Long-Term Ecology Studies in Patagonian Seabirds: A Review with the Imperial Cormorant as a Case Study

Flavio Quintana, Rory Wilson, Nicolás Prandoni, Walter S. Svagelj, and Agustina Gómez-Laich

Global Change and Seabirds

As it has been mentioned in different chapters of this book, it is now widely accepted that global change, and particularly climate variability, has strong and persistent effects on marine ecosystems (Harley et al. 2006; Hoegh-Guldberg and Bruno 2010). In addition to climate change, marine environments (i.e., food webs, biological diversity, and others) are also changing rapidly across the globe for a suite of reasons, some of them as a consequence of anthropogenic activities, including pollution (via heavy metals, organochlorides, oil products, and plastics), coastal development, resource use, energy, transport, overfishing, etc. (Halpern et al. 2008; Poloczanska et al. 2013). These effects have altered the phytoplankton-zooplankton

F. Quintana (✉)
Instituto de Biología de Organismos Marinos (IBIOMAR), CONICET,
Puerto Madryn, Argentina
e-mail: quintana@cenpat-conicet.gob.ar

R. Wilson
Swansea Lab for Animal Movement, Biosciences, College of Science, Swansea University,
Swansea, UK

N. Prandoni
Instituto Nacional de Investigación y Desarrollo Pesquero, Buenos Aires, Argentina

W. S. Svagelj
Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET – Universidad Nacional
de Mar del Plata (UNMdP), Buenos Aires, Argentina

A. Gómez-Laich
Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA) y Departamento de
Ecología, Genética y Evolución (EGE), Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina

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ecosystems, thus changing bottom-up processes throughout the pelagic food chain (Richardson and Schoeman 2004; Hays et al. 2005) with consequences for mid-trophic level fish which are the principal prey for several marine top predators (Cury et al. 2000; Frederiksen et al. 2006).

All mentioned natural and human-induced changes are worldwide and recurrent threats to seabirds and have both direct and indirect impacts on this group (see review in Schreiber and Burger 2002). In addition to climate change (and others mentioned above), threats to seabird populations also include habitat loss and degradation due to invasive species, coastal development, physiological stressors due to food shortages and pollution, and mortality due to bycatch in certain types of fishing (Lewison et al. 2012). Particularly, the effects of climatic factors on seabirds appear to be mostly indirect, mainly affecting the local to regional food webs and the pelagic habitat. Seabirds mainly prey upon fish, squids, copepods, and krill that appear to be more sensitive to climatic variations than upper-trophic-level species (Richardson 2008; Sydeman et al. 2012). However, changes in the distribution and abundance of prey are presumed to have direct effects on seabirds through changes in bottom-up food web dynamics (Ware and Thomson 2005) and predator-prey interactions. Despite that, it is clear that climate variability and change influence seabird reproduction, distribution, phenology, and survival in many regions of the globe, both on large and local scales (Barbraud and Weimerskirch 2006; Jenouvrier et al. 2018). In birds, the timing of breeding has been hypothesized to be the reproductive parameter most influenced by climate change (Przybylo et al. 2000). However, studies of seabird breeding phenology have reported a variety of trends over time (Chambers et al. 2014), and the current evidence (see Keogan et al. 2018) indicates that the phenology of species occupying higher trophic levels is less responsive to environmental change than that of primary producers and consumers (Visser et al. 2004; Thackeray et al. 2016), making them particularly susceptible to trophic mismatch and the associated negative demographic consequences (Thackeray et al. 2010; Poloczanska et al. 2013). Previous studies that have combined estimates of phenological change over time or in response to temperature, of multiple high-trophic-level species to global change (Thackeray et al. 2010, 2016; Sydeman et al. 2012; Poloczanska et al. 2013), show that, on average, seabird populations worldwide have not adjusted their breeding seasons over time or in response to sea surface temperature (SST) between 1952 and 2015 (see Keogan et al. 2018). However, marked between-year variation in timing observed in resident species and some Pelecaniformes and Suliformes (cormorants, gannets, and boobies) imply that timing, in some cases, is affected by unmeasured environmental conditions (Keogan et al. 2018).

How different seabird species will respond to coupled climate and ecosystem change is clearly related to many factors, including life history characteristics, food habits, range, and abundance (Furness and Tasker 2000). Some species may fare well in a warming ocean, whereas others may become locally, regionally, or perhaps even globally extinct (e.g., Kitaysky and Golubova 2000; Lewison et al. 2012). So overall, a fortunate number of factors, trophic position, global distribution, and numerous long-term studies, make seabirds a tractable and powerful group with which to study climate change in our oceans. Such an analysis allows us to not only make general inferences about the degree to which seabird ecology has changed both over time and in relation to SST (or other environmental variables) but also about the life history traits underpinning variation in ecological responsiveness. However, this profitable scenario is not equally distributed worldwide. A global view of the geographical distribution of seabird-climate change scenario shows that studies are concentrated in the NE Atlantic (North sea, Norwegian sea) and off the west coast of North America (California current to Gulf of Alaska). While studies are widely distributed, there are many regional oceans with little or no information, notably the tropical and subtropical regions (Sydeman et al. 2012). There are only two studies on how seabirds have changed over time and with climate in the Southwest Atlantic (SWA) between 40 and 50 south degrees (Quillfeldt et al. 2007; Millones et al. 2015). Of these, only one has focused on a seabird species from coastal Patagonia (Millones et al. 2015) (see below).

The Importance of the Long-Term Monitoring in a Global Change Scenario

Seabirds are widely recognized as reliable indicators of marine environmental changes (Velarde et al. 2019) associated with climatic as well as other anthropogenic and natural factors (see Durant et al. 2009 for a review). They are also relatively well studied compared to other marine organisms but are one of the most threatened groups of birds globally, and, overall, their conservation status is deteriorating rapidly (Croxall et al. 2012). Indeed ~25% of seabird species are currently listed as "threatened" or considered "of special concern" (IUCN 2020). Some seabird species that breed along coastal Patagonia, and forage in its jurisdictional area, are classified as "threatened" (Ministerio de Ambiente y Desarrollo Sustentable y Aves Argentina 2017). Moreover, many other seabird species that only forage in Argentinian waters are also threatened (wandering Albatross, grey-headed Albatross, and white-chinned petrel (Favero and Silva 2005)), and Argentina is one of the top ten ranked countries according to the number of seabird species of conservation concern (Croxall et al. 2012).

Since many seabirds face threats that may affect population status, the long-term monitoring of population, breeding, and behavioral parameters, preferably coupled with environmental data acquisition, is essential to assess how they respond to environmental changes and anthropogenic impacts (Bost et al. 2015). Long-term monitoring of seabirds, both at the breeding sites and at sea, is key to understand population drivers over time. Importantly though, a better understanding of the implications of changes in the marine and terrestrial environments for seabird species is required in order to improve their management and conservation status (Chambers et al. 2014).

In a global review, Sydeman et al. (2012) noted that most (85%) of seabird-climate studies reported on continuous (annual) data. Of the 108 references covered, they found a mean study period of ~23 years, with an average of ~20 years of data per study. The longest study covered 41 years (Sidhu et al. 2012). Most long-term research (88%) involved any of five seabird abundance or breeding parameters: reproduction (e.g., breeding success and other measures of reproductive performance), abundance, survival (of both adults and juveniles), phenology, and adult condition. Other measurements, which were more rarely investigated, included chick growth, community change, foraging behavior, and at-sea distribution (Sydeman et al. 2012).

Despite the auspicious global scenario in terms of long-term research described above, marine experts advise some degree of caution. Sydeman et al. (2012) pointed out that our interpretations are still limited because, despite having some of the best biological time series of the marine realm, seabird datasets are still of insufficient duration to separate natural inter-decadal variability from human-induced climate change effects. They strongly emphasize the need to maintain, and possibly enhance, existing long-term research and monitoring programs, even in times of financial limitations. These programs are necessary to develop the time series required to provide strong inference relating to seabird ecology under global change and most notably anthropogenic global warming (Sydeman et al. 2012). Such long-term empirical studies must focus on interdisciplinary research. Only through such an integrative approach will accurate predictions of change in seabird populations be possible, thereby facilitating seabird conservation in a changing world.

