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Biological effects of El Niño on the Galápagos penguin

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ABSTRACT

Long-term monitoring of physical and biological parameters is essential for understanding the effects of El Niño on bird populations, particularly for small or declining populations. We examined the biological effects of El Niño activity from 1965 to 2004 using instrumental sea-surface temperatures from the Galápagos Islands and 20 years of census counts of the Galápagos penguin. Between 1965 and 2004, nine El Niño events were recorded of which two were strong and seven were weak. The two strong El Niño events of 1982–1983 and 1997–1998 were followed by crashes of 77% and 65% of the penguin population, respectively. The evidence suggests that the increased frequency of weak El Niño events limits population recovery. The 2004 penguin population is estimated to be at less than 50% of that prior to the strong 1982–1983 El Niño event. We discuss the biological effects of increased El Niño intensity and frequency within the context of a 6000-year record of El Niño influence and in the light of increasing anthropogenic threats operating after 1535, when the Archipelago was discovered by Europeans.

1. Introduction

The Galápagos penguin (*Spheniscus mendiculus*) is an endangered species by virtue of its restricted range and fluctuating population size (BirdLife International, 2000). Approximately, 95% of the population of Galápagos penguins is distributed primarily along the westernmost islands of Fernandina (0°22′0″S, 91°31′20″W) and Isabela (0°25′30″S, 91°7′W); this distribution coincides with the major upwelling zones and the most productive waters of the archipelago (Boersma, 1977, 1978). The remaining 5% of the population lives in small populations inhabiting the islands of Floreana (1°17′0″S, 90°26′0″W), Santiago (0°15′30″S, 90°43′30″W), and Bartolomé (0°16′51″S, 90°32′48″W). Birds nest opportunistically throughout the year if conditions permit although peaks in egg laying occur in April–May (Vargas, unpubl. data) and in August–September (Boersma, 1977). Based on capture-mark-resight methods (Vargas et al., 2005), the population size of the Galápagos penguin in 2004 was estimated at 1500 individuals (Vargas and Wiedenfeld, 2004).

Phylogenetic evidence suggests that the *Spheniscus* penguin genus diverged from other penguin species between 100,000 and 800,000 years ago (Akst et al., 2002; Grant et al., 1994), and subsequent association of *S. mendiculus* with the Galápagos means that historic El Niño episodes are likely to have shaped specific breeding and survival strategies in this species for thousands of years. Lake sediment deposits provide evidence that El Niño activity has influenced the climate of the Galápagos Islands for at least the last 6000 years (Riedinger et al., 2002) with it likely affecting the Galápagos penguin (Boersma, 1998a; Valle and Coulter, 1987; Vargas, 1999), as it does other seabirds, through a cascade of events (Chavez et al., 1999) that lead to changes in the food web and predator–prey relationships (Boersma, 1977). Of all the penguin species, only the Galápagos penguin lives on the equator and is able to do so because of the cold oceanic upwelling along the equator and the

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Equatorial Under Current, also known as the Cromwell current (Boersma, 1977, 1978). As the Equatorial Under Current hits the western edge of the Galápagos Archipelago, cold, nutrient-rich water is forced to the surface (Houvenaghel, 1984) and provides the shallow-diving Galápagos penguin (Mills, 2000) with access to its primary prey species.

El Niño events affect the biodiversity of the Galápagos Islands through dramatic changes to the environmental conditions of the Islands. During El Niño, the Equatorial Under Current weakens, the surface water warms, macronutrients are reduced, primary production decreases (Chavez et al., 1999), and fish numbers diminish; data from commercial fisheries indicated that the catch of mullets from the Galápagos during the 1997–1998 El Niño event was half that of the commercial catch in 1999 when there was no El Niño event (Nicolaides and Murillo, 2001). Similarly, the catch of sardines along the coast of mainland Ecuador during the 1998 El Niño year was the lowest of the last two decades (Jácome and Ospina, 1999).

