Specialization to cold-water upwellings may facilitate gene flow in seabirds: new evidence from the Peruvian pelican *Pelecanus thagus* (Pelecaniformes: Pelecanidae)

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Recent research has shown that tropical seabirds specialized to feed on cold water upwellings exhibit low population genetic differentiation and high gene flow across large geographic distances. This pattern is opposite to the general pattern of differentiation reported for tropical seabirds, and led us to hypothesize that specialization to cold-water upwellings facilitates gene flow between colonies. As a test of this hypothesis we characterized population differentiation and gene flow across the range of the Peruvian pelican *Pelecanus thagus*, an upwelling specialist endemic to the Humboldt Current, using an 838 base pair segment of the mitochondrial control region and seven microsatellite loci. In support of our hypothesis we report genetic panmixia across the geographic range of this species and inferred high gene flow between colonies. The high dispersal propensity of upwelling specialist seabirds (adults and/or juveniles) may reduce loss of genetic diversity during population declines, and increase the ability of these species to colonize new islands.

Genetic divergence between populations is considered a precursor to the evolution of reproductive isolation (speciation) in most organisms (Coyne and Orr 2004), and studies of population differentiation are important for determining how new species arise. Speciation increases and/or maintains biodiversity within an ecosystem and biodiverse ecosystems tend to be more stable and resilient than those with a paucity of species (Cardinale et al. 2006, Bracken et al. 2008). It follows then, that understanding the causes and consequences of population differentiation is also important from a conservation and management perspective (Allendorf et al. 2010).

Levels of population genetic differentiation are variable across taxa, environments, and time, and may be influenced by numerous factors (Coyne and Orr 2004). For example, physical barriers may restrict dispersal and gene flow between adjacent populations leading to differentiation due to genetic drift or selection (Coyne and Orr 2004). Physical barriers to gene flow are regularly included in hypotheses concerning population differentiation and speciation (Fitzpatrick et al. 2009). However, numerous non-physical factors can influence population differentiation (Steeves et al. 2005, Niemiller et al. 2008, Nosil 2008, Zheng and Ge 2010, Lee and Lin 2012).

Non-physical barriers to gene flow appear particularly important in generating population genetic differentiation in seabirds (Friesen et al. 2007). Generally, seabirds are highly mobile but exhibit natal philopatry (Hamer 2002), and most tropical populations exhibit strong genetic structure, indicating that behavioural or ecological processes may play a significant role in generating seabird biodiversity (Table 1; Friesen et al. 2007). Choice of foraging habitat, for example, has been found to influence gene flow and differentiation: brown boobies exhibit high levels of population structure attributed to inshore foraging while red-footed boobies exhibit only moderate levels of population structure, putatively due to offshore foraging (Morris-Pocock et al. 2010a, 2011). Examples of the potential influence of foraging habitat can also be found in albatrosses (Burg and Croxall 2001) gulls and alcids (reviewed by Friesen et al. 2007).

The upwelling hypothesis

A diverse set of factors influences the generation and maintenance of population genetic differentiation in seabirds, including foraging ecology and the nature of the habitats on which seabirds rely for foraging (Friesen et al. 2007). The upwelling environments to which a number of seabird species are specialized are unpredictable in space and time: they alternate between periods of high and low prey abundance, and prey distribution can change significantly both

Table 1. Comparison of population differentiation between non-specialist and upwelling specialist tropical and subtropical seabirds.

Species	Upwelling specialist?	Breeding distribution	Markers used	Φ_{ST}/F_{ST}
Red-footed booby *Sula sula*	N	pantropical	control region microsatellites introns	0.80/−
Brown booby *S. leucogaster*	N	pantropical	control region microsatellites introns	0.86/0.23
Nazca booby *S. granti*	N	Galapagos coastal Colombia northern Peru	ND2 Cyt b COI microsatellites	0.07/0.127
Masked booby *S. dactylatra*		pantropical	control region	0.62/−
Great frigatebird *Frigata minor*	N		ND2 Cyt b COI microsatellites	0.007/0.023
Blue-footed booby *S. nebouxii*	Y	Gulf of California Galapagos Panama northern Peru	control region microsatellites	0.05/0.05
Peruvian booby *S. variegata*	Y	Peru/Chile	control region microsatellites	0.005/0.003
Cape gannet *Morus capensis*	Y	South African coast		low*
Cape cormorant *Phalacrocorax capensis*	Y	South African coast		low*
Humboldt penguin *Spheniscus humboldti*	Y	Peru/Chile		−/0.01

masked boobies, Steeves et al. 2003; brown and red-footed (*S. sula*) boobies, Morris-Pocock et al. 2010a, 2011; Nazca boobies and great frigatebirds, Levins and Parker 2012; Humboldt penguins, Schlosser et al. 2009; blue-footed and Peruvian boobies, Taylor et al. 2011a, b; Cape gannets and Cape cormorants, *L. Nupen pers. comm.