Background of Ecological Long-Term Studies in Patagonian Seabirds

Diversity, Abundance, and General Pattern of Distribution and Conservation Status

Coastal Patagonia breeding seabirds include species from five families, Spheniscidae (penguins), Procellariidae (petrels), Phalacrocoracidae (cormorants), Laridae (gulls and terns), and Stercorariidae (skuas), and constitute one of the best-studied groups of higher-trophic-level organisms in the Patagonian coast of Argentina. Seventeen seabird species breed along the 3,400 km coast from southern Buenos Aires (38° 58' S) to Tierra del Fuego (54° 50' S) (Fig. 1). This includes three penguins (Magellanic Penguin, *Spheniscus magellanicus*; Rockhopper Penguin, *Eudyptes chrysocome*; and Gentoo Penguin, *Pygoscelis papua*), one petrel (Southern Giant Petrel, *Macronectes giganteus*), five cormorants (Imperial Cormorant, *Leucocarbo atriceps*; Rock Shag, *L. magellanicus*; Red-legged Cormorant, *Poikilocarbo gaimardi*; Neotropical Cormorant, *Nannopterum brasilianus*; and Guanay Cormorant, *L. bougainvilliorum)*, three gulls (Kelp Gull, *Larus dominicanus*; Dolphin Gull, *L.*

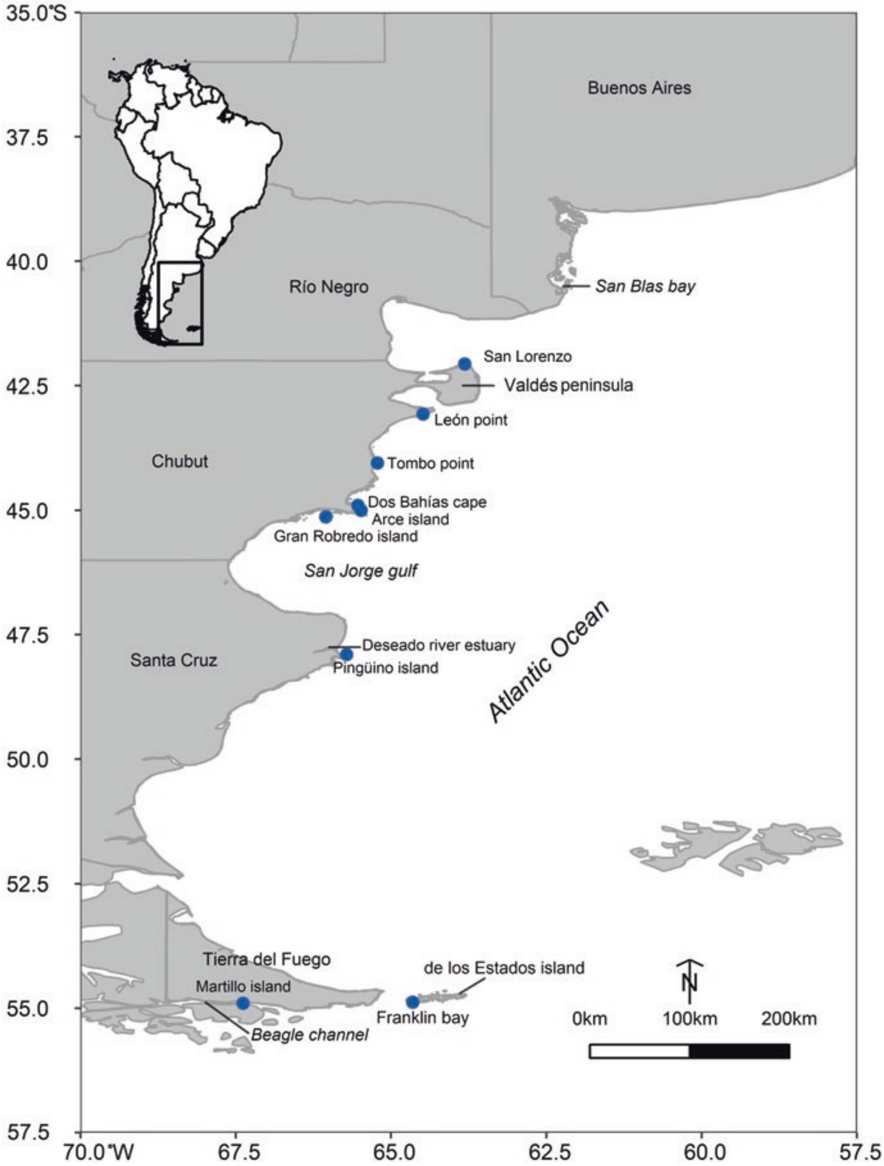

Fig. 1 Geographical location of Patagonian seabird colonies and other sites mentioned in the text

scoresbii; and Olrog's Gull, *L. atlanticus*), three terns (South American Tern, *Sterna hirundinacea*; Cayenne Tern, *Thalasseus eurygnathus*; and Royal Tern, *T. maximus*), and two skuas (Brown Skua, *Catharacta antarctica*, and Chilean Skua, *C. chilensis*) (Yorio et al. 1999; Yorio 2000). Almost the 70% of these species are not abundant and have breeding populations of less than 5,000 pairs (Yorio et al.

1999). The Magellanic Penguin is widely distributed (41° to 55° S) and is the most abundant with a breeding population size of more than one million pairs (BirdLife International 2020), an order of magnitude higher than all other Patagonian seabirds (Schiavini et al. 2005). The list is followed by the Kelp Gull and the Imperial Cormorant with more than 75,000 and 50,000 breeding pairs, respectively (Yorio 2000; Frere et al. 2005), chronologically and correspondingly wide distributions (38°–55° S). Other seabirds, such as the Red-legged Cormorant, the Olrog's Gull, and the Dolphin Gull, have a highly restricted distributions or nest in small colonies at a few sites in Argentina (Yorio et al. 1999). In addition to the 17 breeding seabirds, there are more than 40 non-breeding species which use the Argentine continental shelf as a foraging ground, mostly procellariiforms (Favero and Silva 2005). Despite the fact that the Patagonian coastal zone is one of the few relatively pristine coasts in the world, it is exposed at many locations to fast-growing economic activities such as commercial fisheries, tourism, urban and industry development, etc., with some uncontrolled actions linked to pollution, human disturbance, biological invasions, habitat degradation, and other threats for Patagonian seabirds (Yorio 2000).

In a global context, Southern Hemisphere countries are overrepresented in the number of seabird species of conservation concern, and yet long-term ecological information such as abundance, at-sea distribution, foraging effort, and breeding parameters of many Southern Hemisphere seabirds is limited to a few regions and species. In the Patagonian region, there is no substantial (and published) long-term ecological research with the exceptions detailed below.

Long-Term Research

Even when the ecology of Patagonian seabirds has been studied in a scientifically robust manner, there are only few clear, long-term ecology research approach (i.e., systematically maintained over a period of 10 years or more) in Argentina. Ecology-based research of seabirds inhabiting the Argentinian sea and its coasts has mainly been undertaken for limited periods (single or a few breeding seasons), probably because of logistical challenges of obtaining ecological data across years. Funding programs are also a clear constraint, with most research grants given for 1 to 5 years. Indeed, under the current recession in the global economy, it is hard to predict whether funding will be renewed. Here, we report on the existing long-term studies on seabirds of Argentina after a complete review of published data and personal contacts with seabird researchers who know of unpublished data and ongoing long-term research initiatives. We resume information as follows:

Penguins The Magellanic Penguin is by far the most studied seabird species seen from a long-term perspective, primarily due to the long-term research performed by Dee Boersma and collaborators at the Tombo point colony (44° 02' S, 65°11' W) (Fig. 1) since 1982. Breeding population numbers of this colony have declined 37% since 1987 (Pozzi et al. 2015; Rebstock et al. 2016). Breeding parameters such as breeding success, chick survival, chick growing rate, etc. have also been gathered since 1983 and reported under different research approaches (Boersma et al. 1990; Stokes and Boersma 1998, 2000; among others). At-sea movements and foraging variables (distances traveled and feeding trip durations) of adult breeders during the incubation and chick rearing periods have also been recorded for more than 10 years (Boersma and Rebstock 2009; Boersma et al. 2015). Although the Magellanic Penguin dataset is extensive, there is only one long term-based published article about the potential consequences of climate change on this species. Boersma and Rebstock (2014) studied the effect of storms (rains) on chick survival, based on long-term records of rainfall and air temperature. They found that during a period of 28 years, rain and heat are important sources of mortality in some years but are not the main cause of chick mortality, which was mainly affected by starvation and predation.

Other existing long-term initiatives with more than 5 years of data, including monitoring population numbers, breeding and demographic parameters, records of tagging birds, and foraging variables, are being collected at the Magellanic Penguin in Valdés peninsula (Quintana and Wilson, unpub. data) (see below), Dos Bahías cape (Blanco and Quintana unpub. data), Río Negro and Chubut colonies (Borboroglu et al. unpub. data), Santa Cruz colonies (Millones et al. unpub. data, Barrionuevo and Frere unpub. data), and the Beagle channel (Raya Rey et al. unpub. data) (but see Raya Rey et al. 2014) (Fig. 1).

Long-term studies targeting on the diet of the Magellanic Penguin seem to be reduced to systematic records of stable isotopes from adult breeders of Martillo island (54° 54’S, 67°23’W) (Dodino et al. unpub. data) and a diet study across years at the San Jorge gulf colonies (Yorio et al. unpub. data), both with less than 10 years of continuous data (Fig. 1).

