petrels to cyclones in each of the three regions and three cyclone seasons. For each petrel year we calculated ACE at a range of temporal and spatial scales where cyclones and petrels overlapped for the AS, BoB and SIO (See Table 1 for details), thereby providing a measure of cyclone activity for the areas utilised by petrels during the relevant cyclone season. In the NIO we estimated ACE for AS and BoB in each cyclone season and in the SIO we estimated ACE at three scales: hemisphere scale, i.e. west of 115^0 East (the Australian coast); a regional scale focusing primarily on where petrels were located during the cyclone season, i.e. between $50\text{-}90^0$ East; and a local scale (within 275km of Round Island). The latter was based on data from Meteo services, Mauritius (http://metservice.intnet.mu/cyclone-track.php), on the proximity of cyclones that affected Mauritius between 1958 and 2007 and hence could have directly affected Round Island. Because immature petrels are known to utilise the AS and BoB during both cyclone seasons we generated an annual measure of ACE for these two regions combined. We also generated a measure of overall cyclonic activity throughout the Indian Ocean (IO) (and hence the entire area possibly covered by juvenile petrels) by summing the ACE metrics for the three cyclone seasons in the NIO & SIO. All mapping and spatial analyses were conducted using ARC MAP v10.0 (ESRI, 2010).

Petrel survival

We adopted an analytical approach based upon a series of single-state Cormack-Jolly-Seber (CJS) models and multistate models implemented in Program MARK 6.2 (White & Burnham, 1999). An important assumption underpinning the use of a CMR framework is that the sampling interval (i.e. recapture period) is short in comparison to the intervals between sampling periods (Lebreton *et al.*, 1992, O'Brien *et al.*, 2005) and hence that mortality during this occasion is low. Our sampling regime is year-round; however Round Island petrels typically spend only six months of the year at Round Island (where they can be recaptured) and six months at sea (where they cannot be recaptured). Therefore, by their nature they create sampling periods and corresponding intervals that are broadly equivalent. While this is not ideal, it has been demonstrated that where sampling periods are not brief in comparison to the intervals that any induced bias in survival rates are minimal when survival rates are typically high (O'Brien *et al.*, 2005). As petrels are typically long lived species (>40 years for Round Island petrels – unpublished ringing data) with annual adult survival of >90% (Jones *et al.*, 2011, Waugh *et al.*, 2006) it would be reasonable to assume that short-term survival rates would be so high as not to violate this assumption for Round Island petrels.

We are primarily interested in exploring the potential impact of cyclones on the survival of petrels that frequent Round Island during their adult life history stage (in this case petrels in their second year or older, which can include both sub-adult and adult birds) and the juvenile (i.e. first year) life history stage of petrels fledging from Round Island. We based this division on the premise that juvenile petrels would be substantially less experienced in the marine environment (and associated activities such as flight and foraging) than petrels that have made it through the juvenile life history stage, i.e. sub-adults and adults, and hence more susceptible to the impacts of environmental conditions (such as cyclones) as has been shown for other seabirds (Frederiksen *et al.*, 2008, Horswill *et al.*, 2014, Sidhu *et al.*, 2012). Hereafter, for convenience, we refer to these two life history stages as adult(s) and juvenile(s). Given the potentially mixed origins of petrels on Round Island (see study species section for details), i.e. immigrants and those originating from Round Island, we recognised that a common origin of birds to examine juvenile survival was required and hence we restricted the analyses of juvenile survival to only those birds ringed as chicks on Round Island. In contrast for adults we are interested in the survival of adults known to frequent Round Island, and can therefore include both petrels that originated from Round Island and potential immigrants in any analyses, thereby maximising the use of the data potentially available. Below we describe the discrete analytical approaches we took to explore the impact of cyclones on firstly adult petrel survival and secondly on juvenile petrel survival.

Adult survival

We used recaptures of 2147 adults only (i.e. more than one year old and having completed their first post-fledging migration) from the petrel monitoring programme between 1993 and 2012 (a petrel 'year' runs from 1st June – 31st May) to construct individual recapture histories. For petrels ringed as adults the ringing event was the start of their recapture history and for those ringed as chicks their first capture occasion as an adult was the start of their recapture history. Model notation is as follows apparent survival (Φ), recapture probability (P), (t) time dependence and (.) constant (Lebreton *et al.*, 1992). Initially we tested the fit of our fully time-dependent global model $\Phi_{(t)}\ P_{(t)}$ to the data using a goodness of fit test in U-CARE 2.3.2 (Choquet *et al.*, 2009). Akaike's Information Criteria (AIC) was corrected for over-dispersion (i.e. including a variance inflation factor – see Results: Goodness of fit) as QAICc (Burnham & Anderson, 2002). We then compared a set of models with Φ constrained by six measures of cyclone ACE (using the logit link) with two reference models ($\Phi_{(t)}\ P_{(t)}$ and $\Phi_{(.)}\ P_{(t)}$) using *ANODEV* (Grosbois *et al.*, 2008). Cyclone metrics tested included; SIO, SIO Region, SIO

Local, NIO (May-June), AS (May-June) and SIO+NIO (May-June). The latter metric represented the geographical range of petrels during the two cyclone seasons when combined.

Juvenile survival

Post-fledging many species of seabird leave their natal colony and then embark on a period at-sea, which can encompass multiple years (Croxall & Rothery, 1991, Weimerskirch, 2002), before returning to their natal colony for the first time as sub-adults or adults. During this period at sea individuals are typically unobservable and hence multistate models with an unobservable state representing this period are frequently used (Spendelow *et al.*, 2002) when modelling survival. However, for Round Island petrels we know that this is not strictly true because some individuals are recaptured after only one year at sea (64/473 fledgling petrels from Round Island) and tracking data from GLS deployed on fledglings show that they return to Round Island after only one year away, i.e. during their second year. In light of this an alternative modelling approach would be to use a single state CJS model, where all adult birds, i.e. more than one year old, are assumed to have the same recapture rate. However, in our study system this may not be the case as young birds are likely to be returning to Round Island as visitors (i.e. non-breeders) rather than as breeding petrels and hence have lower recapture rates due to differences in behaviour and time spent at the breeding colony. One potential solution to this is to distinguish between recapture rates for young and older adults in the CJS models, but this could generate imprecise survival estimates for young adults if recapture rates are very low. No distinction between young and older adult survival rates is one solution to the latter issue.

In light of the peculiarities of our study system modelling the impacts of tropical cyclones on juvenile survival in Round island petrels is therefore not a straight forward process. To overcome these issues, and ensure that our findings were not contingent on the choice of model type, we adopted three approaches as follows:

(i) We chose to ignore any potential variation in age specific recapture probabilities of petrels 2 years and older and used a simple CJS model with a two age-class structure (juvenile and adult) in both survival and recapture rate.

(ii) We acknowledged there might be variation in the recapture rates between two-year old and older petrels and implemented a CJS model with a three-age class structure in recapture rates, i.e. juvenile, two year old and three year and older.

(iii) We removed all recapture events of petrels as two-year olds and using a multistate modelling framework created a ‘ghost’ state into which all individuals transitioned, after their first year for at least one year, before transitioning into an adult state following their recapture on Round Island for the first time. In effect petrels spent at least their second year in this state and their annual survival rates are assumed to be the same as those for petrels observed as adults.

We applied each of these approaches to the 853 petrel recapture histories. Approaches based on single state CJS models followed the same methodology as outlined for adult survival, but incorporated age structure in both survival and recapture rates (see SI for details).