inter and intra-annually. These changes are often associated with alternating phases of El Niño Southern Oscillations (ENSO) (Duffy 1994, Camus 2001, Luna-Jorquera et al. 2003, Cushman 2005). Recent research on tropical seabirds that are specialized for feeding on cold-water upwelling systems has revealed very low genetic structure, and even panmixia, across large geographic distances (Table 1). These results led to our hypothesis that specialization to cold-water upwellings, which are regularly influenced by large-scale climatic events, increases dispersal between colonies and may have led to the evolution of more dispersive phenotypes in upwelling specialist seabirds compared to non-specialist seabird species (Taylor et al. 2011b) (hereafter referred to as the upwelling hypothesis).

The data that originally led to this hypothesis comes from three species in the eastern tropical and subtropical Pacific: two sulids and a penguin. Blue-footed boobies *Sula nebouxii* breed in the Gulf of California, the Galapagos, coastal Ecuador and northern Peru and, unlike their close relatives brown (*S. leucogaster*) and Nazca (*S. granti*) boobies, exhibit high gene flow and weak population genetic structure across their entire geographic range (Taylor et al. 2011b). Unlike brown and Nazca boobies, blue-footed boobies feed almost exclusively on prey found in cold-water upwelling systems during the chick-provisioning period (Taylor et al. 2011b). This ecological difference appears to be the driving factor preventing the generation of population genetic differentiation in blue-footed boobies: across similar temporal and geographic scales brown and Nazca boobies exhibit significantly greater population genetic differentiation than do blue-footed boobies (Taylor et al. 2011b, Levin and Parker 2012).

Additional data come from two Humboldt Current endemic seabirds, the Peruvian booby *S. variegata* and Humboldt penguin *Spheniscus humboldti*. The Humboldt Current creates cold-water upwelling where it meets the continental shelf along the coasts of Chile and Peru (Camus 2001, Pennington et al. 2006), and supports a number of endemic seabird species. As for other upwellings within the eastern tropical Pacific, warm water influx during ENSO events reduces upwelling intensity leading to increases in water temperature, and reduces primary productivity causing a number of the seabird species found in the region to disperse long distances to find prey (Juillet-Leclerc and Schrader 1987, Duffy 1990, Luna-Jorquera et al. 2003, Jaksic 2004). Supporting the upwelling hypothesis, both Peruvian boobies (Taylor et al. 2011a) and Humboldt penguins (Schlosser et al. 2009) exhibit weak population structure but high genetic diversity across their respective geographic ranges, which is unexpected for tropical and subtropical seabirds (Friesen et al. 2007).

Movements of reproductive adults to new breeding colonies or foraging areas during ENSO events would be facilitated by the ability of seabirds to learn from others about the presence of foraging areas or additional breeding sites. Recent research in the eastern tropical Pacific on Guanay cormorants *Phalacrocorax bougainvillii* and Peruvian boobies found evidence that pre-foraging rafting behaviour by Guanay cormorants can indicate the direction of foraging areas to other individuals, but that Peruvian boobies tend to rely on individual information combined with sighting foraging conspecifics to locate prey patches (Weimerskirch et al. 2010). These abilities may extend to other upwelling specialist seabirds, facilitating movement to more amenable foraging areas during ENSO events. The possibility also exists that individuals learn of the presence of additional breeding colonies during juvenile prospecting stages; however, these life stages are not well

studied in most upwelling specialist seabirds. Additionally, there is some evidence from blue-footed boobies that southward movement during ENSO events can result in at least temporary relocations of breeding adults (Simeone et al. 2002), but banding data are scarce for most seabird species in the eastern tropical and subtropical Pacific.