Recently, the frequency and severity of El Niño events appear to have increased and this is a concern for the conservation of endangered seabird species. El Niño events now occur 2–7 times more frequently than they did 7000–15,000 years ago (Riedinger et al., 2002; Rodbell et al., 1999). Climate models suggest that most of the warming observed during the last 50 years is attributable to human activities (Karl and Trenberth, 2003) with an increased El Niño pulse in the last three decades (Trenberth and Hoar, 1996, 1997). The 1982–1983 and 1997–1998 El Niño events were the strongest recorded in the last century (Chavez et al., 1999) and had severe biological effects (Barber and Chavez, 1983; Hays, 1986; Valle et al., 1987). Sea-surface temperatures and precipitation data collected from the Galápagos between 1965 and 1999 indicate that 1983 and 1998 were the hottest and wettest years on the Galápagos Islands (Snell and Rea, 1999).

Here, we evaluate the effect of ENSO (El Niño Southern Oscillation) on the population dynamics of the penguin and determine the likely effects of climate change on the conservation of Galápagos penguins. Standard demographic parameters are inordinately difficult to obtain for this species because the penguins are in small groups widely scattered along the difficult terrain of the archipelago. However, we present analysis from two long-running data sets: (1) the number of adult and juvenile penguins recorded since 1970 and (2) the daily sea temperatures logged in the Galápagos since 1965.

2. Materials and methods

We examined the biological effects of El Niño using census data of the Galápagos penguin and instrumental sea-surface temperature data from the Galápagos Islands.

2.1. Penguin data

We conducted complete census counts each year as part of a joint effort of the Charles Darwin Research Station (CDRS) and the Galápagos National Park Service (GNPS). Censuses attempted to count all penguins using methods described elsewhere (Boersma, 1974, 1977; Mills and Vargas, 1997). Sampling bias was minimized by standardizing dates, duration of the census, time of day, number of observers, field equipment, survey zones, travel speed, and types of data collected. The 10-day census occurred in late August and early September across the range of the Galápagos penguin. We counted penguins between 06:00 and 18:00 using a small dinghy to approach the coast as closely as possible. The birds were classified as adults, juveniles, and penguins of unknown age (whose age could not be determined when birds were swimming). Fledged juvenile birds, with juvenile plumage as aged by Boersma (1977), were used as an index of reproduction per year. For our statistical analysis, we assumed no migration and equal detectability of birds across all years (including years of El Niño events). All known nesting areas were checked to determine the extent of nesting activity. Here, we present data on the combined total number of adult and juvenile penguins.

2.2. Sea surface temperature

Sea surface temperature is a good indicator of El Niño events (Trenberth and Stepaniak, 2001), so we used SST data collected between 1965 and 2004 at the meteorological station located at the CDRS (00°44′20′S, 90°18′24″W) on Santa Cruz Island. Sea surface temperature were recorded at 06:00, 12:00, and 18:00 with a hand held thermometer in a bucket of water pulled from the sea surface (Snell and Rea, 1999). We calculated normalized SST anomalies for the period 1970–2004 relative to the base period of 1965–1979 from the same data set. The base period was selected as it was considered representative and not biased by the warming and El Niño events after 1979 (Trenberth, 1997; Trenberth and Hoar, 1996).

We determined El Niño events by identifying periods during which the five-month running mean of SST anomalies was above 0.5 °C for at least six consecutive months. This definition follows the protocols of the Japan Meteorological Agency (J.M.A.) and Trenberth (1997) with adjustment for instrumental sea-surface temperature from the Galápagos Islands. These calculations also enabled us to determine the duration, frequency, and intensity of warm El Niño and cold La Niña events. La Niña events were determined by identifying periods during which the 5-month running means of SST was below 0.5 °C for at least six consecutive months.

The El Niño events were classified as strong or weak depending on the magnitude of the positive anomalies. We considered anomalies between 0.5 and 2 °C as weak El Niño and anomalies >2 °C as strong El Niño events. Despite some differences in measurements of magnitude (intensity), our frequency of ENSO (El Niño Southern Oscillation) events from the Galápagos is in most cases in agreement with the consensus (ENSO) lists (http://ggweather.com/enso/years.htm) and the Multivariate ENSO index (http://www.cdc.noaa.gov/ENSO/enso.mei_index.html). The main difference is that the 1972–1973 event, classified as a strong El Niño by the consensus list, appears only as a weak El Niño event in the Galápagos Islands.