We used a multistate CMR (Brownie *et al.*, 1993) to estimate survival rates, recapture probabilities and state transition rates. Our model was based on three states: state 1 which represents the initial marking of a petrel and its juvenile period (first year); state 2 which is an unobservable ‘ghost’ state into which all petrels transition after the juvenile period; and state 3 where a petrel has returned to the colony and been recaptured. Multistate models can often result in numerous model parameters, many of which are in effect redundant, therefore to avoid this we fixed a number of parameters based on reasonable biological assumptions relevant to our study system (Spendelow *et al.*, 2002) (see SI for details).

We used the programme U-CARE (Choquet *et al.*, 2009) to assess the fit of the data to a Jolly MoVe model. We excluded the tests 3GSR and WBWA, based on the grounds that we will be running an age-structured model as done by Votier *et al.* (2008). Akaike's Information Criteria (AIC) was corrected for any over-dispersion (i.e. including a variance inflation factor) as QAICc (Burnham & Anderson, 2002).

Previous research on the Round Island petrel suggests that petrels are recaptured at Round island for the first time aged two years and above, with the majority returning at around 3 to five years old (Tatayah, 2010). Age is therefore likely to be influential in the transition rates from state 2 to state 3, therefore we explored this as the first step in our analytical framework. This was done be sequentially increasing the maximum age at which petrels could return to Round island for the first time, hereafter known as age of first recapture (AFR) and assessing model fit based on AIC following Burnham and Anderson (2002). Once the appropriate age structure in AFR was established then we constrained juvenile survival by various measures of TC ACE following the approach used in the single state CJS models.

Results

Cyclones

Between 1993 and 2012 there were 301 cyclones in the SIO, 42 in AS and 64 in BoB (see Table S1, SI, for details). Cyclones in the SIO reached a maximum sustained wind speed of 260 Km/h and 265 Km/h in the NIO. The tracks of these cyclones are summarised in Fig. 2a and show the three distinct cyclone regions in the IO. Fig. 2b shows where ACE, for the entire period (1993-2012), is concentrated in each of these regions and clearly overlaps with the distribution of tracked adult petrels (particularly in the SIO and AS, Fig. 2c) and the migration routes of juvenile petrels (particularly in the AS & BoB, Fig. 2d). ACE metrics for the IO, SIO and NIO (Annual and the AS and BoB in May/June only) are shown in Fig. 3a-d. At Round Island local annual ACE metrics ranged from 0.00-13.72 (see Fig. 4a for annual estimates).

Adult survival

There was some evidence for trap-dependence and transience (Table S2, SI) in our global model ($\Phi_{(t)}$ $P_{(t)}$). We calculated an over-dispersion coefficient ($\hat{c}$) of 1.39 and applied this in Program MARK as a variance inflation factor.

We found no compelling evidence for an impact (either negative or positive) of cyclones on annual adult survival between 1993 and 2012 (Table 2). The constant survival model (model 2) was preferred to a time-dependent model, suggesting that adult survival showed little temporal variation, which was then not significantly explained by any of the cyclonic metrics. Annual adult survival was estimated at 0.96 (95% CIs: 0.959; 0.968) from model 2, Table 2 and the annual average recapture probability across the whole study period was 0.31 ranging from 0.07 to 0.47.

Juvenile survival

The median $\hat{c}$ GOF test applied to our global model ($\Phi_{j(t),a(t)}$ $P_{j(.),a(t)}$) indicated that there was some overdispersion in the data (see Table S2, SI) with an estimated $\hat{c}$ of 1.238, which we applied as a variance inflation factor in Program MARK to both of the single state CJS models.

Two-age class CJS model

Model selection confirmed that adult survival was constant and juvenile survival was time dependent (model 5, Table 3a). Cyclones in the vicinity of Round Island had a strong negative impact on the apparent survival of juvenile petrels, at both the local and the regional scale (slope coefficients; +/- 95% CIs for influence of SIO local ACE: model 2, Table 3a; -0.109, [-0.156; -0.061] and SIO Regional ACE: model 6, Table 3a; -0.013, [-0.021; -0.005]), reducing apparent survival to 0.36 (Fig. 4a) in the 2001 extreme year. The addition of SIO Regional ACE to a model containing SIO Local ACE was not significantly influential (model 3, Table 3a), probably due to the close correlation between Local and Regional ACE (Pearson's correlation coefficient = 0.72). Contrastingly, cyclones in the NIO appeared to have a strong positive effect on apparent juvenile survival (slope coefficient; +/- 95% from model 4, Table 3a; 0.036 [0.015 & 0.059]). However, when NIO ACE was added to a model constrained by SIO Local ACE it was no longer found to be significantly influential (model 1, Table 3a). There is no evidence for a correlation between SIO Local Ace and NIO ACE ($R^2 = 0.091$).

The relationship between SIO Local and Φ_j appeared to be largely driven by one year (2001) with an exceptionally high ACE metric (see Fig. 4a), which was primarily due to the very severe tropical cyclone Dina that passed within 50km of Round island in January 2002. The estimates generated from the model (model 2, Table 3a) appeared not to mirror the additional background variation (44%) in survival from one year to the next (Fig. 4a). This is further illustrated by constraining Φ_j by Local ACE, but excluding 2001 from this constraint and fixing that year as a constant. Applying *ANODEV* to then test the influence of Local ACE on Φ_j (excluding 2001) provided no evidence (F=0.01, P=0.913, $R^2<0.01$, see model 5, Table 3b) of an influence. Therefore, in order to be confident that we had not overlooked the potential influence of the other spatial measures of cyclone activity in the Indian Ocean we again constrained Φ_j to be a function of three (IO, SIO Region and NIO Annual) measures of cyclone activity in turn, for all years except 2001. In this instance the constant model in the reference set for *ANODEV* was a model were survival was constant across all years except 2001, which was fixed at a different constant (model 3, Table 3b). This approach identified only NIO Annual as having a significant, positive influence on juvenile survival (slope coefficient; +/- 95% CIs from model 1, Table 3b; 0.021, [0.0001; 0.042]), whereby apparent juvenile survival improved with increasing ACE in the NIO (Fig. 4b) from ~0.6 in years of low ACE to ~0.79 in years of high ACE. Juvenile survival was estimated at 0.33 for the 2001 cohort from models 1, 2, 3, & 4, Table 3b.

Three-age class CJS model

Cyclones in the vicinity of Round Island had a strong negative impact on the apparent survival of juvenile petrels, at both the local and the regional scale (slope coefficients; +/- 95% CIs for influence of SIO local ACE: model 1, Table 4a; -0.115, [-0.163; -0.066] and SIO Regional ACE: model 4, Table 4a; -0.014, [-0.023; -0.005]), reducing apparent survival to 0.36 in the 2001 extreme year. Contrastingly, cyclones in the NIO appeared to have a strong positive effect on apparent juvenile survival (slope coefficient; +/- 95% from model 2, Table 4a; 0.036 [0.013 & 0.06]). The addition of SIO Regional ACE or NIO ACE to a model constrained by Local ACE did not improve model fit as was the case in the two-age class CJS model (for brevity models not shown in Table 4a). As before, in the two-age class model, we constrained Φ_j to be a function of three (IO, SIO Region and NIO Annual) measures of cyclone activity in turn, for all years except 2001. This approach identified NIO Annual as having a positive influence on juvenile survival (slope coefficient; +/- 95% CIs from model 1, Table 4b; 0.02, [-0.002; 0.042]). Under this modelling approach apparent juvenile survival improved with increasing ACE in the NIO (Fig. 4c) from ~0.64 in years of low ACE to ~0.79 in years of high ACE.