The most comprehensive (in terms of number, quality, precision, and sample rate of the variables recorded) long term-based data series of the at-sea behavior of the Magellanic Penguin has been undertaken at San Lorenzo colony (42° 05’S, 63°51’W) in Valdés peninsula (Fig. 1) (Quintana and Wilson unpub. data, but see Sala et al. 2012, 2014; Wilson et al. 2015). Since 2008, more than 500 breeding adults have been instrumented with cutting-edge technologies to study at-sea distribution, diving behavior, prey capture, energy expenditure, and other indicators of the foraging effort of birds during the breeding season (Quintana and Wilson unpub. data). One of the relevant aspects of this long-term initiative is the use of advanced electronic technology for the study of animal behavior in relation to the environment. In fact, latest equipment allows the recording and quantification of environmental variables such as water temperature, depth, atmospheric pressure, and light with high precision (Sala et al. 2017). Thus, a comprehensive, long dataset of foraging movements and at-sea behavior can be coupled with oceanographic long-term records from operational oceanography, remote sensing, models, and/or bio-logging to link movement and/or foraging behavior with issues related with global change as well as other environmental consequences of anthropogenic-based stressors. In the current context of climate change and the rapid modification of the marine habitat, understanding the environmental factors that determine animal movements, behavior, and penguin at-sea distribution is becoming crucial to predict their ability to respond to changing conditions and ultimately the subsequent consequences on bird population dynamics (Fort et al. 2012). The consistent long-term database of the at-sea movement and behavior of the Magellanic penguin that is being built up, year after year, represents the seminal step for the next academic challenge: to analyze these data within the frame of a global change scenario.

The other two species of penguins breeding in coastal Patagonia, the Rockhopper and the Gentoo Penguin, have received less attention in long-term studies. The diet of both species has been monitored through stable isotopes over 10 and 8 years, at Franklin bay (54° 53’ S, 64°39’ W), de los Estados island, and the Beagle channel, respectively (Raya Rey et al. unpub. data) (Fig. 1). Population trends of the Rockhooper Penguin at the northern limit of its breeding range (Pingüino island, Santa Cruz, 47° 54’ S, 65°43’ W) (Fig. 1) have been studied for 35 years (1985–2020) with 27 years of census data (Gandini et al. 2017; Frere et al. unpub. data), and 16 years of unpublished breeding success data also exists for the same colony (Morgenthaler et al. unpub. data). Population numbers of a newly established colony of Gentoo penguins at Martillo island (Fig. 1) have been continuously monitored since 2000 (Raya Rey et al. 2014; unpub. data).

Cormorants The Imperial Cormorant is the only species of cormorant that has been comprehensively studied using a long-term research approach at a single colony in Patagonia, Argentina. Breeding parameters and the pelagic ecology of the Imperial Cormorant have been systematically studied since 2004 by some authors of this chapter. In the section below, we present, as a case study, our original data and results of this long-term study through time. Over 16 years, we examined the inter-annual variability of breeding and foraging variables of birds from León point, Chubut (43° 04’ S, 64° 29’ W) (Fig. 1), one of the two biggest colonies (> 6,000 pairs) of the species in its breeding range in coastal Patagonia Argentina (Frere et al. 2005). In addition, over 26 years, Yorio et al. (2020) have recently reported population numbers of Imperial cormorants in northern coastal Argentine Patagonia. Occasional data of breeding population numbers have also been reported for colonies from the Beagle channel (see Raya Rey et al. 2014).

The other existing long-term population data of a Patagonian cormorant species is maintained by E. Frere and collaborators for the Red-legged Cormorant from Santa Cruz colonies. Published data on its population trends for a period of 20 years appear in Millones et al. (2015), and the effect of oceanographic conditions (SST and chlorophyll-a) on these trends was analyzed, suggesting that coastal ocean productivity could be an important factor affecting temporal variations in the Argentinian Red-legged Cormorant population.

Petrels Population numbers of the Southern Giant petrels breeding in northern Patagonia, Argentina (Arce island 45° 00’ S, 65° 29’ W and Gran Robredo island 45° 08’ S, 66° 03’ W) (Fig. 1) have been monitored since 1987, and petrel population trends were reported up to 2004 by Quintana et al. (2006). Annual data of breeding pairs and total number of fledgling have been systematically gathered since 1995 (Quintana and Blanco, unpub. data).

Other Species and Multispecies Approaches In general terms, species pertaining to the other Patagonian seabird families (Laridae (gulls and terns) and the Stercorariidae (skuas)), are the least studied over the long term. The most extensive breeding population record of the abundant and widely distributed Kelp Gull is over 7 years for at only three of the 68 northern Patagonian colonies of Río Negro and Chubut provinces (Lisnizer et al. 2011). Breeding population numbers of Dolphin Gull colonies from the Deseado river estuary, Santa Cruz (Fig. 1), have been annually monitored since 2007 to the present (Millones et al. unpub. data) and few occasional counts (four over 20 years) reported by Raya Rey et al. (2014) at the two colonies in the Beagle channel. The foraging areas and other feeding parameters of Olrog's Gull were determined at San Blas bay, south of Buenos Aires (39° S, 61° W) (Fig. 1) for a 5-year period (Suarez and Yorio, unpub. data). There are no medium-/long-term records of any ecological variable for the three species of terns and the two species of skuas from coastal Patagonia Argentina.

Long-term multispecies approaches only relate to the seabird-fisheries interactions. Favero et al. (2013) reported the seabird bycatch in the Argentinian demersal longline fishery for a 10-year period (2001–2010). They characterized, in space and time, the occurrence and intensity of seabird mortality as consequence of the interaction with demersal longline fisheries operating in the Argentine Sea. However, their long-term database extends over the period 1999–2019 and includes bycatch of seabirds in other types of fisheries and related operational and environmental variables (i.e., wind, sea state, etc.) (Favero et al. unpub. data).

In summary, long-term ecological research approaches are not common in Argentina. Only two species (the Magellanic Penguin and the Imperial Cormorant) from single colonies have been systematically studied for continuous period > 10 years in a broad sense (i.e., not only population counts). Even the few existing long-term population data of these and other species are focused on a single species at a particular location/area, and population trends are based on sporadic counts over time, having to resort to mathematical models to present population data with confidence.

Although the non-breeding period is critically important for the population dynamics of seabirds since most mortality occurs at this time (Frederiksen et al. 2008), the few long-term studies on Patagonian seabirds are usually undertaken during the breeding season. Thus, a key question in understanding the link between global change and/or prey availability and seabird ecology is the extent to which there have been long-term changes in both breeding and non-breeding season's ecological variables.

To our knowledge, almost no published studies have quantified long-term trends in any ecological variable other than breeding population numbers in Patagonian seabirds (but see some on the Magellanic Penguin above), and almost no study has compared long-term trends with environmental changes over time (but see Millones et al. 2015). Indeed, our understanding of the spatial ecology of Patagonian seabirds facing environmental change is very rudimentary, despite its relevance for the conservation of these vulnerable organisms and for the management of South Atlantic marine ecosystems. It is thus clear that long-term-based research on seabirds must be continued and results interrogated (including the development of new approaches) to integrate processes occurring at various scales, so as to track the population responses of these long-lived vertebrates to environmental changes.

In the next section, we offer unprecedented results from a long-term dataset (16-year period) on demographic, breeding, and at-sea ecological variables for the imperial cormorant from León point, Chubut. Our research is given only as an example of the database gathered under a long-term ecological research needed to understand the potential effects of global change on Patagonian seabirds.

A Model of Long-Term Ecological Research on a Patagonian Seabird: The Imperial Cormorant

As mentioned, it is only recently in Argentina that seabird ecology studies have focused on inter-annual variability over the long term. Such long-term studies are necessary if we want to have a better understanding of how birds make use of the surroundings of a breeding colony (Corman et al. 2016; Warwick-Evans et al. 2016) because this will help us identify important areas for conservation in the form of marine protected areas or other management and conservation tools (Thaxter et al. 2012). Long-term approaches integrating population and breeding parameters with at-sea performance are as rare as they are essential, even when they are key to wholly understanding the status and health of seabird populations (Inchausti et al. 2003).

The Imperial Cormorant colony of León point is one of the two largest colonies (> 6,000 pairs) of the species at its breeding range in coastal Patagonia Argentina (Frere et al. 2005). Previous studies performed at this breeding site have analyzed several aspects of the bird's at-sea distribution and diving and foraging behavior by means of miniaturized data loggers (Global Positioning System, time depth recorders, daily diaries, and accelerometers; Shepard et al. 2009; Quintana et al. 2011; Wilson et al. 2012; Gómez-Laich et al. 2013; among others). Most of these studies have been focused on specific behaviors related to diving performance and energy management, among others, with no more than 2 or 3 years of data. In the present work, we capitalize on a long-term data series (i.e., 14 years of records over a 16-year period from 2004 to 2019) including breeding parameters and foraging patterns, to describe inter-annual variation. Firstly, we examine the variation over time of some foraging trip parameters, the use of marine habitat, and the foraging range of both males and females. Secondly, we examine how both sexes exploited the depth-dependent "energy landscape" (landscape-dependent energy expenditure, see Wilson et al. 2012) of the area around the colony over time, and thirdly, we analyze the inter-annual variations of some breeding parameters. We then discuss the importance of long-term tracking, breeding, and population data for ecological studies and their implications for conservation and management plans.