3. Results

Analysis of SST indicates two strong (1982–1983 and 1997–1998) and seven weak (1965–1966, 1968–1969, 1972–1973, 1976, 1986–1987, 1991–1992 and 1993) El Niño episodes in the Galápagos during the study period (Fig. 1). The two strong El Niño events, in addition to showing anomalies greater than 2 °C, also lasted for 17 and 18 months, respectively. The average duration of the weak episodes was 11.4 months (±3.4 SD, range 6–16). The 1982–1983 and 1997–1998 strong El Niño events were associated with reductions in the penguin population of 77% and 65%, respectively, and the frequent, weak El Niño events coincided with years when recovery in the penguin population faltered (Fig. 1). The change in penguin numbers was significantly and strongly correlated with mean normalised SST anomalies (Fig. 2). This model ($F_{1,15} = 71.1$, $p < 0.001$, $b_{(adj)} = 0.81$) predicts that strong El Niño events, characterized by a rise in SST anomalies >2 °C above baseline temperature, result in population crashes greater than 50% (Fig. 2). In contrast, La Niña events, defined as a drop in SST anomalies to −0.5 °C or lower below baseline temperatures, are associated with periods of recovery in the population of Galápagos penguins (Fig. 2).

Fig. 1 illustrates that in the years of strong El Niño, the census revealed fewer adults and juveniles than in other years suggesting an association between El Niño, reduced fledgling success (measured as the number of juveniles) and adult survival. Counts during weak El Niño events showed a low recovery rate of the population indicating poor reproduction and recruitment. The censuses also indicated an uncharacteristically low recovery rate of the penguin population between 1983 and 1997 coincident with a high frequency of weak Niño events between the two strong events (Fig. 1).

During the 2004 census, we counted 858 penguins. Although this represents nearly a doubling of the numbers (444) after the last strong 1997–1998 El Niño event, the 2004 penguin numbers are less than half of numbers in the 1970s.

4. Discussion

4.1. *Increased frequency and intensity of El Niño*

The CDRS SST data show that between 1965 and 1981 there were no strong El Niño events in the Galápagos that were comparable to those of the 1980s and 1990s. We assert that during these earlier years, the oceanographic conditions produced resources sufficient to support the high numbers of penguins that we recorded in the first three counts of the 1970s and early 1980s (Fig. 1). In fact, recent investigations suggest that a decrease of 25% in oceanic upwelling around the equator after 1970 may have led to an increase of 0.8 °C in SST (McPhaden and Zhang, 2002), probably reducing food resources in Galápagos. After 1980, the large fluctuations and the slow recovery of the penguin population were probably linked to the increasing intensity and frequency of both strong and weak El Niño events and the associated unproductive oceans.

Historically (before 1980), we presume that the penguin population would recover in years following an El Niño, or during cold La Niña events, with the associated abundance of food. Our census data indicate that population recovery during La Niña events have been only moderate (Fig. 2) and have failed to restore the numbers typical of the period prior to the 1980s (Fig. 1).

The modern pattern of more frequent and intense El Niño episodes, including some events that are extreme by histori-