Multistate model

There was no compelling evidence from any of the four GOF tests applied in U-CARE for significant overdispersion in the data and $\hat{c}$ was estimated at 1.1 (see Table S3, SI), which we applied as a variance inflation factor in Program MARK to the multistate models.

There was compelling evidence for age-structure in the transition rates (hereafter known as age of first return or AFR) from the unobservable state to adult state, Table 5a, Models 5 and 7. AFR was fixed at zero for one-year olds to reflect their inability to return to the colony during their first year, but estimated at 0.31 (+/- 95% CIs: 0.24-0.391) for two year olds, 0.46 (+/- 95% CIs: 0.346-0.584) for three year olds and 0.23 (+/- 95% CIs: 0.134-0.347) for four year olds (estimates from Model 5, Table 5a). This implies that all petrels had returned to the breeding colony for the first time before they were 5 years old.

Cyclones in the vicinity of Round Island had a strong negative impact on the apparent survival of juvenile petrels, at both the local and the regional scale (slope coefficients; +/- 95% CIs for influence of SIO local ACE: model 1, Table 5a; -0.158, [-0.218; -0.099] and SIO Regional ACE: model 2, Table5a; -0.014, [-0.022; -0.005]), reducing apparent survival to 0.36 in the 2001 extreme year. Contrastingly, cyclones in the NIO appeared to have a strong positive effect on apparent juvenile survival (slope coefficient; +/- 95% from model 3, Table 5a; 0.154 [-0.03 & 0.339]). The addition of SIO Regional ACE or NIO ACE to a model constrained by Local ACE did not improve model fit as was the case in the two/three-age class CJS models (for brevity models not shown in Table 5a). As before, in the two-age class model, we constrained Φ_j to be a function of three (IO, SIO Region and NIO Annual) measures of cyclone activity in turn, for all years except 2001. This approach identified NIO Annual as having a significant, positive influence on juvenile survival (slope coefficient; +/- 95% CIs from model 2, Table 5b; 0.03, [-0.01; 0.068]). Under the multistate modelling approach apparent juvenile survival appeared on average to be higher than in the single state models and improved with increasing ACE in the NIO (Fig. 4d) from ~0.76 in years of low ACE to ~0.89 in years of high ACE. Juvenile survival was estimated at 0.38 for the 2001 cohort from models 1, 2, 3, 4 & 5, Table 5b. It is worth noting that the only other difference in terms of outputs between the single state and multistate modelling approaches is the positive influence of IO ACE on juvenile survival in the multistate model (slope coefficient; +/- 95% CIs from model 1, Table 5b; 0.008, [-0.001; 0.017]), when examined independently of 2001.

Unsurprisingly, using a two-age class or three-age class modelling approach does not change the estimates of (time-independent) juvenile survival (0.63 +/- 95% CIs: 0.578-0.671) or adult survival (0.97 +/- 95% CIs: 0.959-0.983). However, the multistate modelling approach, in response to excluding any recapture information on two year olds, estimates a higher (time-independent) juvenile survival rate (0.75 +/- 95% CIs: 0.685-0.812) and a lower adult survival rate (0.96 +/- 95% CIs: 0.946-0.972). Despite this variation our different modelling approaches all indicate that in different regions of the Indian Ocean tropical cyclone activity has contrasting effects on juvenile petrel survival; strong tropical cyclones in close proximity to the breeding colony reduce juvenile survival while greater cyclone activity in the Arabian Sea and Bay of Bengal improve juvenile survival. Our results also indicate, irrespective of the modelling approach, that once the negative impact of TCs on juvenile survival in 2001 was accounted for the impact of TCs at the IO scale were always positive, but not necessarily statistically significant (i.e. $p<0.05$). This suggests that at an ocean-wide scale (IO) and regional scale (NIO) the overall impacts of TCs on juvenile survival are typically positive.

Discussion

Using the long-term CMR data we provide (to the best of our knowledge) the first robust estimate of annual adult survival for a tropical procellariid and only the second estimate of this important demographic parameter for a *Pterodroma*. Annual survival for adult Round Island petrels falls at the upper end of published estimates for procellariidae, which range from 0.78-0.97 (Descamps *et al.*, 2015, Dobson & Jouventin, 2010, Jones *et al.*, 2011). Juvenile survival is still relatively poorly documented and ours are the first estimates for a tropical species and comparable to the few available for procellariidae (Jenouvrier *et al.*, 2005, Jones *et al.*, 2011). The breeding colony and migration routes of adult and juvenile Round Island petrels encompass the three cyclone regions in the Indian Ocean and to the best of our knowledge is the only species of seabird breeding (at one single colony) in the Indian Ocean that does so. Each year Round Island petrels are therefore exposed to cyclones at different stages in their annual cycle and this has different consequences for the survival of different life history stages. While adult petrels are largely unaffected by cyclone activity at either the breeding colony or during migration, cyclones appeared to have a significant impact on juvenile petrels during their first year at sea. The latter finding was observed, irrespective of the analytical approach used. Each approach identified the reduced juvenile survival in the 2001 cohort associated with the high level of TC activity in the vicinity of the breeding colony and described a positive relationship between TC activity in the NIO and juvenile survival during their first year at sea. While absolute juvenile survival rates did not differ between the two single state models these were lower (~16%) than those estimated by the multistate model. However, this did not appear to affect our overall findings, which highlight the importance of not only identifying when and where species are exposed to environmental variation across their life history and life cycle, but also that the environmental factor needs to be considered as potentially having both a regular ‘mild’ impact (i.e. on a continuous scale) and a stochastic ‘extreme’ impact (see Jenouvrier *et al.*, 2009a).

Round Island petrels are asynchronous breeders (Tatayah, 2010), therefore not all fledglings and adults are exposed to cyclones in the vicinity of the colony. However the peak period for chicks/fledglings at the colony overlaps with the cyclone season (December to April) in the southern hemisphere (Fig. 1). Therefore the majority of breeding adults and most fledglings are potentially exposed to cyclones in the vicinity of the breeding colony. Juvenile Round Island petrels fledge, i.e. leave the colony, and spend up to two weeks in the vicinity of the colony before dispersing into the wider Indian Ocean. During this period they are gaining their powers of flight and initial experiences in foraging and could therefore be particularly prone to mortality due to extreme weather events, in this case cyclones. We surmise that in January 2002 the passage of the very severe cyclone ‘Dina’ close to the breeding colony resulted in the mortality of a significant proportion of the ringed, fledged and near-fledged petrel chicks at that time rather than another causal agent. This conclusion is supported by anecdotal information from the ringing programme; with 34% of petrel chicks ringed two months prior to the event (i.e. in November) recaptured later in life compared to 0.56% of those ringed in the month (December) immediately preceding the event. As a comparison between 2002 and 2006, when there were no cyclones in the vicinity of the colony, 51.8% (73/141) of petrels ringed as chicks in November and 49.4% (40/81) ringed in December each year were recaptured as adults on Round Island.

Once fledglings have left the south-west Indian Ocean our tracking data, currently limited to six individuals, indicates that they typically move into the northern hemisphere, primarily into the extremely productive Arabian Sea (Lévy *et al.*, 2007, Piontkovski & Claereboudt, 2012) and also the Bay of Bengal (Fig. 2d). Both of these areas are prone to cyclones during two short seasons each year and during our study period experienced a wide range of cyclone activity (NIO ACE range: 7.4 - 61.9), including six super cyclonic storms (Table S1). Published evidence suggests that given elevated levels of cyclone activity in these regions we might have expected a decrease in juvenile petrel survival primarily through ‘inland wrecks’ as found in the Atlantic and Caribbean (Bugoni *et al.*, 2007, Hass *et al.*, 2012, Spendelow *et al.*, 2002), but we found no evidence to support this. On the contrary we found that improved juvenile survival was associated with increased levels of cyclone activity in these regions. On the assumption that our limited tracking data of petrels during their first year at sea is typically representative of the majority of juvenile petrels from Round Island - Why might this occur?