The Peruvian pelican

The Peruvian pelican (Pelecanidae: *Pelecanus thagus*; SACC 2006) is endemic to the Humboldt Current, and regularly breeds from Isla Lobos de Tierra in northern Peru (02°S) south to Isla Mocha (38°S) in Chile (Fig. 1; Murphy 1936, Nelson 2005). It was originally considered a subspecies of brown pelican *Pelecanus occidentalis*, but is significantly larger than any brown pelican subspecies and also exhibits plumage differences (Nelson 2005). Recent genetic work supports the species status of the Peruvian pelican and dates the divergence of this species from the brown pelican at 0.75 million years ago (Kennedy et al. 2013). Peruvian pelicans are upwelling specialists that feed on anchovies and other pelagic species, both diurnally and nocturnally, through plunge-diving and sit-and-wait surface water feeding. They will also feed on offal from fishing boats, and will steal prey from other seabirds, such as Guanay cormorants (Anderson et al. 1982, Nelson 2005, Zavalaga et al. 2011). During El Niño events, Peruvian pelicans normally desert their breeding grounds (causing total mortality of eggs and chicks) and undergo extensive southward movements in search of better environmental conditions and food (Murphy 1925, Tovar et al. 1987, Duffy 1990).

A test of the upwelling hypothesis

As an upwelling specialist, the Peruvian pelican is an ideal candidate to test our hypothesis that specialization to cold water upwellings leads to increased dispersal and gene flow
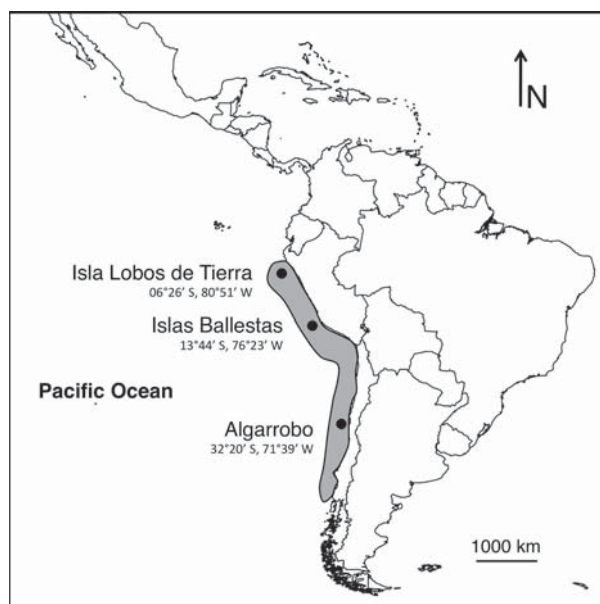

Figure 1. Sampled colonies (black circles) within the Peruvian pelican breeding range (grey shaded region).

compared to non-specialist tropical seabirds. To test the hypothesis we examined population differentiation across the bulk of the range of the Peruvian pelican using seven microsatellite markers and an 838 base pair fragment of the mitochondrial control region. If specialization to a variable foraging environment promotes long-distance dispersal, or the evolution of more dispersive phenotypes in upwelling specialist seabirds, levels of gene flow between Peruvian pelican colonies should be high. Likewise, population differentiation between colonies should be weak, even between colonies at the northern and southern limits of their breeding range. If population differentiation exists between Peruvian pelican colonies the hypothesis will be falsified. If differentiation does not exist this will provide mild support for our hypothesis: a genetic pattern of low differentiation is consistent with other scenarios of population admixture.

Methods

Sampling and DNA extraction

Blood samples were collected from 83 Peruvian pelican nestlings (one per nest) or juveniles from crèches (one per crèche) either from the leg or using gular pouch vein puncture (Zavalaga et al. 2009), from three colonies that span the majority of the breeding range of the species (Table 2, Fig. 1). DNA was extracted from the blood samples using a standard phenol-chloroform protocol (Sambrook and Russell 2001). Blood samples and DNA extractions are archived at Queen's Univ. at $-80°C$.

Lab procedures

Mitochondrial control region
Although the Peruvian pelican mitochondrial genome has yet to be fully sequenced, the recently inferred sulid mitochondrial gene order (Morris-Pocock et al. 2010b), along with primers used to amplify the control region from the American white pelican *Pelecanus erythrorhyncos* (Oomen et al. 2011), provided a basis for primer design. The genes for tRNA-Glu and a partial cytochrome b flank the target fragment of the control region. Primers were designed from an existing sequence of this fragment from an Australian pelican *P. conspicillatus* targeting the first section in the potentially duplicated control region (tgluF 5′–CCAAGATCTGTGGCCTGAAAAGCCACCG–3′; polytR (Pthagus) 5′–GCCGCGATCACGGACGAAAAT GGTAG–3′; Gibb et al. 2007). Due to sequencing ambiguities caused by a substantial poly-thymine repeat in Domain II, additional forward and reverse primers were designed to sequence the remainder of the fragment past the poly-T region (polytF 5′–GGGGCGTCTTCACTCT GCCCTCCC–3′; cytbR (Pthagus-cytb-degen-R) 5′–GGT GAAGTAGCTGAGGGAGGCTAATTG–3′).