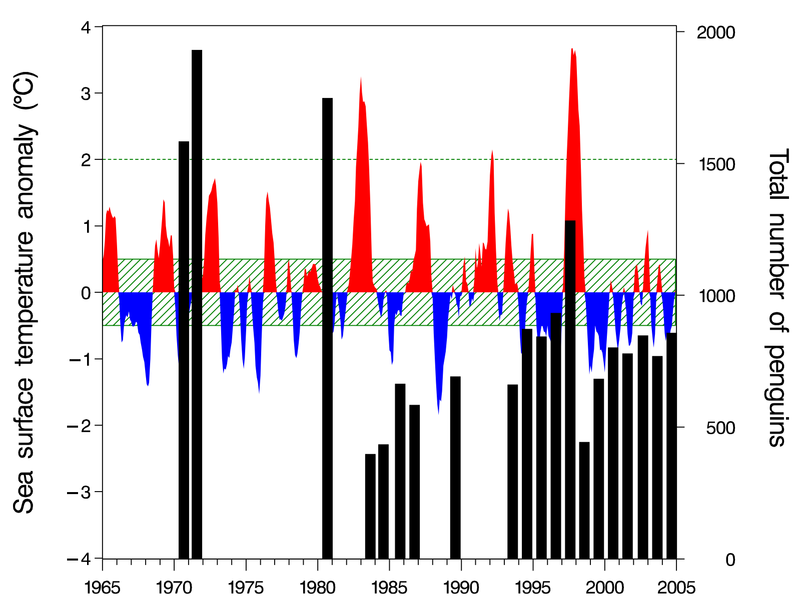

Fig. 1 – Sea-surface temperature (SST) anomalies from the Charles Darwin Research Station, Isla Santa Cruz, Galápagos, Ecuador. We calculated the normalized temperature anomalies (red and blue areas) by comparing the 5-month running mean for SST of each month to the baseline SST from 1965 to 1979. SST anomalies that remain above 0.5 °C or below −0.5 °C (beyond grey striped area) for at least six consecutive months define El Niño (*n* = 9) or La Niña (*n* = 9), respectively. The positive temperature anomalies that exceeded 2 °C (dashed line) indicate strong El Niño events. Black bars are total number of penguins. (For interpretation of the references to color in this figure legend, is referred to the web version of this paper.)

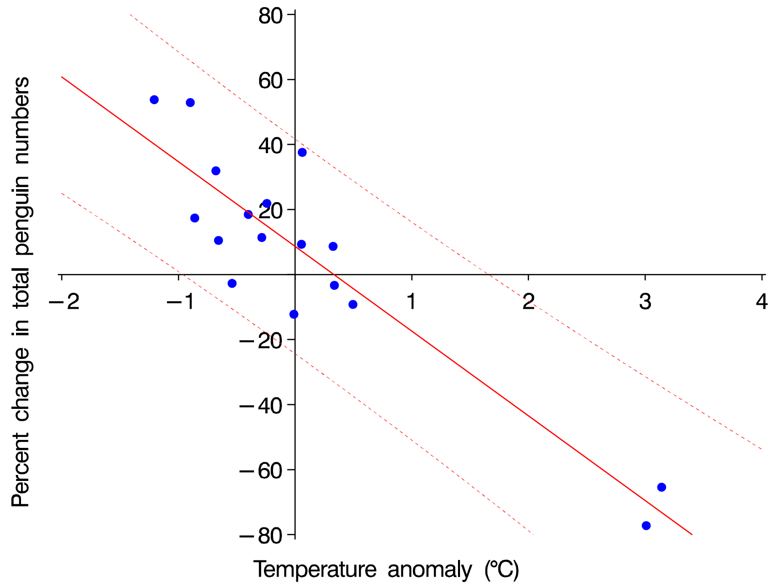

Fig. 2 – Percent change in penguin numbers in relation to the mean normalized sea-surface temperature (SST) anomalies for the period December–April that preceded each penguin count. We calculated changes in the penguin population for counts that were not more than 3 years apart ($n = 17$) ($F_{1,15} = 71.1$, $p < 0.001$, $b_{(adj)} = 0.81$). We also tested the relationship without the 2 strong El Niño events in 1983 and 1998 to determine that the relationship remained significant without these extreme values ($F_{1,13} = 10.2$, $p = 0.007$, $b_{(adj)} = 0.40$). Dotted lines are 95% confidence limits. (For interpretation of the references to color in this figure legend, is referred to the web version of this paper.)

cal standards (1982–1983, 1997–1998), has cumulative effects that diminishes the capacity of the penguin populations to recover from previous El Niño events before the next event occurs. This cycle leads to long-term reductions in penguin numbers.

4.2. *Strong El Niño events and population crashes*

Our analysis indicates that strong El Niño events are catastrophic for the Galápagos penguin causing declines greater than 50% in the population of adult and juvenile birds (Fig. 2).