Primary production typically takes place when nutrient rich waters are pumped into the euphotic zone, via a variety of mechanisms (Lin *et al.*, 2003). One such mechanism involves strong winds causing vertical entrainment and upwelling in tropical oceans (Eppley & Renger, 1988, Marra *et al.*, 1990). Tropical cyclones generate extremely strong winds and have been proposed as drivers of vertical entrainment, but this has only recently been explored and the extent to which primary production can be modified by tropical cyclones quantified (Chang *et al.*, 2008, Lin *et al.*, 2003, Rao *et al.*, 2006, Subrahmanyam *et al.*, 2002, Zhao *et al.*, 2008). The passage of tropical cyclones through an area of the ocean, although brief, can result in a marked cooling of SSTs (Rao *et al.*, 2006), large-scale upwelling (Chang *et al.*, 2008) that result in localised increases in primary productivity (Lin *et al.*, 2003, Subrahmanyam *et al.*, 2002, Zhao *et al.*, 2008). These temporary alterations of a largely oligotrophic environment can occur within 1-2 weeks after the passage of the cyclone (Lin *et al.*, 2003, Subrahmanyam *et al.*, 2002, Zhao *et al.*, 2008) and can lead to a <30 fold increase in chlorophyll-a abundance (Lin *et al.*, 2003) and an associated 4-9 fold increase in primary productivity (Lin *et al.*, 2003, Rao *et al.*, 2006). These positive impacts of cyclones have been described in the Bay of Bengal (Rao *et al.*, 2006) , the Arabian Sea (Subrahmanyam *et al.*, 2002), the Pacific Ocean (Fiedler *et al.*, 2013) and the South China Sea (Chang *et al.*, 2008, Lin *et al.*, 2003, Zhao *et al.*, 2008) and in the latter, single cyclones have been estimated to generate up to 4% of new primary productivity and to contribute up to 20-30% of the annual regional primary productivity (Lin *et al.*, 2003, Zhao *et al.*, 2008). We therefore suggest that the passage of cyclones in the Arabian Sea and Bay of Bengal are generating localised patches of higher productivity leading to improved foraging opportunities for the juvenile petrels and that in years of higher cyclone activity (as recorded by ACE) this can lead to improvements in survival.

For adult petrels we found no compelling evidence for an influence of cyclones on their apparent annual survival at either the breeding colony or migration grounds. Although, for all models constrained by cyclone ACE, the influence on survival was positive but non-significant. Adult petrels are primarily exposed to cyclones during their time at the breeding colony (Figure 2c), but do not exhibit the same elevated levels of mortality associated with very severe cyclones that juveniles do. This could in part be explained in accordance with life history theory (Roff, 1992, Stearns, 1992), whereby experienced individuals show improved performance in reproduction and survival in comparison to relatively inexperienced individuals (Forslund & Part, 1995, Reid *et al.*, 2003). This has been demonstrated for both survival and reproductive success in seabirds in response to environmental variation, through improved foraging capabilities, (Nevoux *et al.*, 2007) and it would therefore not be unreasonable to suggest that through experience adult Round Island petrels are better prepared to deal with very severe cyclones compared to recently fledged juveniles. Very severe cyclones in proximity to mainland coastlines have resulted in ‘wrecking’ in adults of other petrel species (Bugoni *et al.*, 2007, Hass *et al.*, 2012), but there is no evidence to suggest that this occurs for adult Round Island petrels. This may in part be due to their pelagic nature whereby they remain away from mainland coastlines during the period where their migration corresponds with regional cyclone seasons, but also the relative isolation of their breeding colony from substantial land masses (as shown by Fig. 2c). Both of these traits would therefore limit opportunities for adult petrels to be ‘wrecked’ by cyclones.

Under projected climate change scenarios the recently observed general trends in cyclone metrics are to continue for cyclones in the NIO and SIO with; a decline in frequency, an increase in the frequency of strong cyclones and an increase in the maximum wind speeds (Gualdi *et al.,* 2008, Knutson *et al.*, 2010). However, there are some more subtle regional scale variations in cyclone frequencies, which could have important implications for the first year survival of Round Island petrels. In the SIO there is a predicted general decline in cyclone frequency, but in the south west Indian Ocean region, which includes the Mascarenes (Mauritius, Reunion & Rodrigues), a significant increase in cyclone frequency is predicted in association with changing SST and CO_2 levels (Sugi *et al.*, 2014). Regional variation is also apparent in the NIO with a predicted increase in cyclone frequency in the western north section of the Arabian Sea only and a decrease elsewhere including in the Bay of Bengal (Murakami *et al.*, 2014, Sugi *et al.*, 2014). Therefore while there is potential for an increase in the frequency of detrimental impacts associated with cyclones in the vicinity of the breeding colony (Round Island) during the SIO cyclone season, there is the intriguing potential for this to be (partially) offset by changing conditions in the Arabian Sea. Exactly how these contrasting effects might affect Round Island petrel demography and population dynamics is unclear, because at present our understanding of breeding success (e.g. numbers of fledglings produced) within and outside of the SIO cyclone season is limited. In addition as petrels breed at Round Island all year round, only some fledglings (or chicks close to fledgling) are potentially exposed to cyclones, at or in the vicinity of the breeding colony, while current tracking data (be it from a limited number of individuals) indicates juvenile petrels are potentially exposed to cyclones in the Arabian Sea. While the next logical step might be to explore the within-year variation in first year survival of petrels fledging during or outside of the cyclone season, this is currently not possible due to the relatively low numbers of fledglings produced outside of the cyclone season - only 18.5% of 1178 chicks ringed between 1993 and 2012 were ringed outside of the cyclone season - and the requisite post-fledgling recapture period. Therefore further long-term monitoring of annual breeding success and survival and tracking of juvenile petrels is required to understand how these two regionally contrasting impacts of cyclones might shape Round Island petrel population dynamics.

Our study has demonstrated that cyclones can have contrasting effects on a single species raising the intriguing prospect that the projected changes in cyclones under current climate change scenarios may have positive as well as the more commonly perceived negative impacts on marine biodiversity. These positive impacts may have the potential to mitigate (in part at least) for the more commonly perceived negative impacts. However, our study also highlights the need for comprehensive data sets not only on cyclone metrics, which are readily available, but also on species demography and year-round tracking data in order to effectively understand this process.

Acknowledgements

This work would not have been possible without the dedication, over the last 20 years, of numerous staff and volunteers from the Mauritian Wildlife Foundation (MWF) and the National Parks and Conservation Service (NPCS) to establishing a comprehensive ringing and recovery programme on the Round Island petrel. Of particular note are the contributions made by Vimul Nundlaul, Daryl Birch, Pete Haverson, Nicolas Zuel, Martine Goder, Richard Baxter, Pat Banville, Katherine Booth Jones, Lucy Rouse and Helen Gath in facilitating the petrel research programme on the island. The petrel tracking programme and Malcolm Nicoll were supported by the Natural Environmental Research Council (UK) (Grant NE/H5081500) with in-situ support from MWF and NPCS. The authors have no conflict of interest to declare.

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Supporting Information

Title: ‘Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean’.

The information provided in supporting information relates to additional details on the methods used to (i) establish where adult petrels migrated to (ii) explore the impact of tropical cyclones on juvenile survival, (iii) summary information on tropical cyclones in the Indian Ocean and (iv) the results of goodness-of-fit tests for both single state and multistate models used to explore the impact of tropical cyclones on juvenile survival.