Polymerase chain reactions (PCRs) were conducted in 25-µl volumes using a thermocycler under standard conditions (Taylor et al. 2011b). PCR products were sequenced at Genome Quebec (McGill Univ., Montreal). Sequences for 78 individuals were aligned in Clustal as implemented in BioEdit (ver. 7.0.9).

Table 2. Colony, location, number of individuals sequenced and genotyped, haplotype diversity ± SD (h), nucleotide diversity ± SD (π) and results of neutrality tests (Ewens–Watterson and Chakraborty's) for colonies of Peruvian pelicans based on mitochondrial control region sequences. Obs = observed value, Exp = value expected under neutrality. Values in bold are significantly different from zero (p < 0.05).

Colony	Location	n (mtDNA/ nDNA)	Haplotype diversity (h)	Nucleotide diversity (π) (%)	Ewens–Watterson		Chakraborty's	
					Obs	Exp	Obs	Exp
Isla Lobos de Tierra	06°26′S, 80°51′W	14/14	0.58 ± 0.14	0.091 ± 0.080	0.44	0.31	5.0	3.4
Islas Ballestas	13°44′S, 76°23′W	26/30	0.47 ± 0.12	0.081 ± 0.070	0.54	0.22	**8.0**	3.1
Algarrobo	32°20′S, 71°39′W	38/39	0.61 ± 0.095	0.081 ± 0.070	0.41	0.12	**15**	4.6
Total	–	–	0.56 ± 0.07	0.085 ± 0.070	0.45	0.09	**0.45**	4.74

Microsatellites

Seven microsatellite loci were amplified from all individuals. Two loci, PEL149 and PEL185, were amplified using great white pelican *P. onocrotalus* primers (Ponte Machado et al. 2009). The other five loci, PeEr 02, PeEr 03, PeEr 05, PeEr 07 and PeEr 09, were amplified using American white pelican primers (Hickman et al. 2008). PCRs were conducted in 5-μl volumes using a thermocycler under standard conditions (Taylor et al. 2011b). DNA fragments were sized at the Queen's Univ. Dept of Biology Core Genotyping Facility (Kingston, ON). Random samples comprising 5% of the dataset were amplified more than once to check for repeatability in allele scoring: repeatability was > 99%. Following amplification and scoring, each locus was tested for the presence of null alleles, large allele dropout, and stutter using Micro-Checker using default settings (Oosterhout et al. 2004).

Data analysis

Mitochondrial control region

Sequence variation in the 838 base pair control region fragment was evaluated using Arlequin (ver. 3.11, Excoffier et al. 2005). Ewens–Watterson (Ewens 1972, Watterson 1978) and Chakraborty's (Chakraborty 1990) tests of selective neutrality were conducted to determine if control region variation deviates from mutation-drift equilibrium. Arlequin was also used to index population genetic structure by calculating Φ_{ST} between colony pairs, and to determine the statistical significance of genetic differences between colonies. Analyses of control region haplotypes were conducted using Kimura two-parameter distances (Kimura 1980) with a rate parameter (α) of 0.45 as determined using MrModelTest (ver. 2.3; Nylander 2004). Significance was determined by comparison to 10 000 random permutations of the sequence data. Mutational relationships among control region haplotypes were inferred by constructing a statistical parsimony network in TCS ver. 1.21 (Clement et al. 2000). The network was redrawn using Microsoft PowerPoint 2007.

Because results from both marker types indicate that the entire population is panmictic (Results) we examined the growth rate of the total population using Fluctuate (Khuner et al. 1998). The program uses mitochondrial sequence data to address the null hypothesis that population growth rate is zero. This was determined by testing whether g, from Fluctuate, was significantly different from zero using a log-likelihood ratio test which involved multiplying 2 by the difference between the log-likelihood of g

at maximum theta and the log-likelihood of g at theta = 0. The result was compared to the critical value of χ^2 at α = 0.05 with one degree of freedom.