Starvation is the likely cause of this elevated mortality. Similar mortality in seabirds, due to starvation, has been documented in productive ecosystems, such as those of the Bengala Current during severe El Niño events. (La Cock, 1986). The severity of strong El Niño, measured as duration and extent of SST anomalies, explains this drastic effect on the Galápagos penguin. Only 29 juveniles were counted in the two censuses of 1984 following the 1982–1983 El Niño event (Valle and Coulter, 1987). In September 1997, the effects of El Niño (initiated in March 1997) on the penguin population were still imperceptible (Fig. 1), and we counted 1284 penguins in the Archipelago of which 17% were juveniles. The 1997–1998 El Niño ended in July 1998. By the time of the census of September 1998, no nests or juveniles were recorded, and only 444 adults were observed. These two strong warm events occurred when they would have had the maximum impact on breeding success during two consecutive breeding seasons (1982–1983 and 1997–1998).

Although penguins can breed year round, the onset of a strong El Niño events coinciding with the critical period of pre-breeding food acquisition could have detrimental effects on the population. Since one known preferred breeding time is from April–May, it could have been that the two strong El Niño events that started in May 1982 and March 1997 were particularly detrimental to penguins because of the lack of available food.

The high annual adult survival in penguins in general (Crawford et al., 1999; Weimerskirch et al., 1992) would tend to make their population trends extremely sensitive to small changes in annual survival (Ratcliffe et al., 2002). Consequently, the estimated low adult survival values of 0.23–0.35 for the Galápagos penguin during strong El Niño events, in addition to the direct impact on the dynamics of the breeding population, could also reduce the penguin life expectancy (Croxall et al., 2002) and affect the overall population trend in the manner described in this paper. Therefore, we consider adult mortality to be the main effect of El Niño on the Galápagos penguin.

4.3. *Weak El Niño events and slow recovery rate of penguin population*

Weak El Niño events appear to affect only reproduction and not adult survival because no population crashes were recorded during weak El Niño events. During the weak 1972–1973 El Niño, Boersma (1998b) recorded only one surviving chick from 92 nests. This suggests that penguins do lay eggs during weak El Niño events, but we deduce that the food supply could be insufficient to achieve the survival and recruitment of fledglings. The cumulative effects of weak El Niño events on reproduction provide a plausible explanation for the low recovery rate of the penguin population between 1983 and 1997 (Fig. 1). In fact, some authors have identified the period between 1990 and 1995 as the longest El Niño on record (Trenberth and Hoar, 1996). Poor recruitment rates associated to post-fledgling mortality during repetitive weak

El Niños are also expected to have a lag effect on population size.

4.4. *The mechanisms of El Niño events*

Sinclair and Krebs (2002) state that food supply is the primary factor determining the growth of animal populations. Furthermore, there is accumulating evidence that changes in the availability of food limits the production and survival of the young, and that these changes are often driven by the weather (White, 2004). At present, little is known about the diet of the Galápagos penguin. There are only opportunistic observations of penguins foraging close to the shore that indicate that prey species such as sardines (*Sardinops sagax*), piquitingas (*Lile stolifera*), and mullets (*Mugil* sp.) are likely of primary importance to the penguin diet (Mills, 2000; Vargas, unpubl. data). If these schooling fish species migrate away from the Galápagos archipelago during El Niño events, the penguin will not have access to prey. The Galápagos penguin will be constrained to the coastal areas by its inability to travel long distances (see Crawford and Shelton, 1978). In fact, research on foraging behaviour suggests that feeding is exclusively taking place in upwelling waters less than 2 km from the coast where penguins perform dives of not more than 50 m (Mills, 2000; Steinfurth et al., unpubl. data).