Table 1. Regions and cyclone seasons for which accumulated cyclonic energy (ACE) was estimated in both the northern and southern hemispheres, based on the overlap of Round Island petrels and cyclone activity in the Indian Ocean.

	Indian Ocean (IO)	Northern hemisphere (NIO)	Arabian Sea (AS)	Bay of Bengal (BoB)	Southern hemisphere (SIO)	SIO Region (50-90^0 E)	SIO Local (within 275Km of Round Island)
May-June	-	✓	✓	✓	-	-	-
November	-	✓	✓	✓	-	-	-
Annual	✓	✓	-	-	✓	-	-
November-April	-	-	-	-	-	✓	✓

Table 2. Outputs from models and ANODEV tests used to examine the impact of cyclones on annual adult Round Island petrel survival. NP – number of model parameters. Model notation is as follows apparent survival (Φ), recapture probability (P), (t) time dependence and (.) constant. Cyclone metrics follow the notations from Table 1. Models are ordered by QAICc values. Covariate Deviance = (QDeviance $\Phi_{(.)} P_{(t)}$ – QDeviance of specified covariate model); Total Deviance = (QDeviance $\Phi_{(t)} P_{(t)}$ – QDeviance $\Phi_{(.)} P_{(t)}$) and R^2 = ((Covariate Deviance/Total Deviance)*100).

#	**Model**	**QAICc**	**NP**	**Q Deviance**	**ANODEV F statistic**	**ANODEV P-value**	**Covariate Deviance**	**Total Deviance**	**R^2 (%)**
1	$\Phi_{(IO)} P_{(t)}$	16271.08	21	5205.58	1.47	0.245	2.626	29.479	8.90
2	$\Phi_{(.)} P_{(t)}$	16271.70	20	5208.21	NA	NA	NA	NA	NA
3	$\Phi_{(SIO\&NIO:May\text{-}June)} P_{(t)}$	16272.01	21	5206.51	0.92	0.353	1.701	29.479	5.80
4	$\Phi_{(AS:May\text{-}June)} P_{(t)}$	16272.24	21	5206.73	0.78	0.388	1.474	29.479	5.00
5	$\Phi_{(SIO)} P_{(t)}$	16272.57	21	5207.06	0.605	0.449	1.143	29.479	3.88
6	$\Phi_{(SIO\ Local)} P_{(t)}$	16273.31	21	5207.81	0.208	0.655	0.403	29.479	1.37
7	$\Phi_{(NIO:May\text{-}June)} P_{(t)}$	16273.46	21	5207.96	0.128	0.726	0.249	29.479	<1
8	$\Phi_{(SIO\ Region)} P_{(t)}$	16273.69	21	5208.20	0.009	0.925	0.018	29.479	<1
9	$\Phi_{(t)} P_{(t)}$	16274.48	36	5178.73	NA	NA	NA	NA	NA

Table 3. Outputs from two-age class, single state models and ANODEV tests used to examine the impact of cyclones on annual juvenile Round Island petrel survival. (a) All years are included the analysis of juvenile survival, (b) All years except 2001 are included in the analyses of juvenile survival. NP – number of model parameters. Model notation is as follows apparent survival (*Φ*), recapture probability (*P*), (t) time dependence, (.) constant, juvenile (*j*) and adult (*a*). For brevity of model notation, where recapture (*P*) is not shown it is modelled as $P_{j(.),a(t)}$. Model 9 is the global starting model. Cyclone metrics follow the notations from Table 1. Models in bold include single measures of tropical cyclone metrics that were found to influence juvenile apparent survival.

#	Model	AICc	NP	Q Deviance	ANODEV F statistic	ANODEV P-value	Covariate Deviance	Total Deviance	R^2
a									
1	$\Phi_{j(\text{SIO LOCAL+NIO}),a(.)}$*	5454.51	22	2287.20	2.66	0.134	3.33	15.88	20.98
2	**$\Phi_{j(\text{SIO LOCAL}),a(.)}$***	**5455.80**	**21**	**2290.53**	**13.82**	**0.003**	**19.96**	**35.84**	**55.69**
3	$\Phi_{j(\text{SIO LOCAL+REGIONAL}),a(.)}$*	5457.83	22	2290.52	0.004	0.952	0.01	15.88	<1
4	**$\Phi_{j(\text{NIO}),a(.)}$**	**5462.35**	**21**	**2297.09**	**6.57**	**0.026**	**13.40**	**35.84**	**37.40**
5	$\Phi_{j(t),a(.)}$	5462.49	32	2274.65	NA	NA	NA	NA	NA
6	**$\Phi_{j(\text{SIO REGION}),a(.)}$**	**5464.11**	**21**	**2298.84**	**5.29**	**0.042**	**11.64**	**35.84**	**32.49**
7	$\Phi_{j(.),a(.)}$	5473.72	20	2310.49	NA	NA	NA	NA	NA
8	$\Phi_{j(\text{IO}),a(.)}$	5475.41	21	2310.14	0.11	0.751	0.34	35.84	<1
9	$\Phi_{j(t),a(t)}$	5485.48	49	2262.27	NA	NA	NA	NA	NA
b									
1	**$\Phi_{j(\text{NIO-ex 2001}),a(.)}$**	**5450.58**	**22**	**2283.27**	**5.09**	**0.047**	**4.39**	**13.01**	**33.7**
2	$\Phi_{j(\text{IO-ex 2001}),a(.)}$	5451.29	22	2283.98	3.94	0.075	3.68	13.01	28.3
3	$\Phi_{j(\text{.-ex 2001}),a(.)}$	5452.93	21	2287.66	NA	NA	NA	NA	NA
4	$\Phi_{j(\text{SIO REGION-ex 2001}),a(.)}$	5454.95	22	2287.64	0.02	0.89	0.02	13.01	<1
5	$\Phi_{j(\text{SIO LOCAL-ex 2001}),a(.)}$	5454.95	22	2287.64	0.01	0.913	0.02	13.01	<1
6	$\Phi_{j(\text{SIO LOCAL}),a(.)}$	5455.80	21	2290.53	NA	NA	NA	NA	NA
7	$\Phi_{j(t),a(.)}$	5462.49	32	2274.65	NA	NA	NA	NA	NA
8	$\Phi_{j(.),a(.)}$	5473.72	20	2310.49	NA	NA	NA	NA	NA

Notes: * When testing the effect of adding a second covariate to a model using ANODEV, the reference models are the fully time dependent model and a model containing only the first of the two covariates listed in the model being examined.

Table 4. Outputs from three-age class (in recapture rates), single state models and ANODEV tests used to examine the impact of cyclones on annual juvenile Round Island petrel survival. (a) All years are included the analysis of juvenile survival, (b) All years except 2001 are included in the analyses of juvenile survival. NP – number of model parameters. Model notation is as follows apparent survival (*Φ*), recapture probability (*P*), (t) time dependence, (.) constant, juvenile (*j*) and adult (*a*). For brevity of model notation where recapture (*P*) is not shown it is modelled as $P_{j(.),(.),a(t)}$. Cyclone metrics follow the notations from Table 1. Models in bold include single measures of tropical cyclone metrics that were found to influence juvenile apparent survival.