At-Sea and Breeding Performance Data Gathered Through Time

Fieldwork was conducted at León point colony (43° 04’ S, 64° 29’ W), Chubut, Argentina (Fig. 1) over 16 breeding seasons (in late November–early December of 2004–2019). A total of 567 Imperial cormorants brooding chicks < 10 days old were fitted with GPS loggers. Of those, 207 were equipped with GPS loggers (Earth and Ocean Technologies, Kiel, Germany), 229 were fitted with Mini-GPS loggers (Earth and Ocean Technologies, Kiel, Germany), six were instrumented with GiPSy-4 loggers (TechnoSmart, Rome, Italy), and 125 were fitted with Axy-Trek loggers (TechnoSmart, Rome, Italy) (Table 1). All of the devices were programmed to record time, latitude, longitude, and ground speed (GPS-based) every second. Each animal was sexed by its vocalizations following Svagelj and Quintana (2007) and gently removed from its nest using a specially designed pole with a crook. Devices were attached to the feathers of the lower back using Tesa tape following procedures outlined in Wilson et al. (1997) and retrieved after ≤ 24 h. All of the equipped birds continued to breed normally during the study period.

Only completed foraging trips (departure from and arrival to the nest) were included in the analyses. Most cormorants performed a single foraging trip before the logger was retrieved; however a small number of individuals (< 5%) performed two or more trips. In these cases, only the longest trip performed by the animal was considered for further analyses to avoid pseudo-replication. Identification and classification of the different behaviors performed by cormorants in each of the foraging trips were described in Quintana et al. (2011). Fixes were categorized into three classes: traveling (flying), floating, and diving (see Quintana et al. 2011 for details). This classification allowed us to calculate a series of five foraging trip parameters for each bird composed of: (1) times (in h), trip duration (from departure until returning to the colony) and total foraging duration (time between the first foraging dive until the last); (2) distances (in km), foraging path length (total distance traveled) and commuting distance (distance from the nest to the first dive plus the distance from the last dive to the nest); and, finally, (3) the number of dives per total foraging time. During 2014, devices did not record data in exactly in the same regime as the other years, and we only computed data of total trip duration, total distance traveled, and commuting distance (see Table 1).

To describe the pattern of variation of each studied variable across years, we calculated an overall mean which was obtained by calculating the weighted mean of yearly means using the *weightedMean* function from the R library *matrixStats* (R Core Team 2019). The latter was used because the number of samples differed significantly between years and we wanted each year’s mean to contribute the same to the overall mean. Since at-sea movements and behavior differ between males and females (Quintana et al. 2011; Gómez-Laich et al. 2012), overall mean calculations were performed for males and females separately. After this, for each bird, we calculated the difference between each foraging trip parameter and the overall mean

Table 1 Total number of instrumented Imperial cormorants and recorded tracks during a 16-year period. The mean value and the standard deviation of the total trip duration, the foraging time, the total distance traveled, the commuting distance, and the number of dives per hour per sex per year are also shown

Year	Sex	Total instrumentations	Tracks with data	Trip duration (h)	Foraging time (h)	Total distance traveled (km)	Commuting distance (km)	Number of dives per hour foraging
2004	Female	8	7	5.53 ± 2.53	4.4 ± 2.0	60.3 ± 28.7	33.4 ± 16.0	14.3 ± 3.2
2004	Male	8	7	6.06 ± 1.49	4.4 ± 0.8	93.6 ± 47.6	41.3 ± 12.9	13.5 ± 4.9
2005	Female	8	8	6.73 ± 1.91	5.2 ± 1.7	74.8 ± 30.6	35.4 ± 15.0	25.6 ± 12.8
2005	Male	8	6	5.18 ± 0.95	4.1 ± 0.6	64.0 ± 22.8	21.1 ± 13.6	11.8 ± 4.1
2007	Female	8	5	5.75 ±1.36	2.3 ±0.6	90.3 ± 25.1	65.2 ± 23.2	19.9 ± 13.9
2007	Male	7	5	4.49 ±0.81	2.1 ±0.4	68.5 ±20.1	35.2 ±17.1	17.4 ±6.7
2008	Female	22	18	6.61 ± 1.28	5.3 ± 1.1	64.8 ± 22.5	28.6 ± 10.8	11.5 ± 3.2
2008	Male	20	15	6.53 ± 1.40	5.1 ± 1.3	75.3 ± 15.3	19.5 ± 7.6	22.1 ± 11.3
2009	Female	31	13	6.18 ± 1.97	4.3 ± 1.5	69.8 ± 27.2	27.3 ± 15.8	13.9 ± 4.0
2009	Male	30	16	4.56 ± 2.16	3.6 ± 1.9	53.7 ± 24.4	16.6 ± 9.9	20.1 ± 8.9
2010	Female	48	25	7.47 ± 1.27	5.9 ± 1.2	78.6 ± 25.0	40.9 ± 18.4	13.6 ± 4.0
2010	Male	50	24	5.88 ± 1.46	4.3 ± 1.5	75.4 ± 33.0	26.1 ± 14.2	15.8 ± 7.2
2011	Female	29	11	7.93 ±1.34	6.1 ±1.0	68.0 ±23.1	38.1 ±21.6	12.2 ±2.4
2011	Male	13	6	6.48 ±0.52	5.1 ±0.8	68.7 ±13.6	28.8 ±6.2	18.8 ±11.3
2012	Female	15	10	10.14 ± 1.70	4.8 ± 1.6	72.1 ± 30.1	38.6 ± 16.7	20.1 ± 16.0
2012	Male	15	7	8.89 ± 2.63	4.5 ± 1.7	70.3 ± 16.4	24.9 ± 10.3	12.1 ± 4.1
2013	Female	18	10	6.15 ± 1.34	4.6 ± 1.3	68.8 ± 22.2	37.1 ± 14.0	15.7 ± 8.3
2013	Male	21	12	6.22 ± 1.81	4.2 ± 1.3	71.5 ± 22.2	35.8 ± 16.5	16.8 ± 9.1
2014	Female	20	6	6.50 ± 0.91	-	76.7 ± 14.4	41.3 ± 15.7	-
2014	Male	21	7	7.38± 0.47	-	63.2 ± 12.8	38.6 ± 15.0	-

(continued)

Table 1 (continued)

Year	Sex	Total instrumentations	Tracks with data	Trip duration (h)	Foraging time (h)	Total distance traveled (km)	Commuting distance (km)	Number of dives per hour foraging
2015	Female	19	17	6.46 ± 1.40	5.1 ± 1.2	78.8 ± 20.8	31.2 ± 15.7	15.8 ± 11.6
2015	Male	21	14	6.61 ± 2.88	3.2 ± 1.7	67.3 ± 27.5	36.3 ± 13.7	16.7 ± 8.6
2016	Female	32	15	6.87 ± 1.38	5.5 ± 1.2	81.6 ± 22.9	22.8 ± 13.3	12.8 ± 3.8
2016	Male	28	16	5.43 ± 1.60	4.2 ± 1.3	70.8 ± 15.8	29.2 ± 8.1	8.0 ± 2.0
2017	Female	21	12	8.72 ± 1.38	7.4 ± 1.5	73.3 ± 29.3	31.6 ± 20.5	17.3 ± 4.7
2017	Male	20	16	5.65 ± 2.23	4.0 ± 2.4	96.3 ± 18.2	44.1 ± 12.8	15.7 ± 6.1
2019	Female	12	8	6.97 ± 1.07	5.3± 0.9	59.5 ± 28.6	30.9 ± 19.1	11.8 ± 4.2
2019	Male	14	9	5.66 ± 1.62	4.3 ± 1.5	75.4 ± 20.9	38.0 ± 15.4	9.8 ± 4.3
	Female weighted mean			7.0 ± 1.20	5.1 ± 1.1	72.7 ± 8.1	35.9 ± 9.7	15.7 ± 3.9
	Male weighted mean			6.14 ± 1.03	4.1 ± 0.8	72.4 ± 10.8	31.0 ± 8.3	15.3 ± 3.9

for that parameter (hereafter, deviation from the overall mean), and this difference was used in the following analyses.