Microsatellites

Arlequin was used to calculate F_{ST} both for the global sample and for pairwise comparisons of colonies. Structure ver. 2.3.1, (Pritchard et al. 2000) was used to determine the most probable number of genetic clusters. Analyses were performed using an admixture model, correlated allele frequencies, a burn-in period of 50 000 cycles, and 500 000 additional cycles (determined from test runs to be sufficient for parameter stabilization). Using the no admixture model and sampling sites as prior information did not produce significantly different results (data not shown). Analyses were repeated 20 times for each K = 1 to 3, where K = the number of genetic populations, and posterior probability, ln[P(D)], was used to infer the most likely number of genetic populations as described in Pritchard and Wen (2004).

Results

Mitochondrial variation

Twenty-three haplotypes, defined by 23 variable sites, were found in 78 individuals (Supplementary material Appendix 1, Table A1; GenBank accession numbers KC331602–KC331620). Fifty-two individuals shared a single haplotype; all other haplotypes occurred in only one to three individuals each. The haplotype network generated by TCS was star-shaped and did not reveal any phylogeographic structure (Fig. 2). Accounting for sample size, no colony contained significantly more private haplotypes (Fisher's exact test: all p > 0.4).

Haplotype diversities ranged from 0.47 at Islas Ballestas to 0.61 at Algarrobo (Table 1). Nucleotide diversity ranged from 0.0081 to 0.0091 (Table 1). Chakraborty neutrality tests for the Algarrobo and Islas Ballestas populations were both significantly different from expected values; however, the rest of the neutrality tests were not significantly different from expected values (Table 1). Neither the estimates of Φ_{ST} between colony pairs (all $\Phi_{ST} = 0$) nor the global estimate of Φ_{ST} ($\Phi_{ST} = 0.01$) were not significantly different from zero (all p > 0.25).

Estimates of growth rate of the entire Peruvian pelican population from Fluctuate using various transition/ transversion ratios were significantly positive compared to a χ^2 value at α = 0.05 and one degree of freedom.
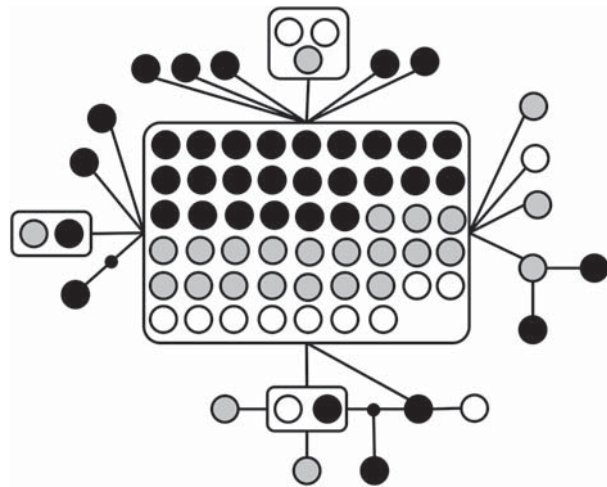
Figure 2. Statistical parsimony network for mitochondrial control region haplotypes. White circles represent individuals from Isla Lobos de Tierra (northern Peru), grey circles represent individuals from Islas Ballestas (central Peru), black circles represent individuals from Algarrobo (Chile). Boxes represent shared haplotypes, un-boxed circles represent haplotypes found only in a single individual. Each line represents a single mutational step; small black circles represent a haplotype missing from the population.

Nuclear microsatellite variation

Between four and 26 alleles were found per microsatellite locus, with an average of 12 alleles per locus (Supplementary material Appendix 1, Table A2). There was no evidence of large allele dropout at any locus; however, locus PeEr05 showed weak evidence of null alleles and possible stutter. Micro-Checker did not reveal null alleles or stutter at any of the other six loci. Subsequent population genetic analyses were conducted with and without locus PeEr05; however, the results from each set of analyses were the similar and we present analyses using the full seven microsatellite dataset. Genotype frequencies deviated significantly from HWE for one locus at Isla Lobos de Tierra, two loci at Islas Ballestas, and three loci at Algarrobo; however, there were no significant deviations from HWE either within a single locus across colonies or within a single colony across loci (Supplementary material Appendix 1, Table A2). That being said, the results indicate that mating may not be random, or a sampling artefact.