#	Model	AICc	NP	Q Deviance	ANODEV F statistic	ANODEV P-value	Covariate Deviance	Total Deviance	R^2
a									
1	**$\Phi_{j(\text{SIO LOCAL}),a(.)}$**	**5413.05**	**21**	**2247.78**	**16.48**	**0.002**	**20.39**	**34.01**	**59.96**
2	**$\Phi_{j(\text{NIO}),a(.)}$**	**5421.61**	**21**	**2256.34**	**5.87**	**0.034**	**11.84**	**34.01**	**34.81**
3	$\Phi_{j(t),a(.)}$	5422.01	32	2234.17	NA	NA	NA	NA	NA
4	**$\Phi_{j(\text{SIO REGION}),a(.)}$**	**5422.28**	**21**	**2257.01**	**5.38**	**0.041**	**11.16**	**34.01**	**32.83**
5	$\Phi_{j(.),a(.)}$	5431.4	20	2268.18	NA	NA	NA	NA	NA
6	$\Phi_{j(\text{IO}),a(.)}$	5433.69	21	2268.42	0.1	0.85	0.24	**34.01**	<1
7	$\Phi_{j(t),a(.)}\ P_{j(.),a(t)}$	5462.69	32	2274.65	NA	NA	NA	NA	NA
b									
1	**$\Phi_{j(\text{NIO-ex 2001}),a(.)}$**	**5408.85**	**22**	**2241.54**	**4.82**	**0.053**	**3.55**	**10.92**	**32.52**
2	$\Phi_{j(\text{IO-ex 2001}),a(.)}$	5408.9	22	2241.59	4.71	0.055	3.5	10.92	32.02
3	$\Phi_{j(\text{.-ex 2001}),a(.)}$	5410.36	21	2245.09	NA	NA	NA	NA	NA
4	$\Phi_{j(\text{SIO REGION-ex 2001}),a(.)}$	5412.30	22	2244.99	0.09	0.767	0.10	10.92	0.92
5	$\Phi_{j(\text{SIO LOCAL-ex 2001}),a(.)}$	5412.39	22	2245.08	0.01	0.936	0.01	10.92	0.06
6	$\Phi_{j(\text{SIO LOCAL}),a(.)}$	5413.05	21	2247.78	NA	NA	NA	NA	NA
7	$\Phi_{j(t),a(.)}$	5422.01	32	2234.17	NA	NA	NA	NA	NA
8	$\Phi_{j(.),a(.)}$	5431.4	20	2268.18	NA	NA	NA	NA	NA

Table 5. Outputs from multistate models and ANODEV tests used to examine the impact of cyclones on annual juvenile Round Island petrel survival. (a) All years are included the analysis of juvenile survival, (b) All years except 2001 are included in the analyses of juvenile survival. NP – number of model parameters. Model notation is as follows apparent survival (Φ), recapture probability (P), age of first return (Ψ), (t) time dependence, (.) constant, juvenile (j), (u) unobservable state and adult (a). For brevity of model notation: where recapture (P) is not shown it is modelled as $P_{j(.)}P_{u(.)}P_{a(\mathrm{t})}$ unless otherwise specified; and where age of first return (Ψ) is not shown it is modelled as a function of four age classes - $\Psi_{(1\text{-}4)}$. Cyclone metrics follow the notations from Table 1. Models in bold include single measures of tropical cyclone metrics that were found to influence juvenile apparent survival.

#	Model	AICc	NP	Q Deviance	ANODEV F statistic	ANODEV P-value	Covariate Deviance	Total Deviance	R^2
a									
1	**$\Phi_{j(\text{SIO LOCAL})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$**	**5881.37**	**24**	**2137.92**	**16.17**	**0.005**	**28.78**	**38.59**	**74.58**
2	**$\Phi_{j(\text{REGION})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$**	**5887.73**	**24**	**2144.29**	**7.63**	**0.008**	**22.43**	**38.59**	**58.12**
3	**$\Phi_{j(\text{NIO})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$**	**5893.40**	**24**	**2149.95**	**4.23**	**0.044**	**16.77**	**38.59**	**43.46**
4	$\Phi_{j(\mathrm{t})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$	5894.21	35	2128.12	NA	NA	NA	NA	NA
5	$\Phi_{j(.)}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$	5906.07	22	2166.72	NA	NA	NA	NA	NA
6	$\Phi_{j(\text{IO})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$	5908.94	24	2165.50	0.18	0.838	1.22	38.59	3.16
7	$\Phi_{j(.)}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}3)}$	5911.04	22	2171.68	NA	NA	NA	NA	NA
8	$\Phi_{j(.)}\Phi_{u(.)}\Phi_{a(.)}P_{\mathrm{j}(.)}P_{\mathrm{u}(.)}P_{\mathrm{a}(.)}\Psi_{(.)}$	5989.08	4	2286.19	NA	NA	NA	NA	NA
b									
1	**$\Phi_{j(\text{IO-ex 2001})}\Phi_{u(.)}\Phi_{a(.)}$**	**5877.40**	**24**	**2133.95**	**6.30**	**0.029**	**3.34**	**9.17**	**36.41**
2	**$\Phi_{j(\text{NIO-ex 2001})}\Phi_{u(.)}\Phi_{a(.)}$**	**5877.75**	**24**	**2134.30**	**5.32**	**0.042**	**2.99**	**9.17**	**32.62**
3	$\Phi_{j(.\text{-ex 2001})}\Phi_{u(.)}\Phi_{a(.)}$	5878.69	23	2137.29	NA	NA	NA	NA	NA
4	$\Phi_{j(\text{REGION-ex 2001})}\Phi_{u(.)}\Phi_{a(.)}$	5880.34	24	2136.90	0.49	0.497	0.39	9.17	4.30
5	$\Phi_{j(\text{LOCAL-ex 2001})}\Phi_{u(.)}\Phi_{a(.)}$	5880.50	24	2137.05	0.30	0.596	0.24	9.17	2.64
6	$\Phi_{j(\text{LOCAL})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$	5881.37	24	2137.92	NA	NA	NA	NA	NA
7	$\Phi_{j(\mathrm{t})}\Phi_{u(.)}\Phi_{a(.)}\Psi_{(1\text{-}4)}$	5894.21	35	2128.12	NA	NA	NA	NA	NA