Kernel analyses to assess habitat use from GPS locations were performed for each year by sex using the fixed kernel density estimator (FKDE, KernelUD function in the R package adehabitatHR, Calenge 2006). We considered the 95, 75, and 50% fixed kernel probability density to represent areas of active use (home range area, HRA) (Hamer et al. 2007). The smoothing parameter (h) was set to 0.012 and the cell size was of 1 km^2. We distinguished between mean home range and mean foraging area used per sex per year by calculating the 95% fixed kernel probability density of each of the instrumented animals. To calculate the mean home range, we used all the GPS positions, while only those positions classified as dives were considered to determine the mean foraging area. Finally, we quantified the annual overlap of the foraging areas between sexes. The degree of overlap was calculated as the percentage of the 95% kernel foraging area used by males that overlapped with those used by females and vice versa. Since the total area from which the percentage was calculated was different for each sex, we calculated a percentage overlap for males with respect to females and a percentage overlap for females with respect to males (Gonzáles-Solís et al. 2000).

Bird locations classified as dives were overlaid over an energy landscape scenario that considered the cost of transport based on the costs of flying to and from the colony to the foraging grounds and the costs of foraging along the seabed (mass-specific energy invested per second, J kg^{-1} s^{-1}, see Wilson et al. 2012). For each year, the density of dives (number of dives per km^2) performed in each of the different energy-demanding environments surrounding an area of 60 km (corresponding to the maximum distance from the colony reached by the tagged birds) around the colony was calculated.

Finally, breeding parameters were collected from a total of 2,553 nests. Over 14 breeding seasons, nests were visited every 3–5 days from the start of the laying period until chicks reached 30 days of age (Svagelj and Quintana 2011). Chicks were considered to have fledged (breeding success) if they reached 30 days of age, due to the high probability of chick survival to independence at that age (Svagelj and Quintana 2011).

For each trip parameter and sex, differences between years in the deviation from the overall mean were tested by means of one-way analysis of variance (ANOVA) using the *aov* function from the stats R package. Only in the case of the number of dives per foraging hour, male's home range and male's foraging area, were Kruskal-Wallis tests performed using the *kruskal.test* function from the stats R package. Finally, multiple comparisons were performed using the *lsmeans* function from the lsmeans R package or the *dunnTest* function from the FSA R package. All algorithms, plots, and statistical tests were performed using the open source statistical software R version 3.6.1 (R Development Core Team 2019) with a level of significance $p < 0.05$. Results of foraging parameters are shown as mean ± standard deviation (SD).

Foraging Trips and Use of Marine Areas Over Time

We recorded a total of 325 complete foraging trips from breeding adults. Of these, 165 (51%) were performed by females and 160 (49%) by males. Since several GPS devices failed to record data, no foraging information was obtained for 2006 and 2018 breeding seasons.

Most adult breeders made a single foraging trip per day to find food for themselves and the offspring. The overall mean foraging trip duration for females and males was 7.0 ± 1.2 h and 6.1 ± 1.0 h, respectively (Table 1). The foraging trip duration was relatively steady across the study period (Fig. 2A, B). In general, yearly foraging trip duration for males and females was similar to the overall mean, except during 2012. During this particular year, males remained at sea 2.8 h longer than average (year effect $p<0.01$, $F_{13,146}=2.7$). As regards females, daily feeding excursions were 3.1 and 1.7 h longer than the overall mean during 2012 and 2017 (year effect $p<0.01$, $F_{13,151}=6.8$, Tukey contrasts between 2012 and the rest of the years but 2017, $p<0.03$; Tukey contrasts between 2017 and 2004, 2007, 2008, 2009, 2013 $p<0.02$), respectively (Fig. 2A). Females always spent more (or equal) time at sea than males, except in 2014 when we recorded the opposite pattern (Fig. 2A).

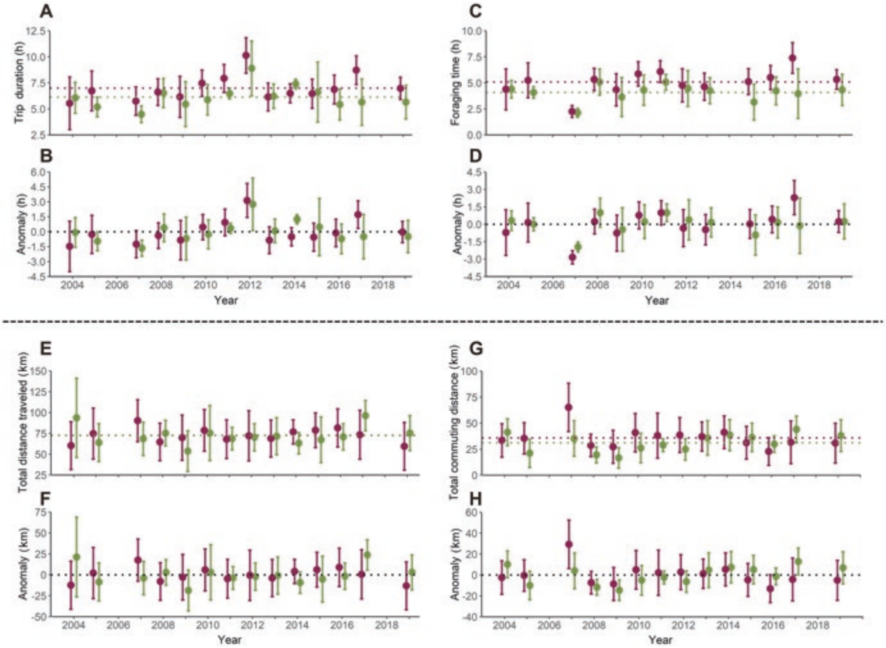

Fig. 2 Foraging parameters (mean ± standard deviation (SD)) over time (a 16-year period) of adult breeders (females in purple circles and males in green circles) of Imperial cormorants from León point, Chubut, Argentina. (**A**) Duration of foraging trips, (**C**) foraging time at sea, (**E**) total distance traveled, and (**G**) commuting distances to and from the foraging sites. Annual deviations from (**B**) trip duration overall mean (i.e., anomaly), (**D**) foraging time overall mean, (**F**) total distance traveled overall mean, and (**H**) the commuting distance overall mean

In general terms, the foraging time at sea was also relatively stable along the 16-year period, and females never spent less time foraging than males (Fig. 2C, D). While at sea, female Imperial cormorants foraged on average 5.1 ± 1.1 h, while males spent 4.1 ± 0.8 h. A clear anomaly of the, otherwise, regular foraging pattern was particularly evident for females during 2007, when birds spent less time foraging than all other years (Fig. 2C). In 2007, female foraging time was 2.8 h less than the overall female mean (Tukey contrasts between 2007 and the rest of the years but 2004, 2009, and 2013, p values <0.03) (Fig. 2C). By contrast, during 2017 (in a manner similar to that observed for trip duration), females spent a particularly great amount of time foraging at sea (2.3 h more than the overall mean) (Tukey contrasts between 2017 and the rest of the years but 2010 and 2011, all p values <0.02) (Fig. 2C).

Total distances covered by adult Imperial cormorants during the at-sea foraging excursions were very consistent over the study period (Fig. 2E, F). The overall mean for females and males was 72.7 ± 8.13 and 72.4 ± 10.8 km, respectively. Females were more consistent than males with respect to the total distances covered while at sea. Contrary to the males, females did not have any distinctive value emanating from particular years (females year effect $p=0.4$, $F_{13,151}=1.0$; males year effect $p<0.01$, $F_{13,146}=2.6$), while the total distance traveled by males was particularly high during 2004 and 2017 (23.9 and 21. 2 km above the overall mean) and particularly low during 2009 (18.8 km below the overall mean) (male Tukey contrasts between 2004–2009 and between 2009–2017, $p=0.02$ and $p<0.01$, respectively) (Fig. 2E).

The flying distances covered by birds during commuting to and from the foraging areas were also relatively constant across seasons (Fig. 2G, H), and the overall mean for females and males was 35.9 ± 9.7 km and 31.2 ± 8.3 km, respectively. Male commuting distance was particularly low during 2008 and 2009 (11.7 and 14.5 km below the overall mean, respectively) and higher during 2017 (12.9 km above the overall mean) (year effect $p<0.01$, $F_{13,146}=5.8$, Tukey contrasts between 2008 and 2015, 2017 and 2019, all p values <0.03; Tukey contrasts between 2009 and 2004, 2013, 2014, and 2017, all p values <0.02) (Fig. 2G). By contrast, it was only during 2007 that females showed any distinctively higher value for their commuting distance (29.3 km above the overall mean) (year effect $p<0.01$, $F_{13,151}=2.8$, Tukey contrasts between 2007 and 2008, 2009, 2015, 2016, 2017, and 2019, p values<0.03).