F_{ST} estimates for pairwise comparisons of colonies and global F_{ST} ($F_{ST} = 0.00$, $p = 0.99$) were low and not significantly different from zero. Bayesian assignment probabilities indicated that all individuals belong to a single genetic population ($K = 1$; $p > 0.999$).

Discussion

As predicted by the upwelling hypothesis, Peruvian pelicans exhibit low population genetic differentiation. Although we did not estimate gene flow, this low population genetic structure suggests high gene flow across the species' range (Slatkin 1987, but see Whitlock and McCauley 1999). Additionally, we detected the signature of population growth from mitochondrial data using Fluctuate.

This growth may be primarily occurring in the Algarrobo and Islas Ballestas colonies, as reflected from Chakraborty neutrality test results. Peruvian pelicans are one of only a handful of tropical and sub-tropically distributed seabird species that exhibit range-wide genetic panmixia at neutral loci (Burg and Croxall 2001, Friesen et al. 2007, Schlosser et al. 2009, Taylor et al. 2011a, b); however, their range also extends into temperate South America. The signature of genetic panmixia is not surprising given the dynamic nature of the system, and the possibility that both adult and juvenile pelicans disperse widely during ENSO events.

The departures from HWE at Islas Ballestas and Isla Lobos de Tierra, and at marker PeEr05 across all colonies, may be the result of non-random mating or sampling artefact. Juvenile pelicans at Islas Ballestas were sampled from crèches, rather than nests, and the possibility that related individuals were sampled cannot be ruled out. Additionally, pelicans from colonies to the south or north of Islas Ballestas, which lies near the centre of the Peruvian pelican distribution, may have recently colonized the island. A mixture of pelicans from different colonies may have been sampled, and assortative mating by these individuals based on arrival time could explain the departures from HWE we report.

As hypothesized for blue-footed and Peruvian boobies, the reliance of Peruvian pelicans on a variable foraging environment (in relation to ENSO events) may have lead to the evolution of increased dispersal tendency of adults and/or juveniles (Taylor et al. 2011a, b). Establishment of the Humboldt Current upwelling system and associated ENSO events occurred before colonization of this marine habitat by Peruvian pelicans (Hartley et al. 2005, Kennedy et al. 2013). As such, the environment may have exerted persistent selective pressures on Peruvian pelicans throughout their evolutionary history.

Several other factors may have also contributed to the evolution of greater dispersal tendency in this species. High levels of ectoparasite infestation have been found in the dense breeding colonies of this species and other Peruvian seabirds (Duffy 1983). Ectoparasite infestations can have significant negative effects on seabird health and behaviour, leading some species to desert nests and relocate (Clifford et al. 1980, Hoogstraal et al. 1985). Additionally, anthropogenic disturbance has promoted seabird dispersal in the Humboldt Current region, especially during the guano era (Murphy 1936, Duffy 1994, Cushman 2005). In the mid 1800s, seabird guano became a valuable resource and overharvesting and increased human presence on guano islands were responsible for seabird colony declines, and potentially increased dispersal between adjacent colonies (Duffy 1994, Cushman 2005).

An alternative hypothesis is that Peruvian pelicans underwent a recent range expansion. This would account for the lack of genetic differentiation across the species' range, the significant neutrality test result, and is supported by the starburst pattern of the mitochondrial haplotype network (Fig. 2). Although this is a plausible hypothesis, a number of lines of evidence suggest that this is not the case. The Peruvian pelican diverged from the brown pelican approximately 0.75MYA (Kennedy et al. 2013), a divergence time congruent with the splitting of a number of brown booby

regional populations within the eastern tropical Pacific, and an earlier date than the divergence of a number of regional Nazca booby populations within this region (Patterson et al. 2010). Though these splitting events took place on similar timescales, both brown and Nazca boobies exhibit strong between colony population genetic structure, even at relatively close geographic distances (Morris-Pocock et al. 2010a, 2011, Levin and Parker 2012). The primary ecological difference between these species is foraging ecology: brown and Nazca boobies are not upwelling specialists while Peruvian pelicans are upwelling specialists. As such, the absence of population genetic structure in Peruvian pelicans is not likely the result of a recent range expansion alone.

The starburst pattern of the mitochondrial haplotype network and significant population growth detected from mitochondrial makers could alternatively be the product of a mitochondrial selective sweep. Mitochondrial selective sweeps have been well documented in other avian taxa and can quickly move through populations and cross species barriers (Irwin et al. 2009). The physiologically challenging environment in which Peruvian pelicans have evolved may have facilitated such a sweep.