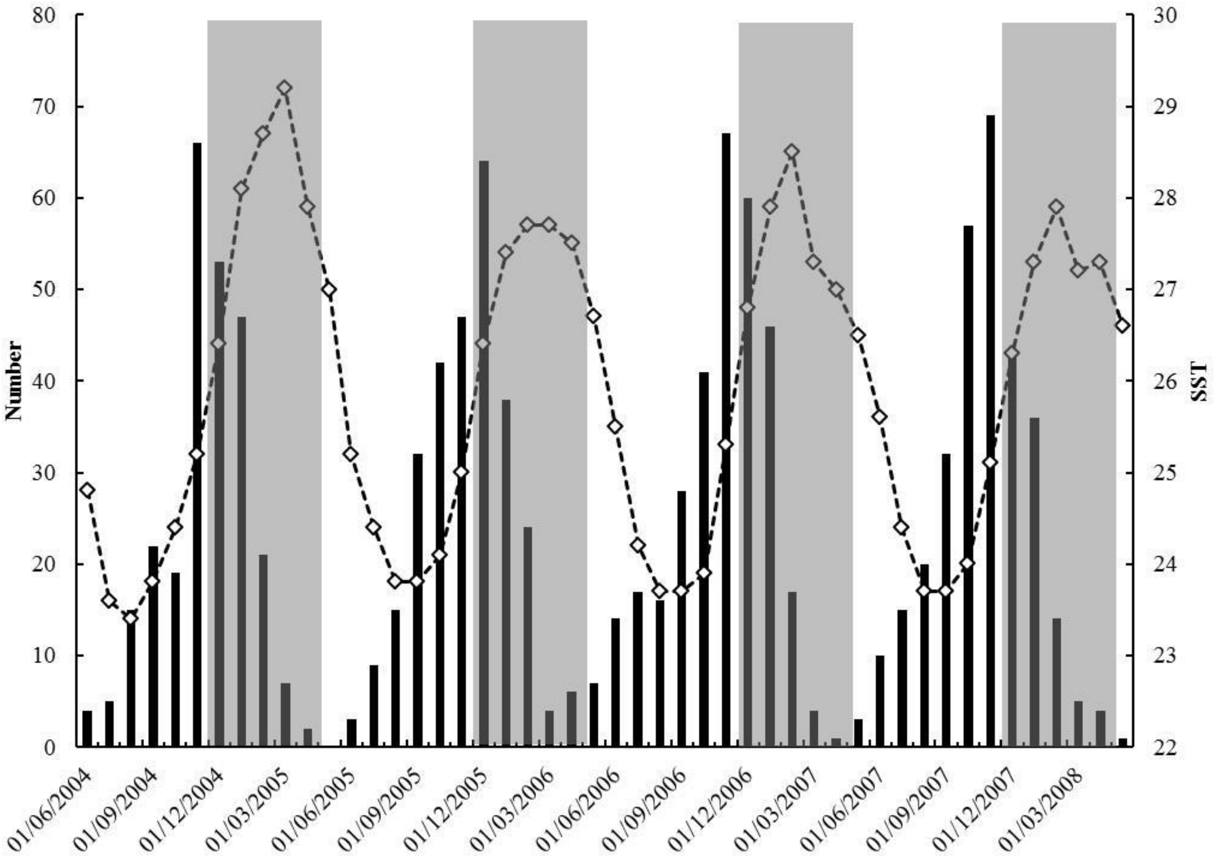

Figure 1. The year round breeding of Round Island petrels at Round Island, Mauritius (June 2004 - May 2008) in relation to Sea Surface Temperature (SST ^{o}C). Black bars represent the number of chicks recorded each month and show the peak in breeding activity from August-December. The dashed line and unfilled diamonds are the monthly average Reynolds satellite SST data for Round island (1^{o} resolution), downloaded from the POET-PODAAC website (http://poet.jpl.nasa.gov/). The dark grey blocks represent the annual cyclone season (December-April) in the south-west Indian Ocean and how this relates to the year-round breeding activity of the petrels at Round Island.

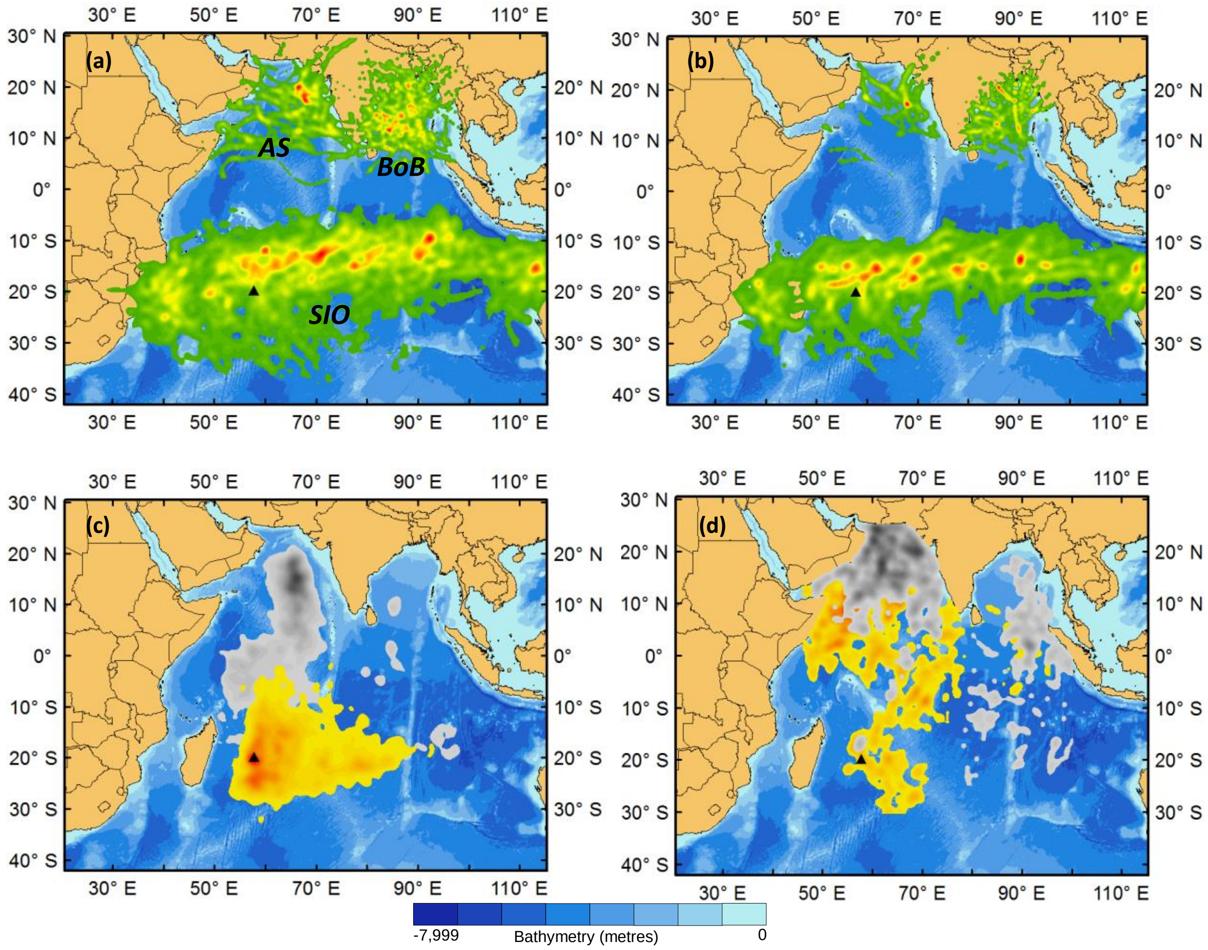

Figure 2. Kernel density maps (95% outer contour) of cyclone activity (1993-2012) (a & b), tracks of 116 Adult Round Island petrels (c) and tracks of six juvenile petrels (d). Black triangle shows the location of Round Island, Mauritius. (a) Cyclone activity (tracks) occurring between 1993 and 2012 in the Arabian Sea (AS), the Bay of Bengal (BoB) and the Southern Indian Ocean west of 115^{o}E. (b) Accumulated cyclonic energy (ACE) between 1993 and 2012 in each region. (c) The locations of 116 tracked adult petrels in December-April (Orange) and May-June (Grey). (d) The locations of six petrels tracked during their first year at-sea after fledging from Round Island in the months of December-April (Orange) and May, June, October & November (Grey)*. In (a) & (b) a progression through green, yellow and orange to red is indicative of an increasing concentration of cyclone activity and ACE. In (c) and (d) an increase in colour intensity indicates an increase in the density of petrel

locations. * In the May-June cyclone season in the Northern Indian Ocean juvenile petrels were found in the AS, and in the October-November cyclone season in the AS and BOB, but for clarity of presentation the locations during both cyclone seasons are shown in one single (grey) kernel density map.