Finally, over the study period, the number of dives performed per hour foraging was less regular than the other foraging variables (Fig. 3A, B). In some years, males performed more dives per unit time foraging at sea than females, although the opposite pattern was also evident. On average, female and male foraging cormorants performed 15.7 ± 3.9 and 15.3 ± 3.9 dives per hour, respectively. Deviations from the overall mean were evident for males during 2016 (7.3 dives per hour below the overall mean) (year effect $p<0.01$, K-W $\chi_{212} = 44.2$) (Fig. 3A). In the case of females,

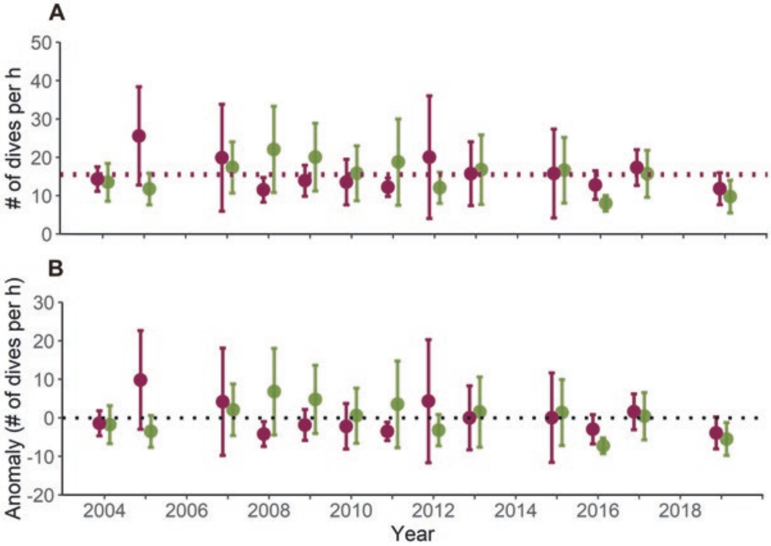

Fig. 3 Number of dives per foraging time (mean ± standard deviation (SD)) of adult breeders (females in purple circles and males in green circles) of Imperial cormorants from León point, Chubut, Argentina, annually performed during a 16-year period (**A**) and annual deviation from the overall mean (anomaly) (**B**)

the number of immersions per hour varied considerably between years (year effect $p = 0.03$, K-W $\chi_{212} = 22.8$). Female diving rate was the highest during 2005 (9.8 more dives per hour than average) and the lowest during 2008 (4.2 fewer dives per hour than average) (Fig. 3A).

Imperial cormorants from León point always foraged within 60 km of the colony and mostly in waters <50 m depth (Fig. 4). A view of all at-sea positions (data for all years together) showed that both females and males from León point exclusively used waters south of the colony to forage at sea (Fig. 4).

From 2004 to 2019, females spread (indicated by the 95% kernel contour) over an average area at sea of 217.4 ± 32.2 km^2 and their home range was very consistent across years ($F_{12,146} = 1.2$, $p = 0.3$) (Fig. 5A, B). Males used a similar area to the females (227.1 ± 43.4 km^2), but deviations from the overall mean were evident during 2009 and 2017 (76 km^2 below and 100 km^2 above the overall mean, respectively) (K-W $\chi_{12} = 23.2$, $p = 0.03$) (Fig. 5A, B).

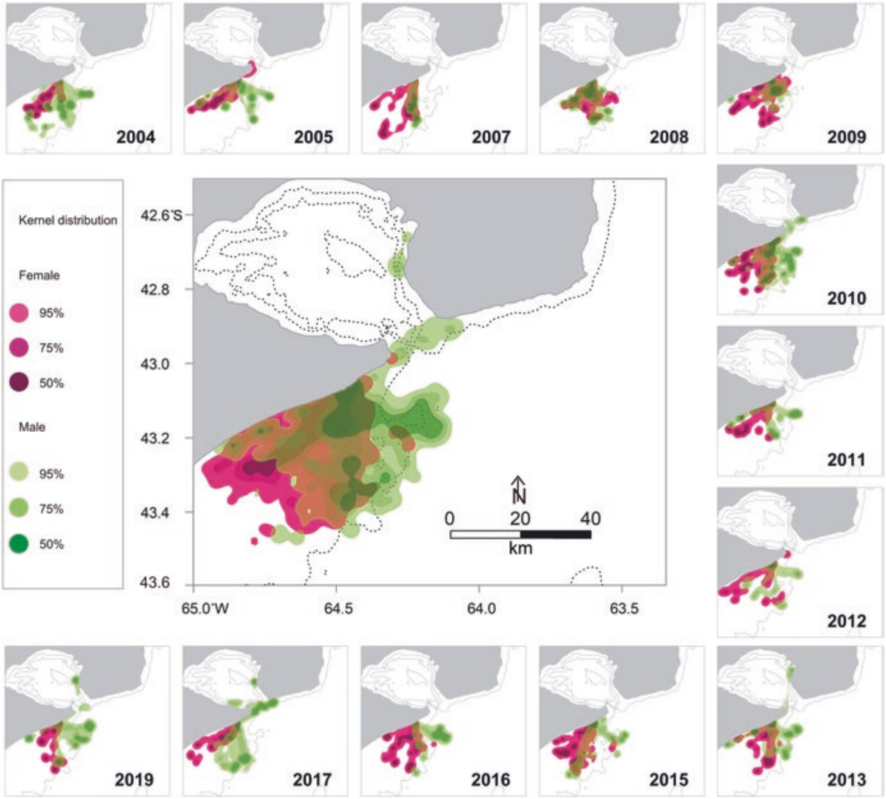

Fig. 4 Imperial cormorants, *Leucocarbo atriceps*. Kernels encompassing 50% (light green), 75% (medium green), and 95% (dark green) of male's and 50% (pink), 75% (medium purple), and 95% (purple) of female's foraging locations from León point between 2004 and 2019. The central map encompasses data from all years in one plot

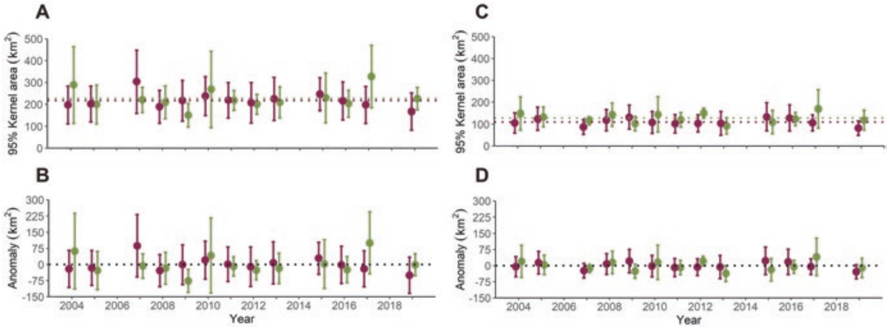

Fig. 5 At sea and foraging areas (mean ± standard deviation (SD)) over time of adult breeders (females in purple circles and males green circles) of Imperial cormorants from León point, Chubut, Argentina. (**A**) Annual variation of the at-sea areas (95% kernel contour of all at-sea-positions) and (**C**) annual variation in the foraging areas (95% kernel contour of dive positions). Annual deviations from (**B**) the at-sea area overall mean (i.e., anomaly) and (**D**) the foraging area overall mean are also shown

Both sexes exhibited some grade of consistency in the use of the foraging areas (given by the 95% kernel contour of foraging locations) along the whole study period (Fig. 5C, D). Females spread out over an average foraging area of 110.5 ± 15.6 km^2 and showed a high consistency across seasons ($F_{12,146} = 1.1$, $p=0.4$) (Fig. 5B). Similarly, the average size of the feeding area used by males was 128.6 ± 21.1 km^2 with no anomalies across time (K-W $\chi_{12} = 20.9$, $p=0.05$) (Fig. 5C, D).

Male Imperial cormorants commonly foraged offshore, to the south-east and near the 50 m isobaths, while females foraged closer to the coast in shallower waters located southwest of the colony. This pattern of sexual segregation in the use of foraging grounds was evident across breeding seasons (Fig. 4). However, foraging females and males overlapped marginally in their foraging areas in every season (mean, 27.7 ± 14.9 and 28.3 ± 20.7% for females over males and males over females, respectively), with a maximum overlap during 2008 and 2009 (Fig. 6A, B).

Based on 22,056 foraging dives, we found that over the complete study period, Imperial cormorants mainly foraged in a virtually homogenous energy landscape (i.e., landscape-dependent energy expenditure, see Wilson et al. 2012) corresponding to the least energetically costly areas (Fig. 7). Overall, females and males concentrated 96–97% of their dives in an area represented by the three least costly fields (Fig. 7). This pattern was also very consistent along the years (Fig. 8). While females systematically foraged mainly on the least costly field (level 1) (Fig. 8A), males allocated their foraging activities equally between the three first energy landscape levels (Fig. 8B). Only between 2008 and 2010 was the number of dives performed per km^2 by males highest in the first field than in the other two (Fig. 8B).