The inability of the penguin populations to recover may not be attributed solely to the time available between successive periods of impoverished food resources. The slow recovery after El Niño events suggests that other factors might also be at play. Boersma (1998b) noted higher mortality of females than of males during strong El Niño events that lead to an unbalanced sex ratio among survivors. The effect of such an imbalance on the mating system of the penguins is unknown, but a higher male:female ratio could dampen the recovery of the population once released from the constraints of food shortage. Flooding associated with El Niño could lead to nest failure and desertion. In 1982–1983, over 2700 mm of rain was recorded at Academy Bay (Santa Cruz) where the annual average (1965–2003) was only 500 mm. Flooding may be a particular problem for Galápagos penguins as has been documented for the Humboldt (Paredes and Zavalaga, 2001) and African penguins (Wilson, 1985). Kelvin waves (eastward propagating waves caused by fluctuations in wind speed at the ocean surface at the Equator) in a strong El Niño create higher than normal sea levels around the Galápagos, (Fig. 3., ftp://ilikai.soest.hawaii.edu/islp/slpp.anomalies) and are expected to increase risks of flooding. Most Galápagos penguin nests are usually sited less than 2 m above sea level (Vargas, unpubl. data). In May 2004, a swell (wave) at Isla Mariela Mediana (0°35′31″S, 91°5′19.5″W) caused the loss of four nests with eggs and chicks (two chicks were drowned in one of these nests, Vargas, unpubl. data).

It is still unknown how the moult affects penguin survival and breeding success during warm El Niño and cold La Niña events. Some unanswered questions are whether penguins are able to moult during El Niño or if penguins are capable of moulting more than once in a year of La Niña when food conditions would be favourable for laying multiple clutches. Moulting requires energy and results in high thermoregulation costs (Payne, 1972). Accordingly, the survival strategy of this species of penguins would require that the penguins: (1) build up energy reserves at sea, (2) moult on land, (3) return to the sea to build up energy reserves again, and (4) begin their breeding cycle. Preliminary data and incidental observations on the Galápagos penguin suggest that, when not moulting, this species is primarily at sea during the day and on land at night (Boersma, 1977).

4.5. *Implications for conservation*

The data that we present here on the effects of El Niño on the Galápagos penguin is important to conservation biology because this species is endemic, rare, and, as we reveal, apparently declining. We have demonstrated that the decline of the Galápagos penguin is associated with a change in climate that is, at least, partly attributable to global human activity (Houghton et al., 2001; Timmermann et al., 1999). Therefore, the Galápagos penguin is predicted to be at higher risk in the 21st century as temperatures and precipitation will very likely continue to rise as the ENSO shifts towards more warming events (Easterling et al., 2000; Houghton et al., 2001).

The fact that the Galápagos penguin has survived for millennia in the face of El Niño (perhaps even stronger that those of 1982–1983 and 1997–1998) is no cause for complacency as other conditions have now changed. Before 1535, the Galápagos Islands were uninhabited by people. Whereas currently, nearly 27,000 humans reside there and about 100,000 tourists visit annually (Boersma et al., 2005). There are several human-caused effects that can lead to further reductions of post-El Niño populations of the Galápagos Penguin. The commercial fishery compete with penguins for the sardines and mullets, particularly during El Niño events when fish populations are reduced, and penguins become entangled in gillnets (Steinfurth, pers. com., see Darby and Dawson, 2000). Furthermore, mosquitoes (*Culex quinquefasciatus*) that arrived on the Galápagos in the 1980s (Peck et al., 1998) because of human actions benefit from the warm and wet conditions of El Niño. The *C. quinquefasciatus* mosquitoes represent a potential new threat for Galápagos penguin (Miller et al., 2001) because *C. quinquefasciatus* are vectors for avian malaria (Fonseca et al., 1998), and penguins in the genus *Spheniscus* are highly susceptible to avian malaria (Fix et al., 1988; Graczyk et al., 1995). There is also concern about the potential arrival to Galápagos of the mosquito-born West Nile virus (Wikelski et al., 2004) that can infect penguins (Travis et al., submitted). The threats outlined alone or in combination (see Huyser et al., 2000) may be exacerbated by the low genetic diversity of the Galápagos penguin that could have arisen from the effects of population bottlenecks imposed by El Niño episodes and coupled with the effects of increased human activity (Akst et al., 2002).