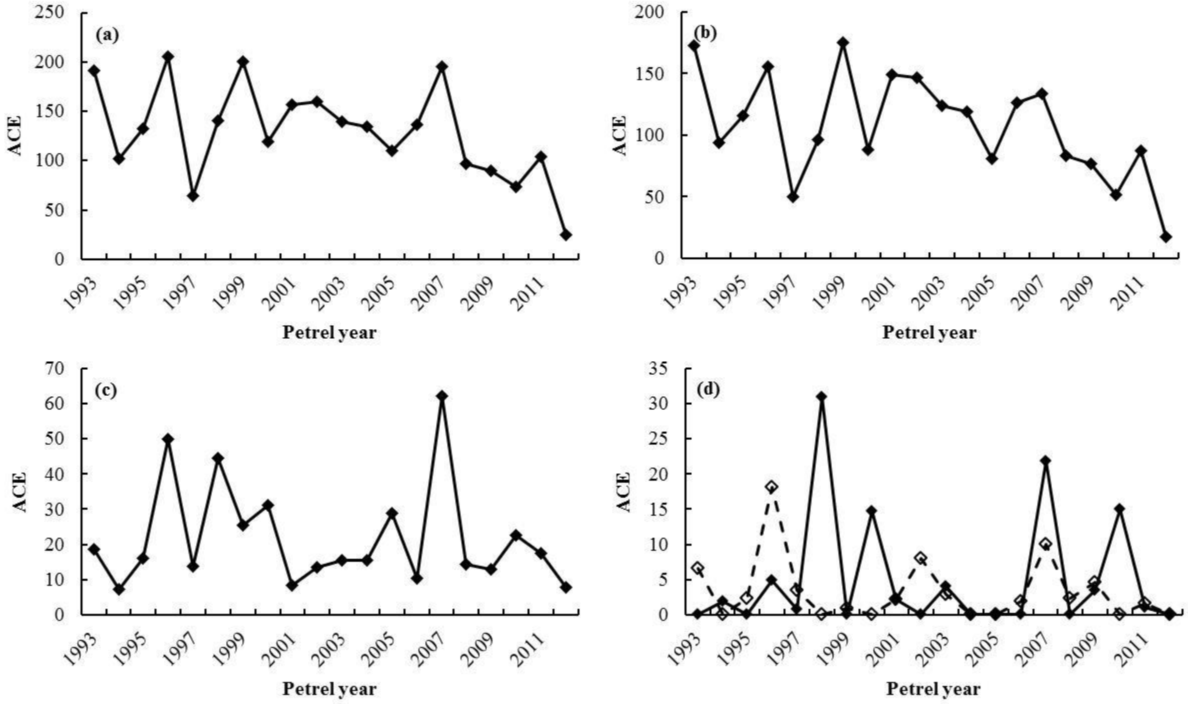

Figure 3. Accumulated cyclonic energy (ACE) for each petrel year (June-May) in: (a) The Indian Ocean west of 115^{o}E, (b) The Southern Indian Ocean west of 115^{o}E, (c) the Northern Indian Ocean and (d) The Arabian Sea (filled diamonds and solid line) and Bay of Bengal (open diamonds and dashed line) in May & June only.

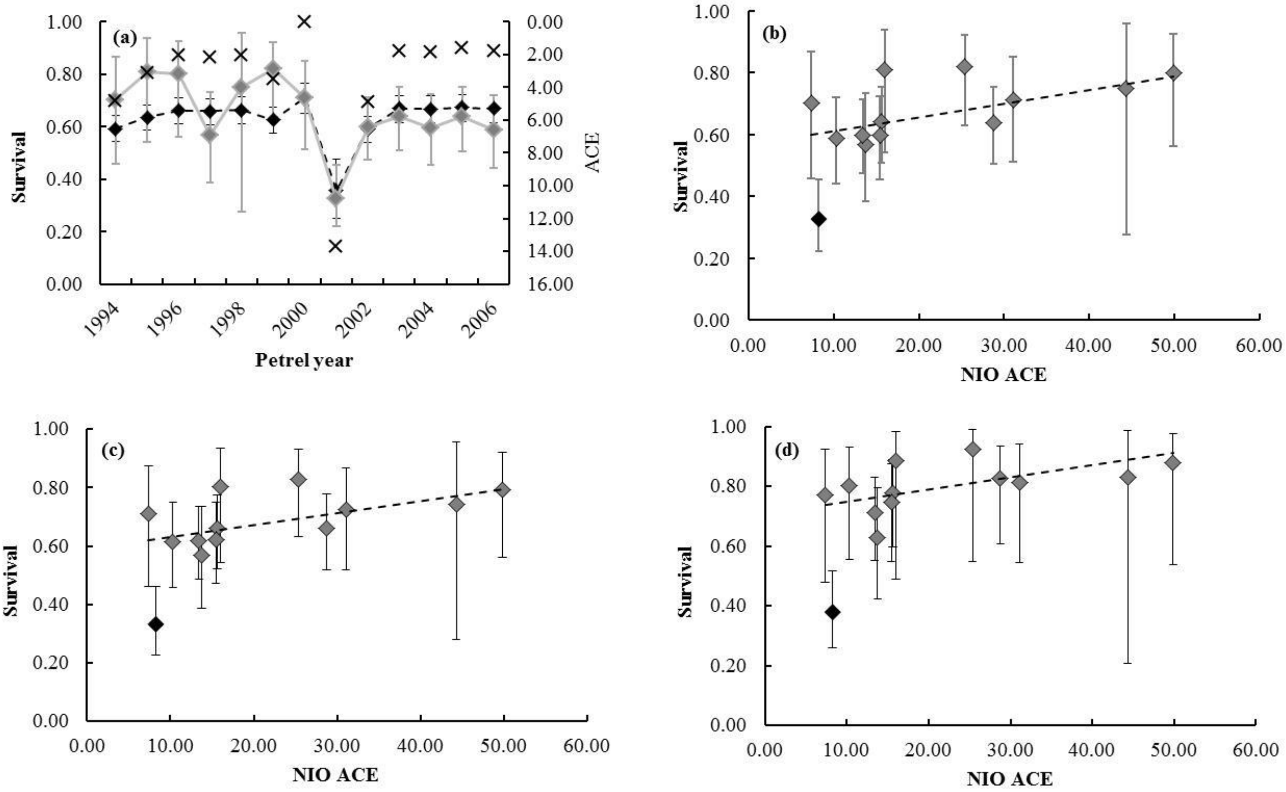

Figure 4. Apparent survival estimates for juvenile Round Island petrels and corresponding tropical cyclone ACE metrics generated from the three different modelling approaches. (a) Two-age class CJS model: Grey line and grey diamonds are time-dependent estimates (model 5, Table 3a) with error bars corresponding to 95% upper and lower confidence intervals. Black diamonds and dashed line are estimates where survival is constrained by SIO local ACE (model 2, Table 3a). For clarity no error bars are shown. The SIO Local ACE for each petrel year is shown by 'X' and the right hand vertical scale is reversed, to correspond with the negative influence of ACE on juvenile survival. (b) Two-age class CJS model: Grey diamonds are time-dependent estimates (model 5, Table 3a) with error bars corresponding to 95% upper and lower confidence intervals. Black dashed line represents the estimates generated from model 1, Table 3b, where survival (excluding 2001) is constrained by NIO ACE. Apparent survival for the 2001 cohort is illustrated by the larger solid black diamond. (c) Three-age class CJS model: Grey diamonds are time-dependent estimates (model 3, Table 4a) with error bars corresponding to 95% upper and lower confidence intervals. Black dashed

line represents the estimates generated from model 1, Table 4b, where survival (excluding 2001) is constrained by NIO ACE. (d) Multistate model: Grey diamonds are time-dependent estimates (model 4, Table 5a) with error bars corresponding to 95% upper and lower confidence intervals. Black dashed line represents the estimates generated from model 2, Table 5b, where survival (excluding 2001) is constrained by NIO ACE.