Similar patterns of gene flow and population differentiation in ecologically similar species, but discordant patterns in ecologically dissimilar species lend support to our hypothesis (Table 1). Sulids specialized to upwellings lack significant population genetic differentiation, even across large geographic distances, while all of the non-specialist sulids exhibit significant genetic differentiation, even at small geographic scales (Steeves et al. 2003, 2005, Morris-Pocock et al. 2010, 2011, Taylor et al. 2011a, b, Levin and Parker 2012). A natural comparison that would facilitate a robust evaluation of the upwelling hypothesis would be an additional within genus comparison to compliment comparisons within the genus *Sula*. We are working on generating this comparative data for brown pelicans within the genus *Pelecanus*, which are the sister taxa of the Peruvian pelican (Kennedy et al. 2013), but the comparison will be complicated by two factors: 1) the California subspecies *P. occidentalis californicus* is also an upwelling specialist and has also experienced drastic declines from DDT use (Schreiber 1980), and 2) introductions of birds from Florida and North Carolina have been used to bolster Louisiana populations and so the genetic signatures in the Gulf of Mexico do not likely represent natural variation (Schreiber 1980). That being said, within eastern North America, the Gulf of Mexico and the Caribbean Ocean there are three brown pelican subspecies, none of which are upwelling specialists. These subspecies have differentiated within a smaller geographic area than that which Peruvian pelicans currently occupy. This represents additional evidence that specialization to cold-water upwellings facilitates gene flow and reduces population genetic differentiation in Peruvian pelicans compared to other non-specialist brown pelican subspecies. This within-genus comparison should be more fully explored.

Dispersive species may be less prone to range collapse and loss of genetic diversity during population declines than are more philopatric species (Pinsky et al. 2010). This may be due to a higher tolerance of these species to disturbance and/or greater ability to adapt to fluctuating environmental conditions. Upwelling specialist seabirds may be resilient to the loss of genetic diversity when facing population declines and range collapses, and may be more able to establish new colonies in response to environmental or anthropogenic stressors. Extra-limital dispersal seems characteristic of a number of species during ENSO events and, although many of the vagrants die, enough may survive so that species occasionally establish themselves in new areas. Duffy (1990) proposed that such could be the case for some seabirds including guanay cormorants, elegant terns *Thalasseus elegans* and blue-footed boobies. Additionally, juvenile upwelling specialist seabirds may be more dispersive than their non-specialist counterparts, which would facilitate range shifts and new colony formation in response to environmental changes. A potential example of the resilience of upwelling specialist seabirds comes from the Cape gannet: apparently in response to increased competition with fisheries on the western Cape, Cape gannet numbers have been increasing at the Bird Island colony on the southeastern Cape of South Africa, predominantly from an influx of dispersive juveniles (L. Nupen pers. comm.). The population as a whole, however, continues to experience significant declines (Distiller et al. unpubl.).

Our results are important for the conservation and management of the Peruvian pelican (which has been recently classified in the Near Threatened category by IUCN), as well as other upwelling specialist seabirds. The results are particularly relevant as climate change may increase the frequency and severity of ENSO events and as competition with fisheries increases globally (Duffy 1994, Thompson and Ollason 2001, Karpouzi et al. 2007).

Summary

The results of this study add to our knowledge of population differentiation and connectivity in marine ecosystems. The observed pattern of low population differentiation and potentially high gene flow in an upwelling specialist seabird is similar to that of other upwelling specialists (Schlosser et al. 2009, Taylor et al. 2011a, b, L. Nupen pers. comm.), but opposite of the usual high genetic differentiation observed in seabird species distributed in the tropics and subtropics (Steeves et al. 2003, Morris-Pocock et al. 2010a, 2011, reviewed by Friesen et al. 2007). A natural extension of this work would be to explore patterns of population differentiation in other marine taxa that are specialized on upwelling systems (e.g. Guanay cormorants, Inca terns *Larosterna inca*, Peruvian-diving petrels *Pelecanoides garnotii*). Increasing our ability to predict patterns of population genetic differentiation in a variety of species will ultimately improve conservation and management of these systems, as well as contribute to our understanding of speciation more generally.

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Supplementary material (Appendix JAV-00004 at < www. oikosoffice.lu.se/appendix >). Appendix 1.