In a population viability analysis (PVA) workshop in February 2005, researchers estimated that under the current El Niño scenario, based on the frequency and intensity of El Niño events described here, the Galápagos penguin has a 30% probability of extinction within the next century (CBSG, 2005; Vargas et al., in preparation). The likelihood of extinction increases when other catastrophic factors such as disease outbreaks, oil spills, or predation by introduced predators are added into the simulations (CBSG, 2005; Travis

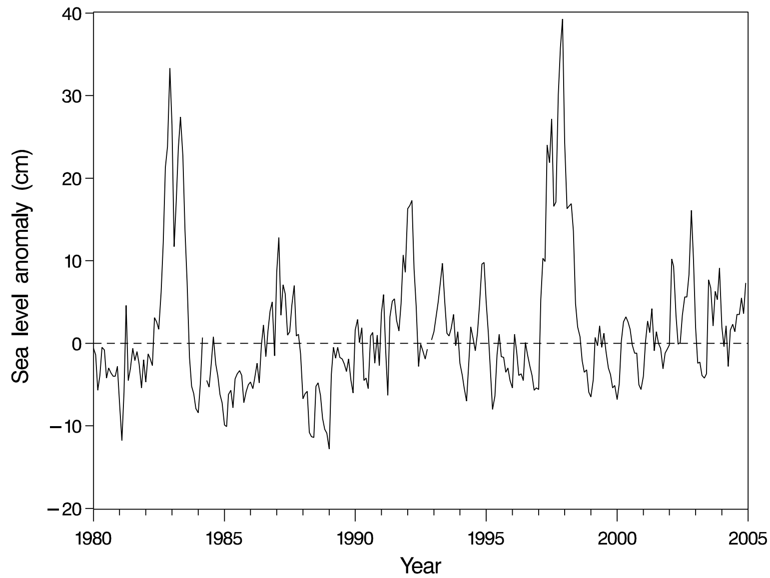

Fig. 3 – Galápagos sea level anomalies from tide gauge at (0°45″S, 90°19″W) Santa Cruz, Galápagos (January 1980–December 2004). The sea level reached 20–35 cm higher than average during the two strong El Niño events of 1982–1983 and 1997–1998. Sea level in December 1997 was slightly higher than the maximum observed during the 1982–1983 El Niño (figure based on monthly data available at: ftp://ilikai.soest.hawaii.edu/islp/slpp.anomalies).

et al., submitted). The Galápagos penguin would be especially at higher risk of extinction after strong El Niño events when the population would be at lower levels.

Of course, direct management of the global human activities that probably underlie the increased frequency and severity of El Niño is beyond the scope of local strategies. However, our results reveal that the situation of the Galápagos penguin is more fragile than previously realized and greater attention should be paid to curtailing human activities that are increasingly affecting this species.

4.6. *Future perspectives and conservation*

The diet of the Galápagos penguin is virtually unknown. Conservation efforts will benefit from determination of seasonal variation in diet. The distribution and abundance of prey species could be better linked to changes in sea temperature, underwater topography, and nutrient levels.

The population dynamics of the Galápagos penguin living in a climatically variable and unpredictable environment still needs further study. Information on the age of first breeding, longevity, annual breeding success and survival rates, recruitment of juveniles, natal philopatry, and movements during ENSO episodes is crucial for the conservation of this endangered species.

Climatologists and wildlife managers should collaborate to conserve the Galápagos penguin. Climate models that successfully predict El Niño events one or two years in advance (see Chen et al., 2004) are of fundamental importance so that timely and effective actions could be undertaken by wildlife managers prior to extreme El Niño episodes.

Conservation actions should focus at reducing mortality of adult birds, which could compensate, at least partially, for the mortality losses during strong El Niño events. Reducing direct and indirect anthropogenic-induced threats to the population will enhance adult survival. Predation by exotic mammals, entanglement in fishing nets, oil spills, and outbreaks of diseases should be prevented (see CBSG, 2005, PVA report for descriptions of research and management recommendations). Therefore, here we recommend the following priority specific conservation actions:

1. Control feral cats (*Felis catus*) on Isabela. In early 2005, cats were reported preying on adult penguins at Caleta Iguana, Southern Isabela (Steinfurth, unpubl. data) Cats could also prey on eggs and chicks in the nest.
2. Prohibit the use fishing nets within foraging ranges of penguins. Fishing nets deployed for mullet and shark are known to cause deaths by entanglement.
3. Prevent arrival of introduced vectors and diseases. Efforts should be aimed at preventing the arrival of vectors (e.g., mosquitoes) and diseases, such as the West Nile virus and avian malaria to which penguins are known to be highly susceptible.

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