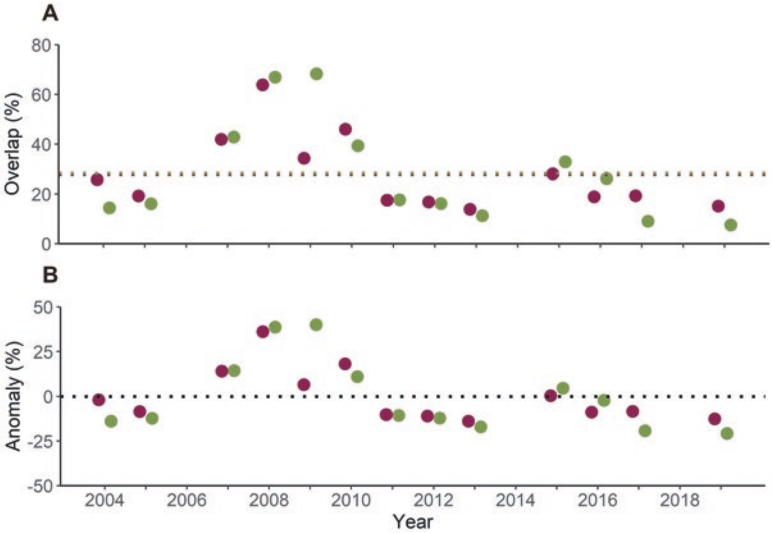

Fig. 6 Annual variation of the spatial overlap (%) in the foraging areas over time of adult Imperial cormorants from León point. (**A**) Overlap of females over males' foraging areas is showed in purple circles at those of males over females in green circles and (**B**) annual deviation from the spatial overlap overall mean (anomaly)

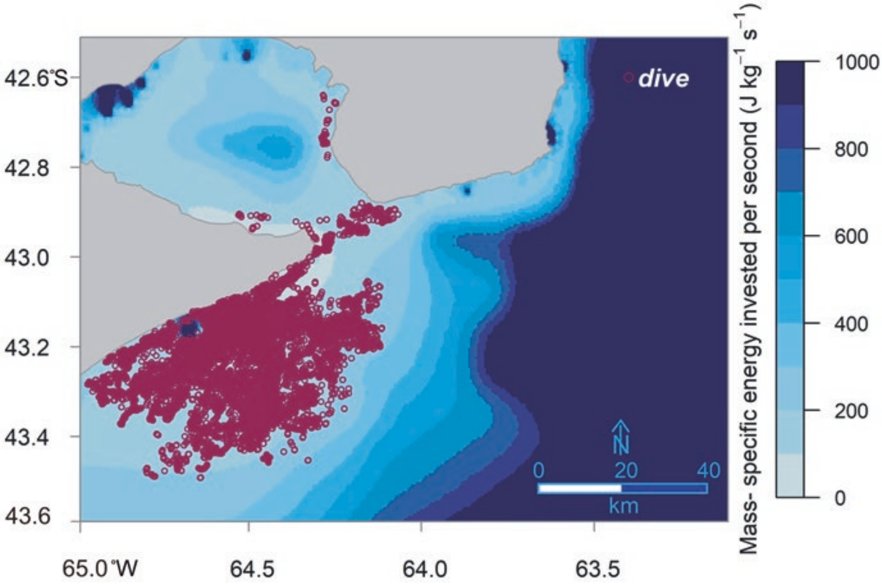

Fig. 7 Use of the energy landscape in the colony surroundings by adult Imperial cormorants breeding in León point. Foraging dives from 2004 to 2019 are represented by purple dots overlaid in the energy levels of the marine landscape (from least energy costly, light blue, to most energy costly, dark blue) (see text)

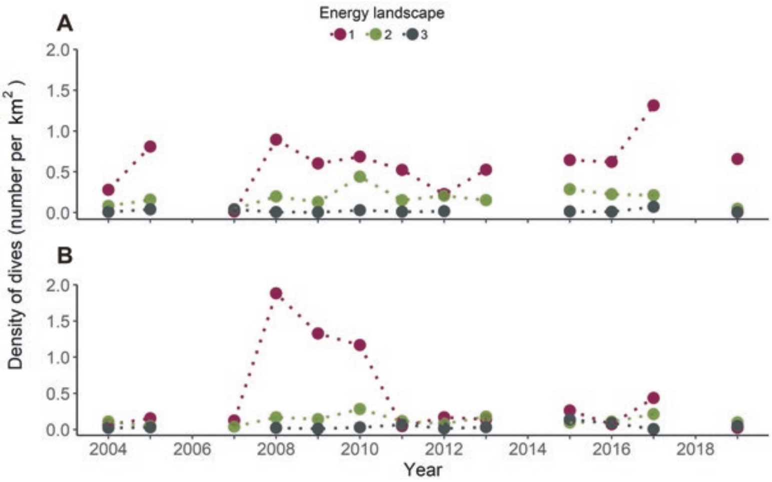

Fig. 8 Annual variation of the number of dives per km^2, performed at the three least costly fields (level 1 to 3) of the energy landscape, by female (**A**) and male (**B**) adult Imperial cormorants of León point during a 16-year period

Breeding Performance and Phenology Through Time

The clutch size and laying date (and consequently hatching date) of Imperial cormorants was very consistent across years (Fig. 9A–D). Mean clutch size for a 16-year period was 2.7 ± 0.6 (range, 2.5–2.8) (Fig. 9A, B). Delays or advance dates of 10 days in laying were very infrequent and were observed in only two breeding seasons (2005 and 2010, respectively) (Fig. 9C). Almost 60% of breeding seasons showed delays or advance dates < 5 days (Fig. 9D). The mean breeding success for the whole study period was 0.9 ± 0.7 chicks per nest and was also extremely consistent across breeding seasons. A clear decrease in breeding success was evident for 2016 (Fig. 9E, F).

Insights and Discussion on the Imperial Cormorant Long-Term Study

In this section we reported, for the first time, the long-term variability of phenology (timing of breeding), breeding traits (clutch size and breeding success), at-sea distribution, and foraging effort (foraging distances, trip duration, number of dives, etc.) of breeding Imperial cormorants from one of the largest colonies (more than 6,000 breeding pairs) of the species along its breeding range in coastal Patagonia, Argentina. These variables have been identified as key response types from previous

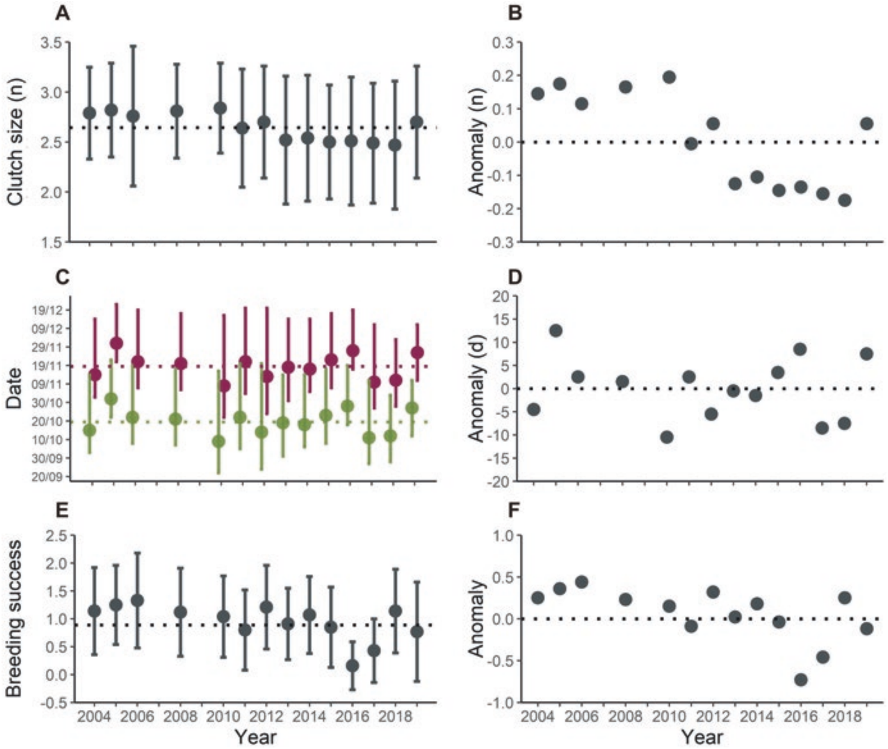

Fig. 9 Annual variation (mean ± standard deviation (SD)) of (**A**) clutch size, © laying (in green) and hatching (in purple) date, and (**E**) breeding success of the Imperial cormorant at León point over 16 breeding seasons. Annual deviations from (**B**) the clutch size overall mean (anomaly), (**D**) hatching date overall mean, and (**F**) breeding success overall mean are also showed

ecological investigations of climate change and other impacts on seabird populations worldwide (Sydeman et al. 2012). Our long-term initiative started at 2004 season recognizing that long-term tracking data coupled with breeding parameters can be employed to obtain ecological indicators about the status of a population (see Grémillet et al. 2006; Lewis et al. 2006).

Long-Term Variability in Foraging Parameters We found a consistent general pattern in the foraging parameters studied over our 16-year period. Both females and males foraged along seasons by performing an almost invariable feeding routine. The number of trips per day, trip duration, foraging time, distances covered while at sea, and the number of dives were particularly consistent over more than one decade in the study area. The long-term stability observed in foraging parameters might be a combination of both intrinsic and extrinsic factors, and the few anomalies recorded seem erratic and difficult to elucidate.

In the particular case of cormorants, intrinsic factors are likely mainly related with the high energy costs associated with flying, which preclude these birds from traveling far (Watanabe et al. 2011). As a consequence, an increase in the time spent flying to and from the colony to the foraging grounds represents a substantial increase in the energy expenditure of the complete foraging trip. For Imperial cormorants, it has been suggested that flying is the most expensive activity that occurs at sea with as much as 42% of the total energy invested during a foraging trip being spent commuting to and from the feeding grounds (Gómez-Laich et al. 2013). Therefore, the energy expenditure associated with this activity will likely restrict the birds both in terms of distances traveled during foraging trips and the distances covered during the breeding season. Superimposed upon this, learned skills, acquired over time, would allow older cormorants to exploit specific profitable foraging areas repeatedly (Patrick et al. 2013; Harris et al. 2014).

Seabird's at-sea behavior is also known to be modulated by extrinsic factors, such as competition for resources (Corman et al. 2016) or changing environmental conditions (Patrick et al. 2013). Our long-term data for the Imperial Cormorant in León point showed that foraging trip duration (and other related foraging variables) was relatively constant across the study period (Fig. 2A, B) and did not show any decrease over time, even the breeding population doubles from 3,000 to 6,100 pairs between 2004 and 2019 (Yorio et al. 2020; Quintana et al. unpub. data). These findings suggest that the Imperial Cormorant from León point is not subject to competition, perhaps because they exploit a predictable and abundant source of food in the vicinity of the colony.

Spatial Consistency of the Foraging Areas and the Energy Landscape Our long-term records showed clear spatial consistency in how chick-rearing Imperial cormorants use the coastal-marine habitat. In general, both female and male foraged primarily within 60 km off the colony in waters < 50 m deep (Figs. 4 and 7). Nevertheless, as indicated by previous studies (Quillfeldt et al. 2011; Quintana et al. 2011), we found clear sexual segregation in the use of foraging areas over time. Even though females generally foraged closer to the coast and males in deeper offshore waters, there was, however, consistent slight overlap in their foraging areas across breeding seasons. The maximum foraging overlap (> 70%) occurred during 2008 (females with respect to males and vice versa) and 2009 (only males with respect to females) (Fig. 6). It has been suggested that intraspecific competition for prey and resources would force this species to develop notable plasticity in their foraging behavior, which would be generally expressed via habitat segregation by sex (Quintana et al. 2011) and/or realized by sex-specific (body-size-driven) physiological differences in diving capacity with respect to depth (Gómez-Laich et al. 2012). However, this elegant and presumably normal, optimal scenario would change if foraging birds have to cope with unusual environmental change, as likely happened during 2008 and 2009 seasons.

Our long-term results on the consistency of foraging areas across years are in accordance with previous findings obtained over 4 years by Harris et al. (2014). The observed repeatability across seasons in the use of foraging areas (and behavior) may be due to a combination of individual characteristics such as learning abilities, breeding experience, and/or health condition, as well as targeted prey type and stability of the environment at this location. Evidence of high consistency in the use of foraging areas among seasons reinforces the notion that the oceanic environment surrounding the colony (Acha et al. 2004; Rivas and Pisoni 2010) and targeted prey are stable across successive breeding seasons. This enables individuals to be successful if they behave consistently, even over the long term. Indeed, our data series highlights the idea of the stability and a predictability of the food source exploited by the Imperial cormorants in this region of coastal Patagonia, reflecting general environmental stability close to the colony. The viability of repeated use of a given foraging area by individuals will depend primarily on how stable the targeted prey system is over time (noting that individual behavior can also be shaped by previous experience). When the probability of prey encounter is high (or the individual was successful in the past), associated with consistent environmental conditions, the memory component of the bird's behavior is enhanced and consistency will increase. On the other hand, if the probability of prey encounter is low, either because of prey mobility or scarcity or because the individual's current assessment of its foraging environment indicates paucity of prey encounter compared to past experience, foraging behavior should become less consistent (Dingemanse et al. 2002; Stephens et al. 2007; Cook et al. 2013). Imperial cormorants breeding at the León point colony are exclusively bottom divers (Gómez Laich et al. 2012) that feed mainly on Cusk-eels (*Raneya brasiliensis*) (Malacalza et al. 1994; Harris et al. 2016). This benthic fish thrives in the stable environment generated each season by the northern Patagonia frontal system (Buratti 2008; Saraceno et al. this volume), generating a predictable and stable food source for Imperial cormorants and making it a suitable scenario to exhibit behavioral consistency of foraging behaviors and areas used by birds over time. Dietary specialization has been linked to consistency in aspects of behavior, such as consistent location or depth of intensively used areas, as individuals fine-tune their behavior to target a particular type of prey (Elliott et al. 2009). A pattern of high consistency would be expected given a patchy spatial distribution of Cusk-eels that, however, remains stable over time.

Across seasons, Imperial cormorants mainly foraged on waters characterized by minimal power requirements compared with other areas in the available marine landscape (Fig. 7), capitalizing on the advantages of foraging in less energy-demanding areas, as expected in the hypothetical energy landscape scenario described by Wilson et al. (2012). The consistency found in the use of low energy-demanding marine landscapes for more than a decade reinforces the idea that the foraging ecology of Imperial cormorants from León point is based in a stable and predictable food source. Finally, successive records of the density of dives at different levels of landscape-dependent energy expenditure across seasons should help to inform us where animals allocate their energy and enable us to link this with potential or real environmental changes (e.g., climate or other global changes), something that should find particular resonance in conservation science.

Breeding Parameter Consistency The idea of long-term environmental stability around the colony is also supported by the high consistency of all breeding parameters recorded over time (clutch size, laying date, and breeding success, Fig. 9). The few anomalies reported in the foraging performance for particular seasons (see above) seem to underpin the idea of some degree of behavior plasticity in the species and the capacity of adult breeders to cope with potential low magnitude environmental changes. This capacity has been reported in other diving seabird species (Wilson et al. 2005; Miller et al. 2009; Dehnhard et al. 2016).

In general, global data have shown that Pelecaniformes and Suliformes (cormorants, gannets, and boobies) vary substantially among years in the timing of breeding, suggesting that these species may adjust egg laying in relation to some aspect of the local environment (weather, oceanographic conditions, and/or food availability) in the lead-up to the breeding season (Dawson 2008). However, our long-term records of laying date of the Imperial Cormorant suggest a low phenological sensitivity (i.e., phenological change over time). Although difficult to assert, the high consistency in time of breeding of Imperial cormorants at the study area can be consequence, at least partially, of a non-changing environment in the vicinity of the colony. Beyond that, the strong stability of clutch size across seasons may also indicate the environmental stability for the species during the winter or at least during the pre-laying period.

Although infrequent, delay/advance dates of 10 days in laying were recorded in 2005 and 2010 breeding seasons though. Among the local environmental drivers of phenology that have been identified, SST is widely reported to correlate with the distribution, abundance, and phenology of both local and migratory prey populations (Cheung et al. 2013). Unfortunately, we were unable to record in situ measurements of such physical variables during our study period, and satellite images of coastal sea surface temperature are not reliable enough to consider a correlational analysis.

A particularly low breeding success was reported during 2016. This anomaly was a consequence of a massive chick mortality event, apparently as an effect of an intense heat wave during the brooding period (Quintana et al. unpub. data). This kind of information results from long-term breeding data concomitant with environmental data continuously recorded over time and can be an important alert of a potential future constraint (under climatic warming scenarios, see Pessacg et al., this volume) on breeding activity, possibly leading to reduced reproductive output of this and other seabird species along coastal Patagonia Argentina.

Conclusion

In summary, the relative consistency of all biotic variables studied over time indicates predictable and stable environmental conditions in the surroundings of León point. However, if unexpected changes in the environment force individuals from this population to change foraging locations, or even develop new search strategies in order to be successful, they may not have the behavioral plasticity required to adapt to the new scenario, as this behavioral response may have been relaxed under long-term environmental stability. Potential inflexibility in breeding phenology in relation to temperature, for example, may leave Imperial cormorants vulnerable to trophic mismatch arising from shifts in timing of their prey. It is therefore interesting to continue to monitor this population over time in order to assess the extent to which behavioral consistency is maintained in the future and, in addition, to monitor other breeding colonies of this species to determine whether behavioral consistency is generalized in this species or is enabled by the prey system and environmental stability surrounding León point.

Finally, our long-term initiative is still in its infancy, and the datasets are still of insufficient duration to link them with inter-decadal variability from both natural and human-induced global change effects. However, they show definitively that a long-term approach, even in times of financial limitations, is possible and highlights the urgent need to maintain and possibly enhance existing long-term research and monitoring programs for this, and other, seabird species along coastal Patagonia.

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